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Differential responses to cadmium stress and competition in *Alternanthera philoxeroides* and *Trifolium repens*: stress resistance and adaptive strategies

Yuanyuan Cui[1,2], Qiaoying Zhang[3], Peng Liu[1], Chang He[1], Tiantian Xie[1], Jing Wan[1], Lin Zhang[4] and Yunchun Zhang[1*]

Abstract

Background Heavy metal pollution, a pervasive and persistent environmental stressor often linked to industrial and agricultural activities, interacts with intra- and interspecific competition as key factors influencing the invasion of exotic plants. *Alternanthera philoxeroides* and *Trifolium repens* exhibit distinct allocation strategies to mitigate resource competition under cadmium (Cd) pollution, yet their differential resistance to Cd remains underexplored.

Results In this study, a greenhouse experiment was conducted to investigate the effects of Cd contamination and competitive interactions on the stress resistance index (SRI) and adaptive strategies of both species. The results indicated that *T. repens* exhibited higher SRI under stronger interspecific competition, demonstrating clear density dependence. *T. repens* primarily enhanced its competitiveness by increasing photosynthesis capacity, though its root system structure contributed more substantially to SRI. In contrast, *A. philoxeroides* increased SRI by forming shorter and thicker root system.

Conclusion Overall, the root utilization strategy of *A. philoxeroides* showed greater advantages than that of *T. repens*. Under intraspecific competition, *A. philoxeroides* improved competitiveness mainly through increased root complexity and optimized photosynthetic efficiency via non-stomatal regulation in light competition. The invasiveness of *A. philoxeroides* can be attributed to the ability to synergistically combine root development and photosynthesis to enhance its stress resistance. This study provides a broader perspective on invasion mechanisms in natural ecosystems and offers a solid theoretical basis for understanding stress tolerance and environmental management of *A. philoxeroides*.

Keywords Cadmium stress, Competition, Stress resistance index, Root development, Photosynthetic efficiency, Adaptive strategy

*Correspondence:
Yunchun Zhang
yunchunzhang@163.com
Full list of author information is available at the end of the article

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Introduction

Heavy metal pollution and biological invasions represent two major environmental challenges exacerbated by societal development, adversely affecting soil productivity, ecological security, and biodiversity (Paini et al. 2016; Wang et al. 2021). Heavy metals inhibit plant growth and threaten ecosystem stability, leading to declines in species diversity and habitat degradation (Pujari and Kapoor 2021). Paradoxically, such degraded ecosystem with low biodiversity can be more vulnerable to plant invasion. Many invasive plants exhibit remarkable adaptability, utilizing a wide range of physiological niches (Prabakaran et al. 2019). During colonization, they engage in both intra- and interspecific competition, which affects their strategies for resource acquisition and utilization. The capacity of an invasive plant to sustain growth and metabolize under stress suggests a degree of resistance that facilitates plant survival and, ultimately, success in niche competition. Notably, organisms with greater stress resistance are likely to gain a competitive advantage (Wang et al. 2024). However, the interactive effects of heavy metal stress and competitive intensity on plants' stress resistance remain unclear, and the underlying adaptive strategies and competitive mechanisms require further elucidation.

Metallic contaminants disrupt a wide range of physiological and biochemical processes in plants, particularly material accumulation and photosynthesis. Excessive soil heavy metal concentrations inhibit photosynthesis, leading to reduced biomass and compromised acclimatization (Emamverdian et al. 2015). For instance, non-essential heavy metals such as Cd, Hg and Pb) can diminish chlorophyll content, induce chlorosis and necrosis (Khan et al. 2023), and ultimately cause plant death by distruption of chlorophyll synthesis and closure of stomatal. Cadmium, in particular, is highly mobile and severely toxic even at low concentrations. It was ranked as the seventh most toxic substance in the 2017 Hazardous Substances and Priority List by the Agency for Toxic Substances and Disease Registry (Mezynska and Brzóska 2018). Once accumulated in plants and biomagnified through the food chain, Cd not only impedes plant growth and development but also poses significant threats to human health (Fan et al. 2023; Zhang et al. 2024).

