

# Responses of seedling growth and physiological characteristics of perennial species *Sophora alopecuroides* to warming and nitrogen deposition in temperate arid habitats, China

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## Research Article

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# Abstract

## Background

It is now undisputed that global warming and nitrogen deposition are having a significant impact on ecosystems. Therefore, it is important to gain a better understanding of how plants are responding to these changes. Of particular interest is *Sophora alopecuroides*, a common and invasive native plant species found in the temperate desert steppes and arid zone temperate steppes of northwestern China. It is of great importance to gain insight into the growth and physiological responses of its seedlings when exposed to conditions of warming and nitrogen deposition. This knowledge is crucial to elucidate the invasion mechanisms of the species and to assess the potential ecological security risks. To study these effects in depth, treatments of nitrogen (N) addition, warming (W), and a synergistic approach of warming and nitrogen (WN) were established.

## Results

The W and WN treatments demonstrated no statistically significant difference in germination rate, index, or potential relative to the control (CK), whereas the N treatment exhibited a notable reduction in germination rate. The W and WN treatments were found to significantly enhance several key growth parameters, including root-to-shoot ratio, stem diameter, plant height, and axial root length. In contrast, the N treatment was observed to significantly reduce these same parameters, with the exception of stem length. In comparison to the control treatment, the nitrogen treatment resulted in an increase in leaf biomass, whereas the water treatment led to a reduction in leaf number. The W and WN treatments were observed to significantly enhance both above-ground and below-ground biomass. The N treatment also resulted in an improvement in leaf biomass ratio and root-to-shoot ratio, while the WN treatment increased stem biomass ratio and root biomass ratio. The N treatment resulted in a reduction in chlorophyll, soluble sugar, and soluble protein contents. In contrast, the W treatment led to a significant decrease in malondialdehyde levels, while the WN treatment increased nitrate reductase activity. Both the N and W treatments elevated enzyme activity, but also had a stronger inhibitory effect on superoxide dismutase enzyme activity.

## Conclusions

The treatments of warming, nitrogen addition, and their combination resulted in significant alterations to the germination characteristics, biomass accumulation, and physiological metabolism of *S. alopecuroides*. These findings are of great significance for advancing our comprehension of the species' influence on ecosystems and for the formulation of efficacious management and control strategies.

## Introduction

In recent years, global warming has become an irrefutable reality [1]. Moreover, as an important environmental factor, temperature exerts a profound influence on the growth and physiological characteristics of plants. Thus, global warming may have a significant impact on plant growth, development, reproduction, phenology, and migration and has become a hot topic in ecology and environmental science. Studies have shown that the effect of warming on plant growth may be beneficial [2], as well as inhibitory [3]. Warming can cause changes in plant traits, with a slower response in reproductivity [4] and a more pronounced and rapid response in plant growth [5]. However, the degree of its impact depends on the species and their environmental conditions. Studies have demonstrated that elevated temperatures enhance the germination rate, aboveground biomass, and reproductive capacity of *Ipomoea cairica* [6]. However, in some invasive plants such as *Hypochaeris radicata* L. and *Leontodon taraxacoides* L., warming has been shown to inhibit seed germination and seedling growth and even lead to vegetation degradation in northern Australia [3]. Climate warming may affect the competitive ability of alien invasive plants and enhance their physiological plasticity.

The Yili Grassland is an important part of the northern grasslands of China, and several important questions about the potential effects of warming need to be addressed: What are the effects of global warming on the composition and distribution of typical communities and the succession of toxic species' communities in the grassland? How do the population life histories of these invasive toxic species respond to warming? What are the specific adaptive regulatory mechanisms in these processes? These are important theoretical issues of biology and ecology in a changing global environment and are also practical problems that need to be solved to control invasive plant species and ensure the security of grassland ecosystems and effective scientific management.

Global emissions of N have been increasing yearly since 2008, and as the demand for animal products increases, the emissions will gradually reach  $135 \text{ Tg Nyr}^{-1}$  by 2100. [7]. Studies have demonstrated that elevated nitrogen deposition can influence plant growth and allocation, alter community composition, and impact ecosystem functions [8]. Continuing nitrogen deposition will also alter nutrient cycling or interspecific competition among species [9] and may even promote the ecological invasion of certain species into new habitats [10]. Most studies have focused on forest and grassland ecosystems with high levels of nitrogen deposition, but relatively little attention has been given to arid and semiarid regions, especially in China. These areas are limited by water and nitrogen. Although water has a significant effect on the primary productivity of plants, nitrogen is the main factor when sufficient water is available [11]. Nitrogen deposition has been shown to have a significant effect on plant growth and community structure in the Chihuahuan Desert [12]. In the arid and semiarid regions of China, research on nitrogen addition has focused mainly on agro-ecosystems but significantly less attention has been given to the potential impacts of nitrogen deposition on natural ecosystems. Previous studies have indicated that nitrogen deposition might reduce biodiversity and alter the composition of herbaceous communities, thereby accelerating ecosystem degradation in desert grasslands [11]. Because of the extreme fragility and sensitivity of ecosystems in these areas, even small increases in nitrogen may have significant ecological effects, which would contribute a much higher proportion of production than in many high-productivity ecosystems [13]. Therefore, it is necessary to study the effects of increased nitrogen

deposition on growth, production, and adaptation strategies in arid and semiarid regions under changing global environment. Such studies will contribute to a comprehensive understanding of the mechanisms by which nitrogen deposition affects invasive plants in arid and semiarid regions and also provide a scientific basis for grassland ecological conservation and management.

