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Research Article

# Effects of plant-soil feedbacks on the invasion and competitiveness of *Aegilops tauschii*

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## Abstract

The interaction between plants and soil is an important aspect that affects the invasive ability of foreign plants and the invasiveness of ecosystems. The study on plant soil feedback of *A. tauschii* can provide reference for its invasion mechanism. Firstly, the effects of *A. tauschii* on the nutrients and enzyme activities of invaded soil were investigated; Secondly, in conjunction with soil sterilization, pot experiments were conducted using the De Wit substitution method to investigate the impact of different degree invasive soils on the development of *A. tauschii* and its interaction with wheat. The results showed that the invasion of *A. tauschii* significantly increased soil organic matter, soluble phosphorus and soluble potassium, while also causing a significant decrease in the concentration of nitrate nitrogen. And according to the changes of morphological and biomass indicators of *A. tauschii*, the results of two-way ANOVAs showed that the invaded soil and its microbiota have a positive feedback effect on the growth of *A. tauschii*. Finally, it can be seen from the value of the competition balance index, the competition ability of *A. tauschii* in different invasion degree soil is greater than that of wheat whether the soil invaded by *A. tauschii* had undergone sterilization treatment or not. In conclusion, the invasion potential of *A. tauschii* is not only derived from its strong competitiveness, but also may be related to the soil conditions.

***Keywords:*** *Aegilops tauschii*; competitiveness; plant soil feedback; plant height; soil sterilization; total biomass

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## Introduction

Soil is an important carrier for ecosystems to run and acts as a medium for interaction between alien and native plants. The alteration of soil characteristics could potentially influence the structure and functionality of the entire ecosystem (Wang *et al.*, 2020). Plants can affect soil chemistry, microbial communities (Bauer *et al.*, 2017), and soil nutrients (Nash *et al.*, 2020) through root exudates (Hinsinger *et al.*, 2006), litter decomposition (Sun *et al.*, 2022), and selective uptake, and these changes in the soil environment subsequently affect plant growth, developing plant-soil feedback (PSF) (Buerdsell *et al.*, 2021). The impact of PSF on plants can be neutral, negative, or positive, determined by the respective roles played by soil-borne enemies, mutualists,

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and decomposers (van der Putten *et al.*, 2016). A lot of studies have demonstrated that PSF can significantly influence species coexistence, plant range expansion and non-native plant invasions (Chen *et al.*, 2019; Crawford *et al.*, 2019). However, studies conducted by Wei et al., (2020) suggest that certain native plants did not exhibit PSF effects that diminished the relative performance of invasive plants, and invasive plants did not manifest PSF effects that improved their own performance. In addition, the causal drivers of the observed varying plant-soil interactions between native and invasive plants have been little explored. As a result, the direction and strength of PSF effects and their role in plant invasions remain largely unpredictable.

As a wild relative of wheat, *Aegilops tauschii* is one of the world's top 10 nefarious weed species. Wild population of *A. tauschii* is widely distributed in the arid and semi-arid regions of central Eurasia (Van Slageren, 1994). *A. tauschii* not only has the characteristics of strong tillering reproductive ability, wide range adaptation, and easy dispersal, but also has very similar growth habit, germination time, and seedling stage characteristics with wheat. Today, *A. tauschii* has invaded more than 10 major wheat producing provinces in China, including Hebei and Shandong (Wang *et al.*, 2019a), and become one of the most difficult weeds to control in winter wheat fields of China (Fang, 2012; Wang *et al.*, 2019a, b). Therefore, the invasion of *A. tauschii* has seriously threatened the safety of wheat production in China. Our previous studies have shown that *A. tauschii* not only has strong allelopathic and competitive abilities (Wang *et al.*, 2019a; Wang and Chen, 2019), but also exhibits certain adaptability to stresses such as drought, flood and saline–alkaline (Wang *et al.*, 2019b; Wang *et al.,* 2021; Wang and Chen, 2023), and these characteristics of *A. tauschii* may play an important role in its invasion process. However, there is no research on the relationship between PSF and the invasiveness of *A. tauschii.* The exploration of the PSF may be provide reference for the study of the invasion mechanism of *A.tauschii*. The purposes of this study are: 1) determine the PSF of *A.tauschii* and evaluate its impact on competition with local plants. 2) evaluate the impact of PSF and competitive ability on the invasion potential of *A. tauschii*.