To mitigate heavy metal toxicity, plants have developed a variety of adaptive strategies, often involving morphological changes and biomass reallocation. These adaptations help offset metabolic costs of detoxification (Maestri et al. 2010). A common reponse is preferential root biomass allocation in metal-polluted soils, which enhances metal sequestration in belowground tissues and stimulates production of defensive phytochemicals (Audet and Charest 2008). Compared to native species, invasive plants often exhibit greater phenotypic plasticity and metal tolerance, granting them a competitive advantage (Wang et al. 2020). In contrast, native plants are frequently negatively affected by invasive-mediated plant-soil feedback. Heavy metal pollution may further create opportunities for invasive plants to establish dominance (Prabakaran et al. 2019), while also rapidly modifying soil conditons—altering the exchangeable forms and availability of heavy metals (Li et al. 2024)—thereby exerting additional pressure on native plant communities in disturbed habitats. Therefore, elucidating the adaptive strategies of both invasive and native plants under cadmium pollution is essential for advancing bio-prevention and phytoremediation approaches.

The phenotypic plasticity hypothesis proposes that invasive species generally demonstrate greater phenotypic flexibility compared to their native counterparts (Huang et al. 2015), enabling rapid adaptation to heterogeneous environments through either adaptive evolution or plastic responses (Williams et al. 2008; Xiang et al. 2024). For instance, invasive plants strategically allocate more resources to stems and leaves under competitive conditions, thereby increasing their light-capturing area and enhancing aboveground space occupancy. In contrast, native plants frequently experience suppressed growth and development due to shading (Kang et al. 2020), placing them at a competitive disadvantage in resource acquisition. Invasive species also commonly demonstrate higher root-to-shoot ratios during competition, conferring greater plasticity and a broader capacity for nutrient uptake compared to native species, which further strengthens their overall competitiveness. Among them, root systems play a vital role in resource storage, nutrient uptake (e.g., water and inorganic salts), and the biosynthesis of essential compounds like phytohormones and amino acids (Wang et al. 2022). As the primary organ in direct contact with soil pollutants, roots initiate a range of adaptive strategies to inhibit toxic metal uptake, modify internal root structure, and regulate translocation to aerial tissues (Fusaro et al. 2025)—all vital mechanisms for heavy metal tolerance. Under heavy metal stress, root architectural traits—including lateral and adventitious root formation, root system topology, and the development of specialized structures—are critical for minimizing metal absorption and managing oxidative stress (Piacentini et al. 2024). Physiologically, one of the earliest plant responses to heavy metal stress is stomatal closure, which directly constrains transpiration. Such stress can also reduce chloropgyll fluorescence emission intensity and chlorophyll content, disrupt "Ca^{2+} signaling", and alter stomatal aperture

(Yang et al. 2025). Additionally, heavy metals impair photosynthetic function by damaging chloroplasts, interfering with electron transport, and inhibiting key enzymes (Bernardini et al. 2016), collectively leading to a decline in photosynthetic performance. However, competitive strategies of invasive and native plants may vary significantly under different intensities of competition, and the mechanistic role of phenotypic plasticity in stress resistance remains inadequately understood. Moreover, the key functional traits that enhance stress resistance under the combined pressure of heavy metal exposure and interspecific competition await further clarification.