*Sophora alopecuroides* L. is a perennial herb or subshrub that grows mainly in western and central Asia. Because of its typical clonal characteristics, it propagates by both considerable amounts of seeds and underground rhizomes, which allows the species to invade and develop mono-dominant communities in farmland, temperate desert steppes, and temperate steppes. As a result, thousands of hectares of *S. alopecuroides* grassland have appeared in the Ili River Valley of China, which poses a serious threat to the local livestock husbandry, biodiversity, and ecosystem security. Therefore, the plant is recognized as a native invasive species in the arid areas of northwestern China [14, 15]. In recent years, how perennial species in temperate arid ecosystems respond to the synergistic effects of warming and nitrogen deposition have gradually attracted the attention of researchers globally, which is crucial to enhancing the understanding of the adaptation mechanisms of plants in changing global climates and environments. In previous studies, we found that *S. alopecuroides* has strong drought and stress tolerance [4], how it responds to new environmental stresses, such as warming and nitrogen deposition, remain unclear. Because it is the typical clonal and native invasive species of Leguminosae in the Ili grasslands and due to its toxicity, vicious invasion, and rapid expansion in arid and semiarid ecosystems, there is an urgent need to carry out studies on its life-history strategies at the population level in changing habitats, especially studies on how it responds to warming and nitrogen depletion. Therefore, in this study, which used *S. alopecuroides* as the research material, we attempted to answer the following two questions through simulated experiments of nitrogen deposition and warming: 1) How do clonal species *S. alopecuroides* cope with the synergistic effects of temperature increase and nitrogen deposition in temperate arid ecosystems? 2) What survival strategies and physiological regulatory mechanisms have been adopted by *S. alopecuroides* seedlings to adapt to elevated warming and nitrogen deposition? These findings will contribute to a deeper understanding of the ecological and physiological strategies used by invasive plants in the region to adapt to arid environments and will also provide some important insights that will enhance our understandings of the scientific prevention and control of various invasive species in these regions.

## Materials and methods

### Materials

In mid-October 2022, mature pods of *Sophora alopecuroides* L. were collected from the suburbs of Yining City, Xinjiang, China, at the end of the growth period. The seeds were sorted, naturally air-dried, and stored in a 4 °C freezer. Before the experiment, uniformly sized and mature seeds were selected and sterilized using 0.01% HgCl<sub>2</sub> and then soaked in distilled water for 48 h. The identification of *Sophora alopecuroides* L. was conducted by Prof. Yan Ping, and its specimen was deposited in the Herbarium of the Institute of Botany, Chinese Academy of Sciences, with the specimen code PE00214699. This plant

is widely distributed in northwest China, commonly found in mountainous grasslands and farmland, and is a highly invasive species that can be obtained without the need for a permit at the time of sampling.

## Methods

Plump and round *Sophora alopecuroides* L. seeds were selected, and a small notch was made on the back of the seeds using a mechanical method to avoid the inhibitory effect of the seed coat [16]. The experiment employed a randomized complete block design with two factors (temperature and nitrogen application). Four treatment groups were established: control (CK), warming (W), nitrogen addition (N), and interaction of warming and nitrogen addition (WN). Each treatment group had four replicates, with four seedlings per replicate. The simulated nitrogen deposition was set at two levels: 0 and 12.5 mmol/L. Based on this research method, daytime (08:00–22:00) ambient temperature was set at 25°C, and nighttime (22:00–08:00) temperature was set at 18°C. For the warming treatment, daytime temperature was elevated to 28°C and nighttime temperature was a constant 21°C, using a light intensity of 6000 lx. Approximately 200 mL of N solution was sprayed on each plant per pot, with spraying conducted once every 7 days for a total of five applications (Fig. 1).

## Indicator measurement

### Growth indicators

During the experiment, seedlings were carefully excavated with their roots intact and gently brushed to remove soil. The plant height and primary root length of *S. alopecuroides* seedlings were measured using a ruler with an accuracy of 1 mm. The basal diameter and root diameter of the seedlings were measured using a vernier caliper with an accuracy of 0.01 mm. The roots, stems, and leaves were separated, and their fresh weights were measured using an electronic balance with an accuracy of 0.001 g. The number of compound leaves per plant was counted, and leaf area analysis software was used to analyze the leaf area of the seedlings in each treatment group.

### Physicochemical indicators

Five healthy *Sophora alopecuroides* L. plants were randomly selected from each treatment, and mature leaves were chosen from each plant. The freshly harvested leaves were promptly placed in a cooler, and 0.1 g of fresh leaf tissue was weighed for determination of physiological and biochemical indicators, such as chlorophyll, soluble protein, soluble sugar, malondialdehyde (MDA), superoxide dismutase (SOD), and nitrate reductase (NR).

### Statistical analysis

Excel 2010 software was used for preliminary data collation, and SPSS (version 26.0) was used for data analysis to compare the significance of differences between different treatments of the same indicator by one-way analysis of variance (ANOVA). Graphs were plotted using Origin 2021 software.