## Materials and Methods

### *Site descriptions and seed collection*

In June 2022, seeds of *A. tauschii* and wheat (*Triticum aestivum* L. 'Xinmai 32') were obtained from the experimental field of Xinxiang Academy of Agricultural Sciences in Henan Province (35°18' N, 113°52' E). The seeds were stored indoors after being sun-dried. In addition, which was the soil collection site for various degrees of invasion by *A. tauschii*. The climate of this region is categorized as temperate continental climate, with an average annual sunshine time of 2144 hours, and an annual temperature of 15.5 °C, and an annual precipitation of 573 millimeters. The type of soil is yellow soil, and the primary accompanying plants in the invasion zone are *Digitaria sanguinalis* and *Elymus dahuricus*. But the PSF experiment was carried out at the Wanmu Garden Nursery Base in Luolong District, Luoyang City, Henan Province. It is characterized by a temperate monsoon climate, with an altitude of 209 meters, an average annual temperature of 14.86 ℃, and an average annual precipitation of 578.2 millimeters, and the type of soil is brown soil.

### *Experimental design*

#### Collection different degree invasion soil

In the experimental field where seeds were collected, four representative habitats were selected as sampling sites in areas with flat terrain and close soil and vegetation conditions based on the degree of invasion of *A. tauschii*. The four selected habitats are: (1) bare soil (blank) i.e., bare land without plant grown; (2) mild invasion, that *A. tauschii* had a coverage of 10-30% in the plot; (3) moderate invasion, that *A. tauschii* had a coverage of 40~60% in the plot; and (4) severe invasion, with *A. tauschii* as the dominant species having a coverage of 60~90% in the plot. The sampling point area is 3 × 3 m, the spacing between sampling points is greater than 5 meters. After removing organic impurities such as ground plants and litter at the sampling point, collect surface soil (0-10cm deep) by using a 5-point sampling method and mix it as a soil sample, and avoid direct sunlight during sampling. The soil samples are packaged in zipper bags, placed in a cooler with ice bags, and then transported to the laboratory for further indicator determination.

PSF experiment of *A. tauschii*

Firstly, select a square plot with side length of 16 m in the Wanmu Garden Nursery Base, and then divide it into 4 rows along the east-west direction. From south to north, the land is divided into bare-, mildly invaded-, moderately invaded- and severely invaded soil. On October 5, 2022, according to the degree of invasion of the soil sampling area (experimental field of Xinxiang Academy of Agricultural Sciences), pre sowing of *A. tauschii* was carried out in each row. Then, two thinning experiments were conducted from germination to early November to match the different degrees of invasion of *A. tauschii* in the invaded soil sampled plots. During the seedling growth process, other weeds were removed and routine field management was carried out. After 90 days, the above-ground biomass of *A. tauschii* was removed. A total of four soil samplings were taken from four rows using the same sampling method as for soils with different degrees of invasion.

Secondly, the four types of soil samples mentioned above were evenly divided into two parts and subjected to sterilization and non-sterilization treatments, followed by comparative pot competition experiments. The soil sterilization treatment followed Trevors' method (1996), which meant the soil was sterilized twice at intervals of 24 hours by autoclaving at 121 °C for 60 min, with an interval of 24 h. The process is as follows: transfer soil samples (sterilization or non-sterilization treatments) with different degrees of invasion into plastic pots (pot diameter 21 cm at the mouth and a height of 19 cm), and 5.5 kg per pot. As per the replacement method (De Wit, 1960), monoculture and mixed planting of *A. tauschii* and wheat. Sow 20 seeds of *A. tauschii* or wheat in each pot, and thinning was performed after germination. Considering the commonly used wheat planting density (500-600 plants·m$^{-2}$) and the pot specification, as well as the edge effect, our plant density was set to 12 plant·pot$^{-1}$, which is same in both monoculture and mixed groups. The slow seedling period lasted for 14 days, and the gaps were filled with seedlings to ensure a constant number of seedlings pot. The seedlings were watered regularly so that they grew normally. After the slow seedling period, the potted plants were randomly placed outdoors. Set 10 pots per treatment and repeat 3 times per treatment, totaling 480 pots.