# Results and analysis

## Effects of nitrogen application, warming, and their interaction on *S. alopecuroides* seed germination

As shown in Fig. 2, for *S. alopecuroides* seeds, in comparison to the control group, nitrogen application alone resulted in significant decreases in germination rate, germination potential, and germination index of 13%, 16.5%, and 20.6%, respectively ( $P < 0.05$ ). However, there were no significant differences in germination rate, germination potential, and germination index compared to the control group under either the warming treatment alone or the combined treatment of warming and nitrogen application ( $P > 0.05$ ). This indicates that nitrogen application negatively affects the germination performance of *S. alopecuroides* seeds, whereas warming treatment alone or in combination with nitrogen application has no significant effect on germination.

## Effects of nitrogen application, warming, and their combination on the growth of *S. alopecuroides* seedlings

In this study, following the application of the different treatments to *S. alopecuroides*, several changes in root diameter, stem diameter, plant height, and primary root length were observed Table 1. Compared to the control group, nitrogen application resulted in significant reductions in stem diameter, plant height, and primary root length of 33.3%, 19.4%, and 24%, respectively ( $P < 0.05$ ). However, root diameter exhibited no significant change ( $P > 0.05$ ). In contrast, under the interaction of warming and nitrogen application, stem diameter and plant height increased significantly compared to the control group ( $P < 0.05$ ). Under the combined treatment of warming and nitrogen application, root diameter exhibited a 7.2% and 28.5% increase, stem diameter exhibited a 23.6% and 19% increase, plant height exhibited a 20.3% and 13.2% increase, and primary root length exhibited a 19.5% and 13.8% increase, respectively. A comparison of the different treatment groups revealed that warming could promote to varying degrees increases in stem diameter, plant height, and primary root length of *S. alopecuroides* seedlings, whereas nitrogen application could inhibit these effects to varying degrees.

Table 1

Effects of nitrogen addition, warming, and their interactions on growth parameters of *S. alopecuroides* seedlings groups

| Group                                                                                                                                                                                  | Root diameter/mm | Stem diameter/mm | Height/cm       | Root length/cm |
|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------|------------------|-----------------|----------------|
| CK                                                                                                                                                                                     | 0.358 ± 0.0303b  | 0.537 ± 0.026b   | 19.05 ± 0.533c  | 6.933 ± 0.416b |
| N                                                                                                                                                                                      | 0.373 ± 0.0191b  | 0.358 ± 0.0251c  | 15.347 ± 0.357d | 5.263 ± 0.254c |
| W                                                                                                                                                                                      | 0.384 ± 0.0188ab | 0.664 ± 0.0204a  | 23.023 ± 0.337a | 8.287 ± 0.247a |
| WN                                                                                                                                                                                     | 0.460 ± 0.0238a  | 0.639 ± 0.0154a  | 21.57 ± 0.264b  | 7.89 ± 0.235ab |
| Notes: All data in the table are average values ± standard error (SE). Values of different lowercase letters indicate significant difference at the $P < 0.05$ level (the same below). |                  |                  |                 |                |

## Effects of nitrogen application, warming, and their combination on biomass accumulation and allocation in *S. alopecuroides*

Table 2 indicates that the combined treatment of warming and nitrogen application significantly increased the root biomass of seedlings by 257.7% and 351.3%, respectively. Furthermore, the leaf area increased by 17.9% and 11.4%, leaf biomass increased by 70.2% and 56.2%, and stem biomass increased by 114.9% and 92%, respectively ( $P < 0.05$ ). However, in the independent nitrogen application treatment, there were no significant changes in root biomass and stem biomass compared to the control group ( $P > 0.05$ ). In contrast, leaves exhibited 87.0% increase in biomass of, but leaf area and leaf number significantly decreased ( $P < 0.05$ ). These findings indicated that *S. alopecuroides* seedlings exhibited a positive response in root growth and leaf development under warming and the combined treatment of warming and nitrogen application, indicating both promoting and interaction effects.

Table 2

Biomass accumulation of *S. alopecuroides* seedlings under nitrogen and warming treatments (mean  $\pm$  SE).

| group | Root Biomass / g     | Stem Biomass / g     | Leaf Biomass / g     | Leaf Area / cm <sup>2</sup> | Number of Leaves     |
|-------|----------------------|----------------------|----------------------|-----------------------------|----------------------|
| CK    | 0.0078 $\pm$ 0.0005b | 0.0771 $\pm$ 0.0207b | 0.0185 $\pm$ 0.0014b | 7.63 $\pm$ 0.273b           | 1.2993 $\pm$ 0.1040b |
| N     | 0.0168 $\pm$ 0.0020b | 0.0491 $\pm$ 0.0055b | 0.0346 $\pm$ 0.0046a | 6.63 $\pm$ 0.242c           | 0.9369 $\pm$ 0.0566c |
| W     | 0.0279 $\pm$ 0.0017a | 0.1657 $\pm$ 0.0076a | 0.0315 $\pm$ 0.0018a | 9.00 $\pm$ 0.267a           | 2.2415 $\pm$ 0.1038a |
| WN    | 0.0352 $\pm$ 0.0070a | 0.1481 $\pm$ 0.0043a | 0.0289 $\pm$ 0.0015a | 8.50 $\pm$ 0.196a           | 2.0716 $\pm$ 0.0860a |

Figure 3 illustrates that sole nitrogen application treatment showed no significant changes in root biomass ratio and stem biomass ratio of seedlings in compared to the control group ( $P > 0.05$ ). However, the leaf biomass ratio and root-to-shoot ratio increased significantly ( $P < 0.05$ ). This indicates that nitrogen application can promote photosynthesis and nutrient absorption in *S. alopecuroides* seedlings, resulting in improved efficiency of leaf tissue and spatial utilization. Under the warming treatment alone, the root biomass ratio and stem biomass ratio increased significantly ( $P < 0.05$ ) compared to the control group, whereas, the leaf biomass ratio and root-to-shoot ratio did not show significant changes ( $P > 0.05$ ). This indicated that the warming treatment could enhance plant root growth and increase plant biomass. Under the combined treatment of warming and nitrogen application, the root biomass ratio and stem biomass ratio increased significantly ( $P < 0.05$ ); however, the leaf biomass ratio and root-to-shoot ratio did not show significant changes compared to the control group ( $P > 0.05$ ). These findings indicate that the combined treatment of warming and nitrogen application promotes plant growth and significantly increases biomass accumulation in both roots and above ground stems.

## Effects of nitrogen application, warming, and their combination on physicochemical indicators of *S. alopecuroides*

Figure 4 indicates that nitrogen application significantly reduced the soluble sugar content ( $P < 0.05$ ) compared to the control group. However, no significant changes were observed in protein, chlorophyll, and MDA contents ( $P > 0.05$ ). However, the warming treatment resulted in a significant increase in soluble sugar content ( $P < 0.05$ ), while protein, chlorophyll, and MDA contents did not show significant changes ( $P > 0.05$ ). The combined treatment of warming and nitrogen application resulted in a significant decrease in the protein and chlorophyll contents of *S. alopecuroides* seedlings compared to the control group ( $P < 0.05$ ). However, no significant differences were observed in soluble sugar content or MDA content ( $P > 0.05$ ). These findings suggest that nitrogen application, warming, and their combined effects have a limited impact on the biochemical indicators of *S. alopecuroides* seedlings.

The enzyme activities of NR and SOD in *S. alopecuroides* seedlings exhibited significant differences among the different treatment groups ( $P < 0.05$ ) (Fig. 5). Under the combined treatment of warming and nitrogen application, the activity of NR was significantly higher than those of the control group and the other treatment groups ( $P < 0.05$ ). Compared to the control group, both the sole nitrogen application and sole warming treatments demonstrated a significant increase in NR activity ( $P < 0.05$ ). The combined treatment of warming and nitrogen application exhibited the greatest increase in NR activity, followed by sole nitrogen application and sole warming treatments. Concerning sSOD, all treatment groups exhibited a significant reduction in enzyme activity compared to the control group. The control group exhibited the highest SOD enzyme activity, followed by the sole nitrogen application treatment, and the combined treatments of warming and nitrogen application showed the lowest activity ( $P < 0.05$ ). The combined treatments of warming and nitrogen application significantly increased NR activity in *S. alopecuroides* seedlings, while exerting a substantial inhibitory effect on SOD activity. The sole nitrogen application and sole warming application also significantly affected enzyme activity, although to a lesser extent than the combined application of warming and nitrogen.

## Discussion

Climate change and human activities exert a multitude of effects on plants. Elevated temperatures markedly enhance the elongation of stems and biomass of invasive plants, impeding their competition with other plants, which in turn causes substantial damage to ecosystems and biodiversity [6]. Piper et al. demonstrated that warming increased the height, biomass, and leaf area of oak seedlings in humid regions and increased seedling survival in arid regions [2]. Elevated temperatures lead to increased biomass and root growth of invasive plants, with growth rates potentially exceeding those of other plants, further exacerbating the pressure placed on and the disruption of ecosystems [6]. For example, studies on *Hordeum jubatum* demonstrated that it only exhibited a competitive advantage over native plants at higher temperatures [5]. The growth and competitive advantages of invasive species may be enhanced by warming, further increasing the risk of invasion and expansion. *S. alopecuroides*, a common perennial plant found across western and central Asia, has become a typical native invasive

species because of its strong environmental adaptability and vigorous asexual and sexual reproductive capabilities [14]. The biomass, height, leaf area, and true leaf number of *S. alopecuroides* seedlings exhibited significant increases under the warming treatment, which is agrees with previous findings [2, 6, 17]. In contrast, Martinez et al. observed that the activity of antioxidant enzymes in plant leaves increased under climate warming, but the MDA content of the leaves remained unaltered [18]. Zhang et al. observed that elevated temperatures significantly increased the chlorophyll and soluble sugar contents of *Leymus chinensis* but had no significant effect on *Phragmites communis* [19]. This study found that warming had a promoting effect on the soluble sugar content and NR activity of *S. alopecuroides* seedlings, had no significant effect on MDA, protein, or chlorophyll content, and had a reducing effect on SOD. This suggests that the plant's antioxidant defense system can mitigate the damaging effects of reactive oxygen species under heat induction.