*Assessment indices and methods*

Soil nutrient and activity of soil enzyme

An appropriate amount of soil with different degrees of invasion was taken from the invasion area and pass it through a 2 mm sieve, and divided into two parts. One part was stored in a refrigerator at 4 °C, while the other part was air-dried indoors for other soil nutrient determinations. The activities of soil urease, protease, invertase and phosphatase were determined according to the method of Yao and Huang (2006), and determination of ammonium and nitrate nitrogen was completed within 15 days. According to Bao's (1981) method, soil organic matter, total nitrogen, total phosphorus, soluble phosphorus, and soluble potassium were determined.

Morphological and biomass indices

The experiment ended after 90 days and a total of 10 plants *A. tauschii* or wheat were randomly selected from each treatment. Firstly, measure the height of each plant; Secondly, separate plant roots from the soil using water flushing method. The leaf area was measured by using a scanner and Photoshop software (Xiao *et al.*, 2005). Finally, the leaves, stems and roots were separated and store them separately in paper bags. Then dry the sample in an oven at 80 °C to constant weight, and measure the weight using a millionth scale. Root mass/Crown mass (R/C) = root biomass/aboveground biomass was estimated (Wang and Feng, 2004).

*Data analysis*

In addition, the relative yield (RY), total relative yield (RYT) and competition balance (CB) index were used to measure the competitiveness of *A. tauschii* and wheat against each other (De Wit, 1960; Wilson, 1988), and they were calculated as described by Wang *et al.* (2021). SPSS software (version 18.0) was used to perform statistical analysis. The effects of different infection degrees on the nutrient and soil enzyme activities were analysed by one-way analysis of variance (ANOVA). Two-way analysis of variance (ANOVA) was used to analyze the effects of soil with different invasion degrees and sterilization treatment or not on the morphology, biomass and competition index of *A. tauschii* and wheat. The significant was tested using the least significant differences (LSD) at $p = 0.05$. Statistical values are expressed as mean (±SE). Microsoft Excel was used to summarize the data and plot figures.

## Results

*A. tauschii invasion on soil nutrient and activity of soil enzyme*

With the increase of the invasion degree of *A. tauschii*, the pH value, organic matter, total nitrogen, total phosphorus, soluble phosphorus, soluble potassium, and ammonium nitrogen of the invaded soil were all increased first and then decreased, but the content of nitrate nitrogen decreased continuously (Table 1). There was a significant difference in the content of organic matter, soluble phosphorus, soluble potassium, and ammonium nitrogen between the mildly invaded soil and the bare soil ($p<0.05$). But there was no significant difference in soil pH, total nitrogen, and total phosphorus between severely invaded soil and the bare soil. In addition, the nitrate nitrogen content in severely invaded soil significantly decreased compared to bare soil ($p < 0.05$).