Within a certain range, moderate nitrogen deposition enhances the nitrogen availability of soil, thereby promoting above ground plant growth and altering the distribution pattern of plant biomass. This subsequently influences the growth of plant seedlings [20]. However, different plants exhibit some variations in their responses to nitrogen addition, with instances of opposing outcomes [12]. For instance, under high nitrogen treatments, the biomasses of *Bouteloua eriopoda* and *Larrea tridentata* significantly increase, whereas lower levels of nitrogen addition may not elicit a response. Wan et al. found that nitrogen deposition significantly promoted the growth of *Solidago canadensis* and rough-fruited *cinquefoil* in terms of biomass allocation to roots, stems, and leaves, leaf number, plant height, and others [21]. Another study found that nitrogen deposition has adverse effects on the stability and positive succession of desert ecosystems [11]. Zhang et al. demonstrated that nitrogen addition increased the chlorophyll content of *L. chinensis*, thereby promoting plant photosynthesis and growth [19]. The results of this study show that nitrogen application alone significantly reduced the germination rate of *S. alopecuroides* seeds and led to significant reductions in stem diameter, primary root length, and plant height. Furthermore, the chlorophyll and soluble sugar contents of *S. alopecuroides* seedlings decreased significantly compared to the control group. Nitrogen application also resulted in a significant decrease in SOD activity while simultaneously increasing NR activity, leaf biomass ratio, and root-to-shoot ratio. These findings indicate that nitrogen deposition exerts a certain degree of inhibition on the growth and physiological status of the plant. The research conclusions of this study provide valuable insights into the responses of desert plant growth and physiology to nitrogen deposition.

The combined treatment of warming and nitrogen application did not significantly affect the germination rate, germination index, or germination vigor of *S. alopecuroides* seeds, despite the concurrent impacts of climate warming and nitrogen deposition. However, it significantly increased the accumulation of aboveground and belowground biomass, as well as the stem biomass ratio. Additionally, the combined warming and nitrogen treatment had a promotive effect on the root biomass ratio. These findings are consistent with those of previous studies, which have demonstrated that the interaction between temperature and nitrogen can enhance plant growth by increasing chlorophyll and leaf nitrogen concentrations [22]. Lu et al. found that the interaction between climate warming and nitrogen addition led to a significant increase in the root biomass of invasive species compared to that of native plants

[22]. Similar results were confirmed in field studies [5, 23]. Furthermore, the combined treatment of warming and nitrogen application significantly increased the NR activity of *S. alopecuroides* seedlings but exerted a significant inhibitory effect on SOD activity. These findings indicate that environmental changes, particularly the combined effects of global warming and nitrogen deposition, facilitate the growth of invasive plants. Consequently, *S. alopecuroides* must exhibit enhanced adaptability to environmental changes such as temperature. The growth advantage and competitive advantage of invasive species may be enhanced by environmental changes (warming and nitrogen addition), further increasing the risk of larger-scale invasion.

## Conclusions

This study aimed to investigate the effects of warming and nitrogen application on the perennial plant, *S. alopecuroides*, and its physiological and ecological response mechanisms, in temperate arid ecosystems. Under the warming treatment alone, there was a significant promotion of growth and accumulation of biomass, particularly the aboveground biomass. Deposition of nitrogen led to a significant decrease in the germination rate of seeds and negatively affected growth characteristics such as plant height, stem diameter, and physiological features, including soluble sugars and SOD. The combined effects of warming and nitrogen deposition on *S. alopecuroides* were more complex, with a continued trend of increase in aboveground biomass but a certain degree of inhibitory effect on physiological metabolism, including soluble proteins, chlorophyll, and SOD, in seedlings. These results highlight temperature as a key factor promoting the growth of *S. alopecuroides*. They also indicate that the combined effects of temperature and nitrogen application, as well as increased nitrogen deposition, play an adaptive regulatory role in the ecological and physiological responses of perennial plants in temperate arid ecosystems. This study provides important insights into the survival strategies of plants facing global climate change and offers scientific evidence for future conservation and management of desert ecosystems.

## Declarations

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### Author Contributions

Hongmei Zhao, Xiaolin Zhang, Zhiyi Zeng, and Zhijie Wangyu contributed to the components of the experiments and data collection. Data analysis was performed by Yu Zhao and Yijun Bai. The experimental design was carried out by Tiancui Shang and Ying Liu. The first draft of the manuscript was written by Hongmei Zhao, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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## Data availability

Data will be made available on request.

## Ethics approval and consent to participate

Not applicable.

## Consent for publication

Not applicable.

## Competing interests

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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## Figures