**Table 1.** Effects of *A. tauschii* invasion on soil nutrient and available nutrients

| Soil type | pH | Organic matter/ $(g\cdot kg^{-1})$ | Total nitrogen/ $(g\cdot kg^{-1})$ | Total phosphorus/ $(g\cdot kg^{-1})$ | Dissolved phosphorus/ $(mg\cdot kg^{-1})$ | Potassium/ $(mg\cdot kg^{-1})$ | Ammonium nitrogen/ $(mg\cdot kg^{-1})$ | Nitrate nitrogen/ $(mg\cdot kg^{-1})$ |
|---|---|---|---|---|---|---|---|---|
| Bare soil | 8.36±0.10 a | 14.23±0.44 a | 1.26±0.02 a | 0.36±0.01 a | 2.50±0.01 a | 102.00±9.39 a | 1.27±0.01 a | 27.45±0.67 b |
| Mild invasion soil | 8.38±0.18 a | 25.45±1.05 b | 2.04±0.04 a | 0.51±0.06 a | 8.50±0.21 b | 252.00±7.83 b | 2.30±0.02 b | 26.95±0.45 b |
| Moderate invasion soil | 8.44±0.09 a | 21.57±0.85 b | 2.06±0.01 a | 0.53±0.02 a | 11.80±0.32 b | 278.00±9.70 b | 1.96±0.01 ab | 18.22±0.25 ab |
| Severe invasion soil | 8.41±0.02 a | 22.58±1.14 b | 1.90±0.02 a | 0.46±0.10 a | 9.60±0.21 b | 228.00±6.82 b | 1.86±0.03 ab | 13.70±0.14 a |

The different lowercase in each column indicates the significant difference at the 0.05 level.

With the increase of *A. tauschii* invasion, the activities of soil urease and protease decreased first and then increased, but the activities of phosphatase and invertase increased first and then decreased (Table 2). Among them, there was no significant difference in urease activity between the severely invaded soil and the bare soil. However, protease, phosphatase, and invertase showed significant differences in mildly invaded soil and the bare soil ($p<0.05$).

**Table 2.** Effects of *A. tauschii* invasion on activity of soil enzyme

| Soil type | Urease $(ug\cdot g^{-1}\cdot 24h^{-1})$ | Proteinase $(mg\cdot g^{-1}\cdot 24h^{-1})$ | Phosphatase $(umol\cdot g^{-1}\cdot 24h^{-1})$ | Invertase $(mg\cdot g^{-1}\cdot 24h^{-1})$ |
|---|---|---|---|---|
| Bare soil | 1007.08±8.40a | 4.12±0.24c | 8.07±0.07a | 74.72±3.23a |
| Mild invasion soil | 921.97±11.48a | 0.96±0.25a | 13.19±0.16b | 126.49±6.19b |
| Moderate invasion soil | 919.34±9.34a | 0.63±0.14a | 16.73±0.45b | 118.89±8.13b |
| Severe invasion soil | 931.28±18.99a | 1.98±0.31b | 14.04±0.03b | 104.69±9.20b |

The different lowercase in each column indicates the significant difference at the 0.05 level.

*PSF of A. tauschii*

The results of two-way ANOVAs showed that the effects of invasion soil on plant height, total leaf area, total biomass and R/C of *A. tauschii* and *T. aestivum* were significant (Table 3, Figures 1, 2, 3, 4). The effects of sterilization treatment or not on plant height, total leaf area and total biomass of *A. tauschii*, and pant height of *T. aestivum* were significant, but there was no significant impact on the R/C of *A. tauschii*, and total leaf area, total biomass and R/C of *T. aestivum* (Table 3, Figure 1, Figure 2, Figure 3). In addition, the effects of invasion soil and sterilize treatment or not, as well as their interaction have significant impact on the competitive balance index of *A. tauschii*, but have no significant impact on its total relative yield (Table 3, Figure 4).

**Table 3.** Analysis of variance results (p values) of growth indicators and competition index of *A. tauschii* with different degrees of invasion soil and sterilized or non-sterilized

| Parameter | ***A. tauschii*** | | | ***T. aestivum*** | | |
|---|---|---|---|---|---|---|
| | **Invasion soil** | **Sterilized or non-sterilized** | **Invasion soil × sterilized or non-sterilized** | **Invasion soil** | **Sterilized or non-sterilized** | **Invasion soil × sterilized or non-sterilized** |
| Plant height | < 0.01 | < 0.01 | < 0.01 | < 0.01 | < 0.01 | < 0.01 |
| Total leaf area | < 0.01 | < 0.01 | < 0.01 | < 0.01 | 0.06 | 0.15 |
| Total biomass | < 0.01 | < 0.01 | < 0.01 | < 0.01 | 0.13 | 0.55 |
| R/C | < 0.01 | 0.21 | 0.19 | < 0.01 | 0.32 | 0.41 |
| RYT | 0.12 | 0.08 | 0.21 | - | - | - |
| CB | < 0.01 | < 0.01 | < 0.01 | - | - | - |

With the increase of the invasion degree of *A. tauschii*, the plant height and total leaf area of the monoculture *A. tauschii* increased in non-sterilized soil, while wheat showed the opposite change. In sterilized soil, the plant height and total leaf area of *A. tauschii* and wheat showed decreasing patterns (Figure 1). In the non-sterilized soil, the plant height and total leaf area of *A. tauschii* were increased by 40.16% and 23.10% in the severely invaded soil compared to the bare soil, while those of the wheat were decreased by 19.81% and 18.69%. In the sterilized soil, the plant height and total leaf area of *A. tauschii* were decreased by 20.01% and 15.28% in the severely invaded soil compared to the bare soil, while those of wheat were decreased by 32.30% and 23.13%.

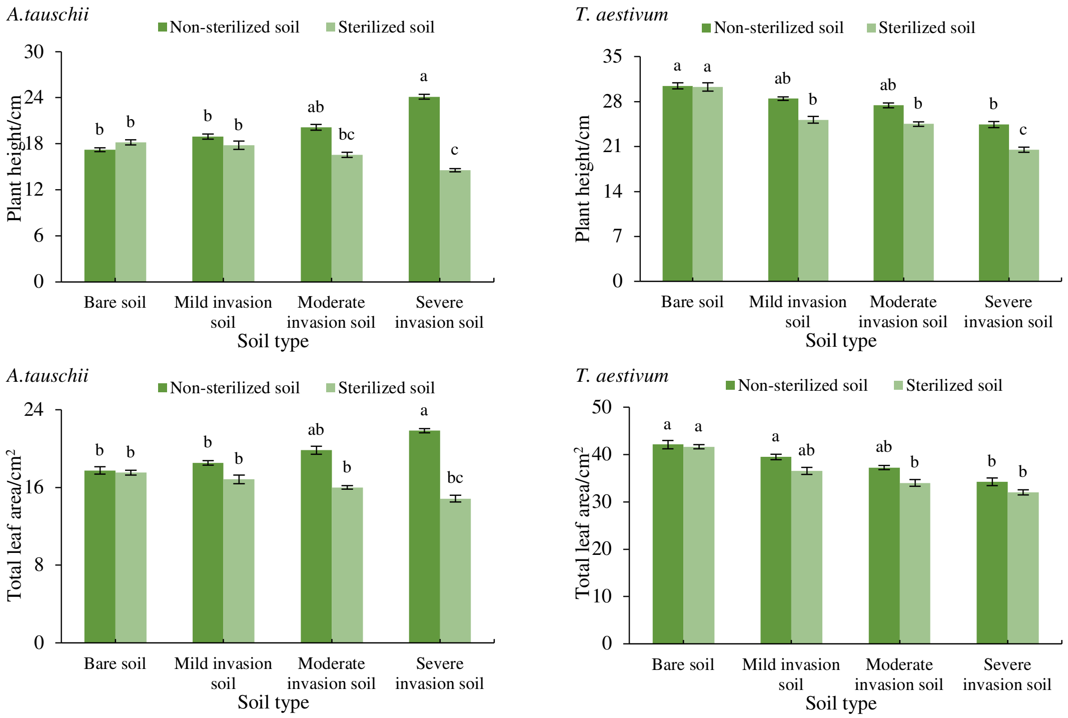

**Figure 1.** Effect of sterilized and non-sterilized soil on plant height and total leaf area of *A. tauschii* and *T. aestivum*

The values are shown as mean ± SE. Different letters above the bars denote significant differences ($p \leq 0.05$) in plant height or total leaf area with Duncan's test under monotculture with sterilized or non-sterilized treatment in different degrees of invasion soil.