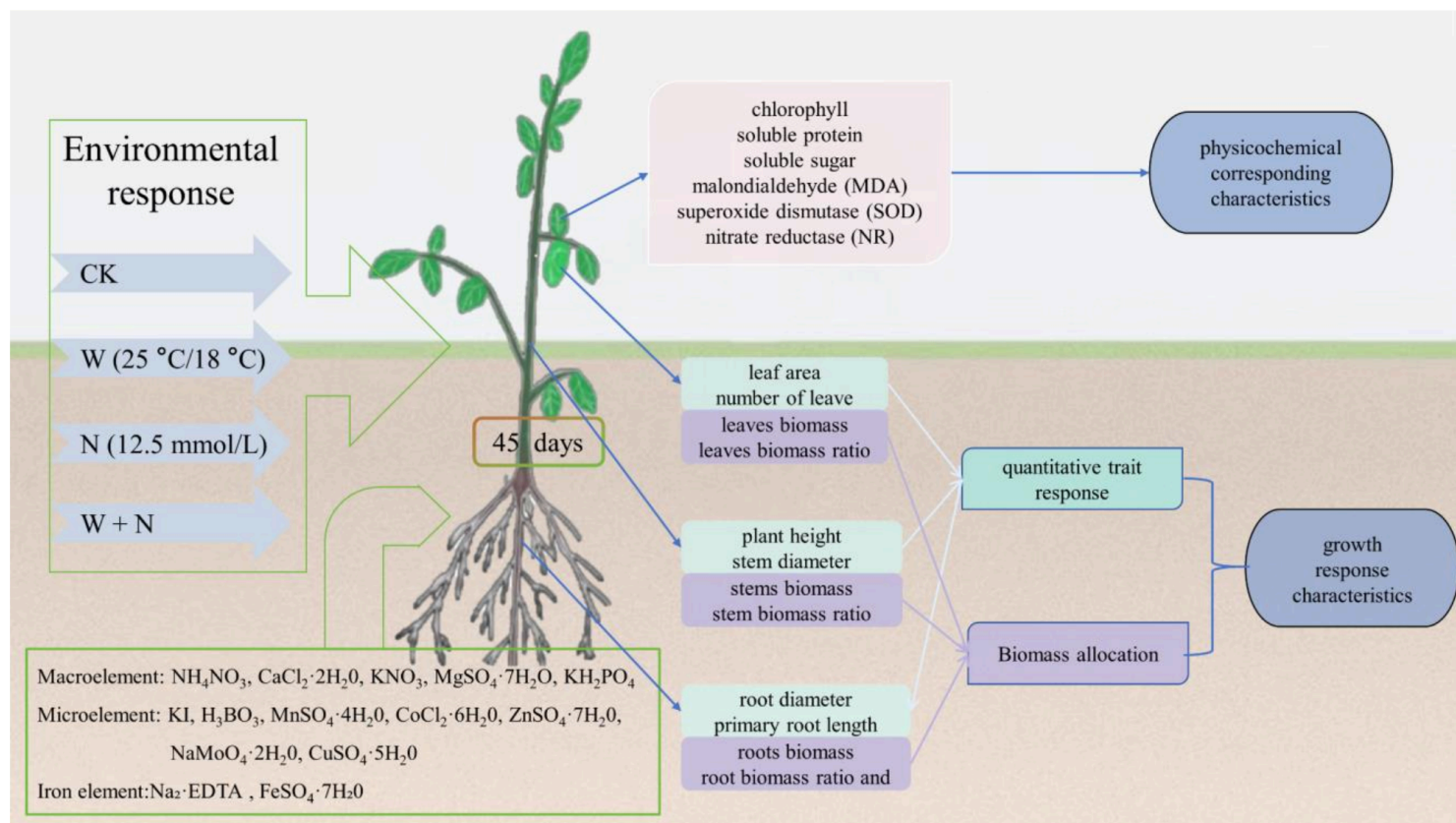


Figure 1

Depicts the experimental layout. *S. alopecuroides* were cultivated in MS nutrient solution for 45 days. Throughout the growth period, various treatments were applied, including a control, warming, nitrogen addition, and the interaction of warming and nitrogen addition.

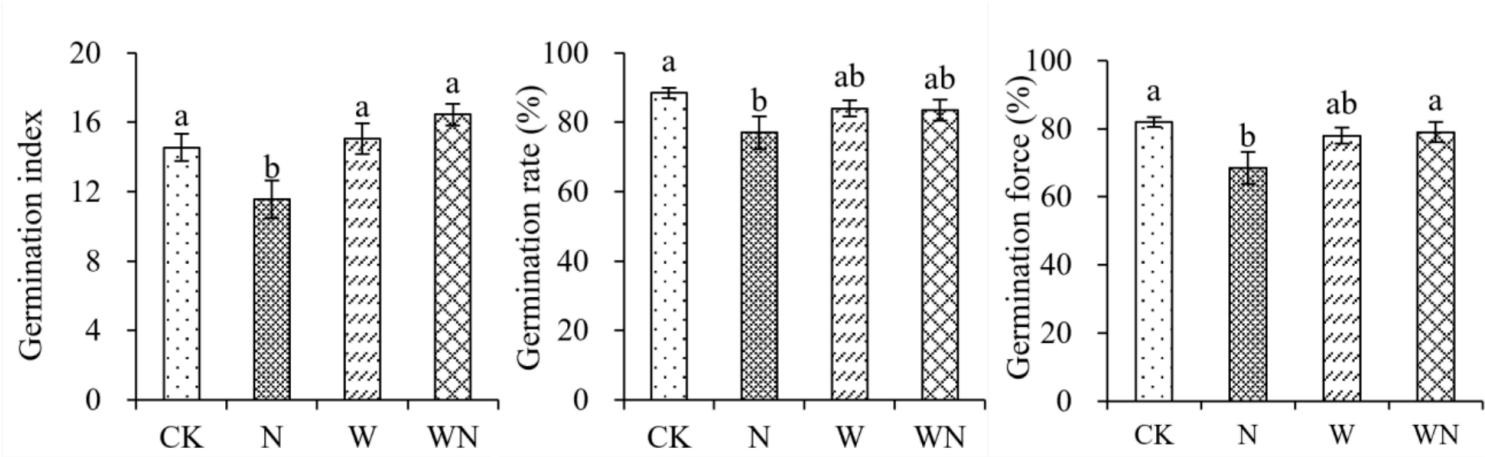


Figure 2

Impacts of nitrogen application, warming, and their interaction on the germination of *S. alopecuroides*.