In the non-sterilized soil, the total biomasses of *A. tauschii* increased with the increase of invasion degree, while the total biomass of wheat showed the opposite change. On the other hand, the total biomass of *A. tauschii* and wheat decreased continuously in sterilized soil (Figure 2). In the non-sterilized soil, the total biomasses of *A. tauschii* increased by 25.47% in the severely invaded soil compared to the bare soil, while the total biomass of wheat decreased by 19.90%. In the sterilized soil, the total biomass of *A. tauschii* decreased by 16.83% in the severely invaded soil compared to the bare soil. While the total biomass of wheat decreased 23.01%.

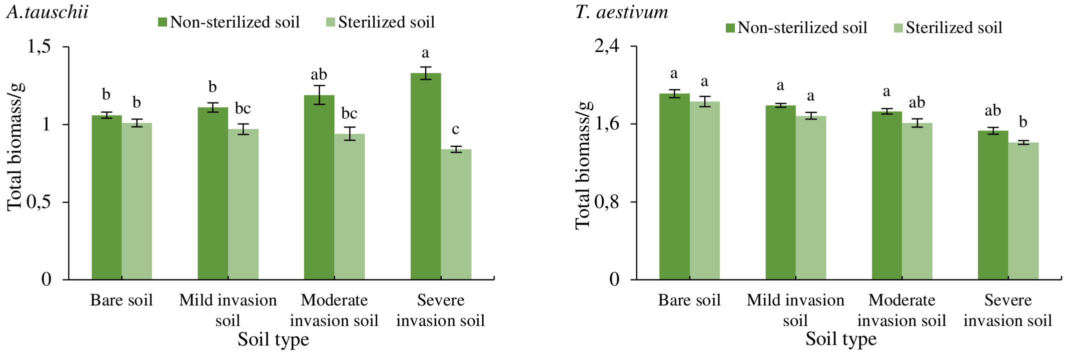

**Figure 2.** Effect of sterilized and non-sterilized soil on total biomass of *A. tauschii* and *T. aestivum*

The values are shown as mean ± SE. Different letters above the bars denote significant differences ($p \leq 0.05$) in total biomass with Duncan's test under monotculture with sterilized or non-sterilized treatment in different degrees of invasion soil.

With the increase of the invasion degree of *A. tauschii*, the R/C values of *A. tauschii* and wheat decreased whether the invaded soil was sterilized or not (Figure 3). In the non-sterilized soil, the R/C values of *A. tauschii* and wheat in the severely invaded soil decreased by 31.38% and 15.60% than those in bare soil. While in the sterilized soil, the R/C values of the monoculture and mixed planting *A. tauschii* and wheat in the severely invaded soil decreased by 37.92% and 17.26%.

Whether the soil was sterilized or not, the RYT of *A. tauschii* was always between 0 and 1, while the CB value increased with the increase of invasion degree of *A. tauschii*, and always greater than 0 (Figure 4).

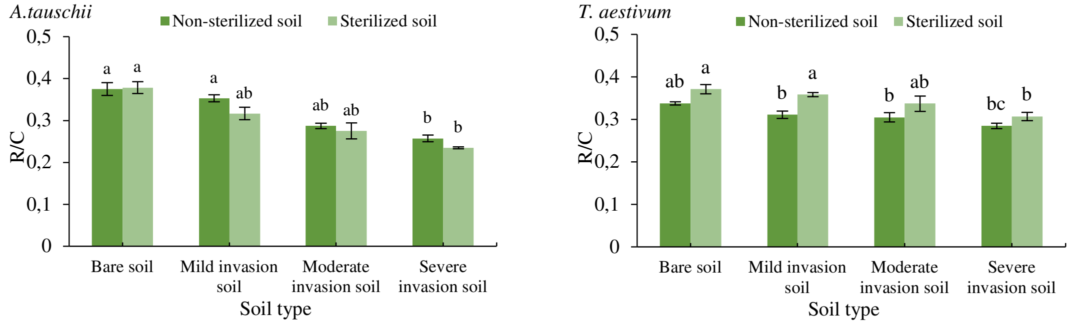

**Figure 3.** Effect of sterilized and non-sterilized soil on the root-crown ratio (R/C) of *A. tauschii* and *T. aestivum*

The values are shown as mean ± SE. Different letters above the bars denote significant differences ($p \le 0.05$) in R/C with Duncan's test under monotculture with sterilized or non-sterilized treatment in different degrees of invasion soil.

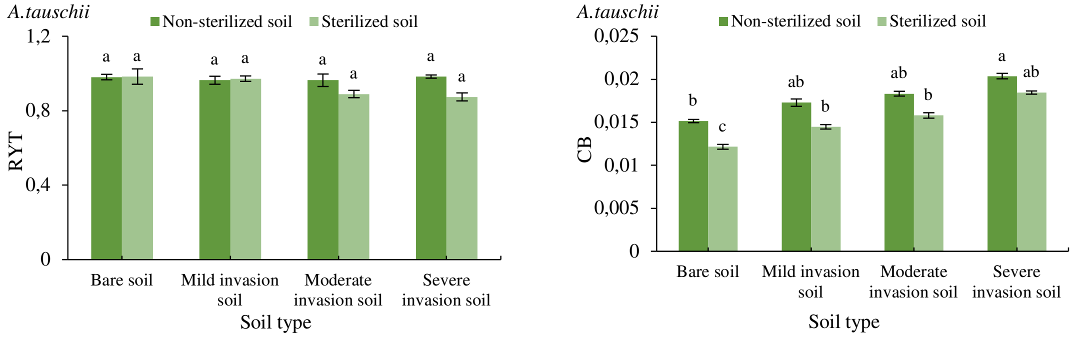

**Figure 4.** Effect of sterilized and non-sterilized soil on total relative yield (RYT) and competitive balance (CB) of *A. tauschii*

The values are shown as mean ± SE. Different letters above the bars denote significant differences ($p \le 0.05$) in RYT or CB with Duncan's test with Duncan's test of sterilized or non-sterilized treatment in different degrees of invasion soil.

## Discussion

In this study, the invasion of *A. tauschii* significantly increased soil ammonium nitrogen but significantly reduced soil nitrate nitrogen, which may be related to its beneficial absorption and utilization of nitrate nitrogen. This result was inconsistent with the results that the invasive plants *Mikania micrantha* significantly increased nitrate nitrogen but decreased ammonium nitrogen in the soil (Chen *et al.*, 2009), and this may be due to the preference of different plant species for nitrogen utilization. Successful invasive plants can influence soil nutrients and significantly alter soil enzyme activities, which may accelerate nutrient cycling and play an important role in improving soil fertility, and ultimately benefit invaders (Liu *et al.*, 2019; Zhou and Staver, 2019). In the present study, the invasion of *A. tauschii* resulted in the decrease of soil urease and protease activities, consistent with the conclusions of the invasion of *Praxelis clematidea* (Quan *et al.*, 2016) and *Spartina alterniflora* (Sun and Zhu, 1989). In addition, the invasion of *A. tauschii* also caused increased activities of soil phosphatase and invertase, and it was also positively correlated with the changes of organic matter and soluble phosphorus in the invaded soil, these results were consistent with the findings about the invasive plants *Spartina alterniflora* (Sun and Zhu, 1989) and *Solidago canadensis* (Wang *et al.*, 2011).