Note: Different small letters indicate significant differences between nitrogen deposition rates (P < 0.05). The same below

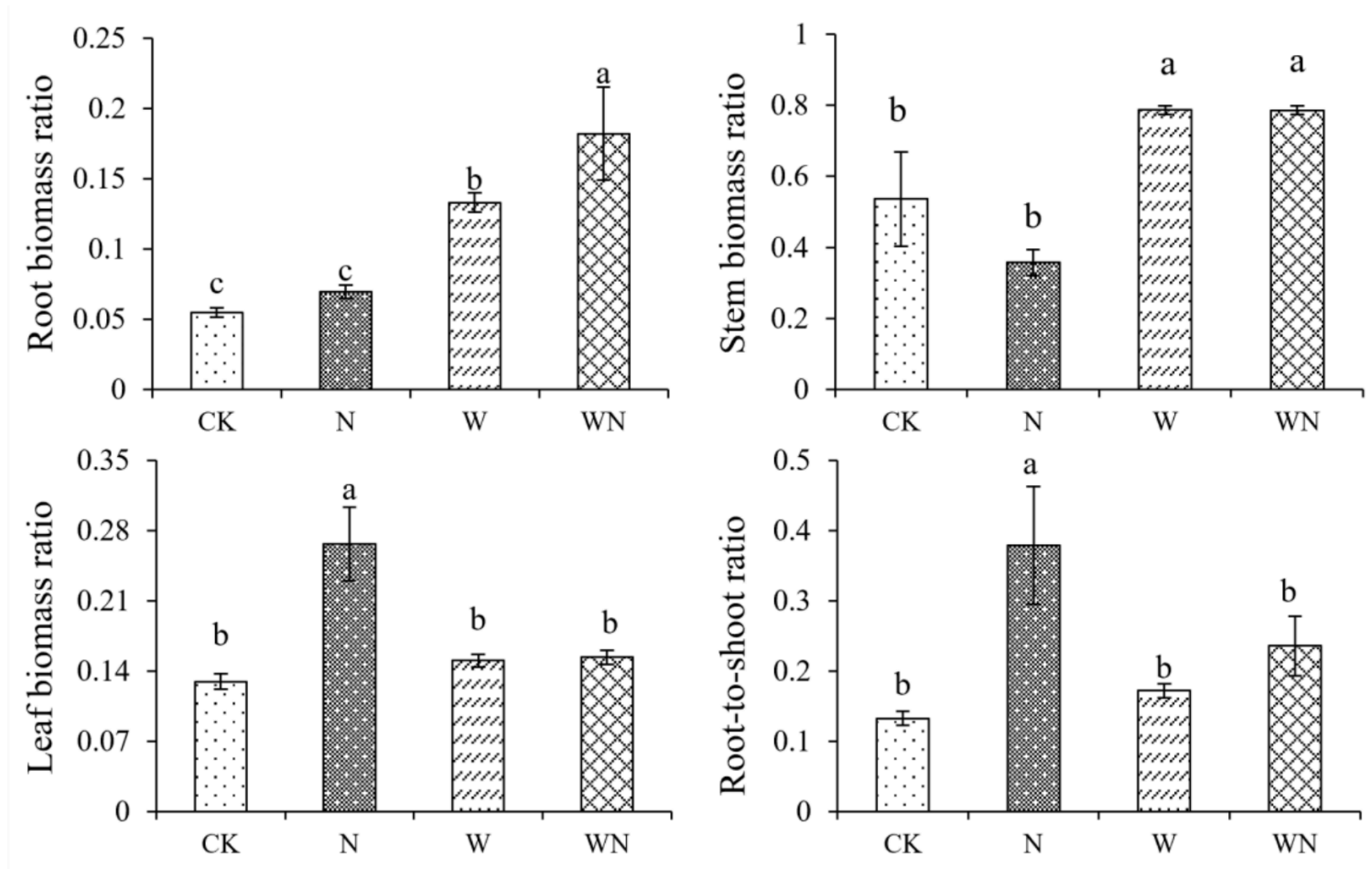


**Figure 3**

Effects of nitrogen and warming treatments on biomass allocation in *S. alopecuroides* seedlings.