Now, more studies have proved that soil microorganisms are an important driving factor for the success of alien plant invasion (Rodríguez-Caballero *et al.*, 2020; Zhang *et al.*, 2020b). In the study of the invasion mechanisms of alien plants, soil sterilization has been widely used to explore the role of soil microorganisms in PSF (Liang *et al.*, 2016; Wang *et al.*, 2022; Xiao *et al.*, 2014). In this study, the plant height, total leaf area and total biomass of *A. tauschii* in the non-sterilized soil increased with the increase of invasion degree of *A. tauschii*, and this indicated that positive feedback of the invaded soil on the growth of *A. tauschii*. However, these morphological and biomass indicators of *A. tauschii* showed a decreasing change after sterilization treatment of the invaded soil. This indicated that the microbiota of invasion soil also promotes the growth of *A. tauschii*, and this result is contrary to the invasive plant *Sorghum halepense* (Wang *et al.*, 2022), which may be due to the different plant species. In addition, the reason why the sterilization treatment of invaded soil inhibited the growth of *A. tauschii* itself may be related to the allelopathic substances in the invaded soil, which consistent with our previous research findings about the allelopathy of *A. tauschii*. The result also confirmed the hypothesis that the successful invasion of alien plant may be a combination of changes in soil microbial communities (Zhang *et al.*, 2020a) and the production of new chemicals by invaders (Reinhart and Callaway, 2006).

It may be an important strategy for the invasive plant such as *Chromolaena odorata* to adapt to the invaded habitats by allocating biomass, and this may also bring greater competitive advantages to invasive plants (Te Beest *et al.*, 2009). In this study, whether the invaded soil is sterilized or not, the root-crown ratios of *A. tauschii* decreased with increase of invasion degree of *A. tauschii*, and this indicates that the invasion adaptation strategy of *A. tauschii* is same as *C. odorata*. Combined with the positive feedback results of invasion soil of *A. tauschii* on its own growth. Our research results indicate that the invasion soil was conducive to the growth of the above-ground part of *A. tauschii* to compete for light resources, and it also inhibited the growth of local associated plants to a certain extent to achieve competitive advantage, consistent with the results of Oduor *et al.* (2022).

The invasiveness of an alien plant species can be reflected by its competitiveness (Vilà and Weiner, 2004). And biomass is one of the essential indicators to measure interspecific competition. In this study, the RTY of *A. tauschii* were both greater than 0 and less than 1 whether the invaded soil was disinfected or not, and this indicating a certain competitive relationship between *A. tauschii* and wheat. The increased CB values indicated that the invaded soil promoted the competitive inhibition of *A. tauschii* on wheat. Under other unchanged conditions, the CB value in sterilization treatment is lower than that in non-sterilized treatment, this may be because that the sterilized treatment eliminated the positive feedback of soil microbiota on the growth of *A. tauschii*, thereby weakening its competitive effect on wheat.

The impact of soil conditions on competitive relationships may affect invasion dynamics (Perkins *et al.*, 2011). The PSF produced by some plants can improve the performance and competitiveness of the same plant species, which may increase their invasive potential (Klironomos, 2002; Kulmatiski *et al.*, 2008). Perkins and Nowak (2012) found that the invasive plant *Agropyron cristatum* generated a higher competitive effect than its native neighbours only in the same soil conditions, and so its invasive potential may come from the soil conditions rather than the competitive ability. In this study, *A. tauschii* not only exhibited a higher competitive effect than wheat in the same conditioned soil, but also showed higher competitiveness in the feedback soil, and this indicated that the invasion potential of *A. tauschii* not only came from competition capacity but also from soil conditions.

## Conclusions

The invasion of *A. tauschii* significantly increased soil organic matter, soluble phosphorus, and soluble potassium content, but significantly reduced nitrate nitrogen content. In addition, the invasion soil and its soil microbiota both showed positive feedback on the growth of *A. tauschii* and promoted its competitive inhibitory effect on wheat. In summary, *A. tauschii* affected the cycling of soil-related nutrients by altering soil enzyme activities and microbial community composition, so that it gained an advantage in competition with local plants.

## Authors' Contributions

NW wrote the manuscript and designed experiments; LW and HC performed out experiments; NW and YWT analysed the experimental results. All authors read and approved the final manuscript.

## Ethical approval (for researches involving animals or humans)

Not applicable.

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## Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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