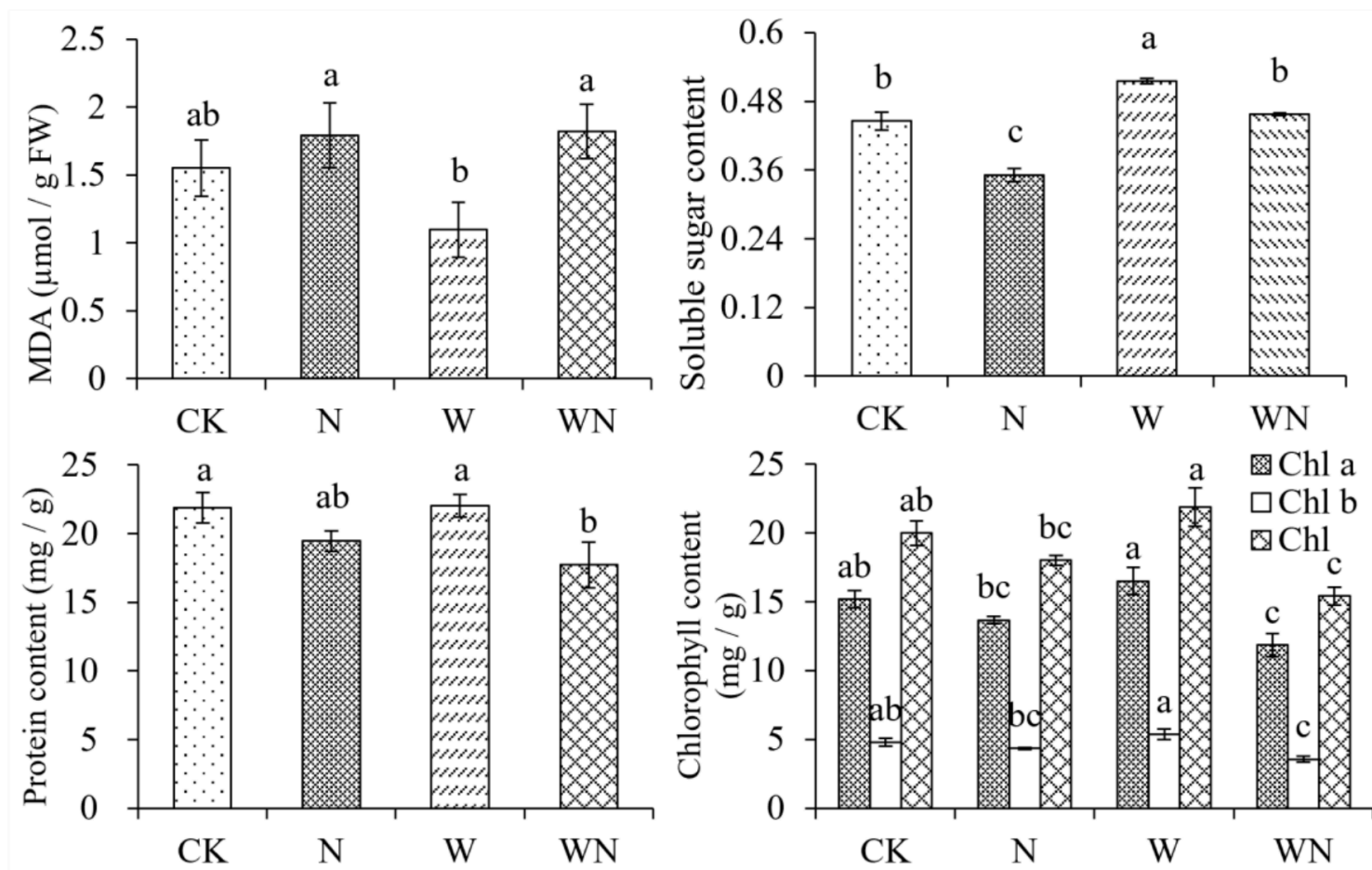


**Figure 4**

Effects of nitrogen and warming treatment on physicochemical indices of *S. alopecuroides* seedlings.

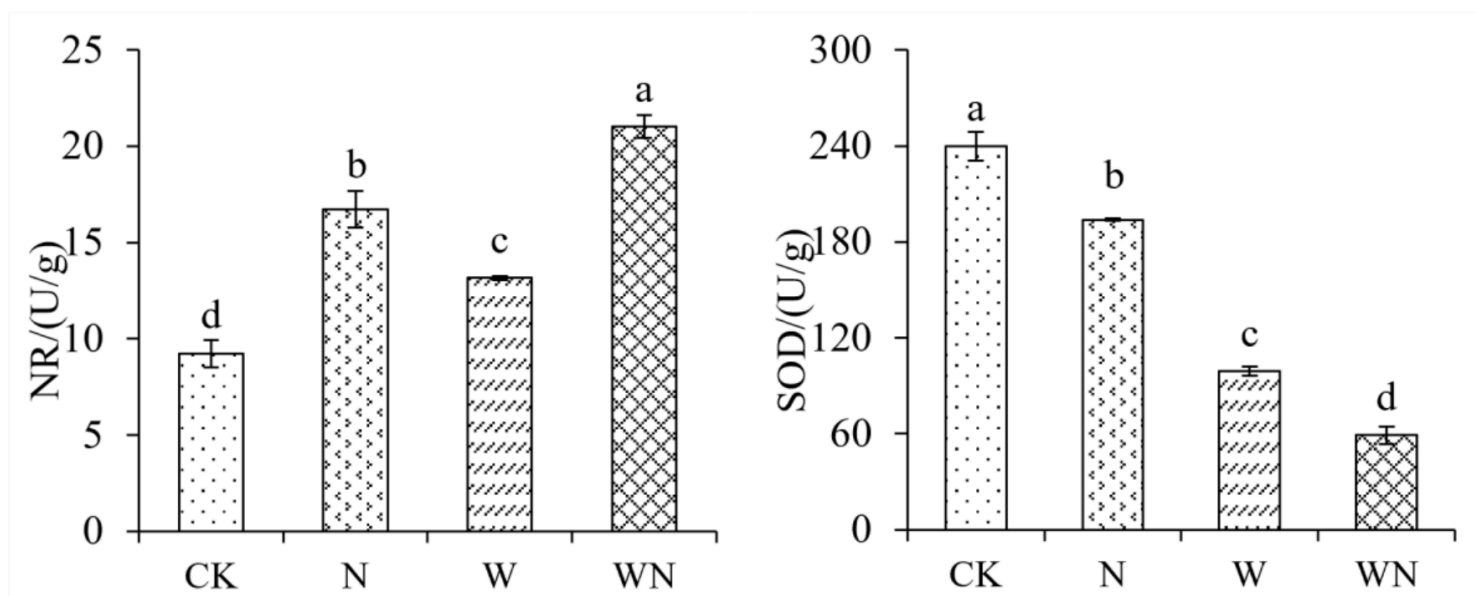


**Figure 5**

Effects of nitrogen and warming treatments on enzyme activities of *S. alopecuroides* seedlings