Alternanthera philoxeroides, a species originating in South America, has become a highly destructive invasive plant in Chinese ecosystems due to its exceptional reproductive capacity and rapid growth (Wang et al. 2021). It has colonized southern China with particular aggressiveness, significantly altering native community structures and disrupting key ecological processes. In contrast, *Trifolium repens*, a high-quality forage grass, valued for its ecological and economic benefits, is widely cultivated in regions south of the Huaihe Rever and in southwestern China (Yu et al. 2024). Both *A. philoxeroides* and *T. repens* are clonal plants (Song et al. 2025), and their competition in heterogeneous environments involves spatial occupation and resource integration. However, under combined cadmium (Cd) contamination and competitive pressure, *A. philoxeroides* exhibits reduced efficiency in resource acquisition. Specifically, Cd stress and competition intensity drive *A. philoxeroides* to allocate more resources to the belowground parts to compete for soil nutrients, whereas *T. repens* invests more in aboveground structures to compete for light (Cui et al. 2022). Despite these insights, the specific competition strategies employed by *A. philoxeroides* and *T. repens* for above- and belowground resources under Cd stress remain poorly understood, particularly regarding their differential stress resistance. Specifically, we aim to address the following questions: (1) Does *A. philoxeroides* exhibit greater stress resistance than *T. repens* across a gradient of Cd exposure? (2) What are the principal competitive mechanisms governing the interactions between *A. philoxeroides* and *T. repens* under Cd stress and competition conditions? (3) Which functional traits enhance the stress resistance of each species under such combined pressures? By adressing these questions, this study seeks to provide deeper insights into the competitive dynamics and adaptive strategies of these two species under environmental stress, thereby informing more effective strategies for invasive species management and native habitat restoration.

Materials and methods

Experimental design

The competition experiment was conducted during the summer of 2021 (June to August) in a greenhouse at China West Normal University (30°48′45″ N, 106°4′1″ E), Nanchong City, Sichuan Province. The study site experiences a subtropical monsoon climate, with a mean annual temperature of 15.6 °C and annual precipitation of 1070.5 mm.

The growth substrate was prepared by mixing native clay soils—which exhibited brown-purple to reddish-brown-purple coloration and low organic matter content—with a commercial nutrient soil at a 1:4 ratio. The nutrient soil contained standardized components including perlite, high-quality peat, and various trace elements. The resulting substrate was characterized as clay loam with the following basic physicochemical properties: pH 7.3 ± 0.13, organic matter content 9.21 ± 0.32 g kg^{-1}, and a background Cd concentration of 0.27 mg kg^{-1}.

In May 2021, uniform stem fragments of *A. philoxeroides* were collected from the campus of China West Normal University and vegetatively propagated using single-node cuttings to maintain genetic consistency. Simultaneously, *T. repens* seeds were germinated under controlled environmental conditions. After 12 days, seedlings of both species with similar growth vigor were selected and transplanted into plastic pots (23.5 cm top diameter × 14 cm height × 13.2 cm bottom diameter), each filled with 3.5 kg of artificially Cd-spiked soil. The soil was contaminated by adding $CdCl_2$ solution to achieve three target contaminations: 0, 100, and 200 mg Cd kg^{-1} (dry weight), referencing China's agricultural Cd guideline (Duan et al. 2016). Prior to planting, the $CdCl_2$ solution was uniformly mixed into the soil, which was then equilibrated for one week to ensure homogeneity. Uncontaminated soil (0 mg Cd kg^{-1}) served as the control. Each treatment was replicated five times.

On 6 June 2021, uniformly sized ramets were transplanted into experimental pots under two culture types: monoculture of *A. philoxeroide*s and mixed culture with *T. repens*. Each culture type was established at two planting densities (5 or 9 plants per pot). In the mixed culture configuration, one central *A. philoxeroides* individual was surrounded by either four or eight evenly spaced *T. repens* plants. This design resulted in six treatments per culture type: Cd0P5, Cd0P9, Cd100P5, Cd100P9, Cd200P5, and Cd200P9. From the start of the experiment until the final harvest on 26 August 2021, all pots were watered daily to maintain optimal soil moisture, randomized weekly to minimize positional effects, and regularly weeded to ensure unrestricted plant growth.

Measurement of gas exchange characteristics

Photosynthetic characteristics of *A. philoxeroides* and *T. repens* were measured under saturating light intensity (PPFD 1500 μmol m^{-2} s^{-1}) using a LI-6400XT portable photosynthesis measurement system (LI-COR Inc., Lincoln, NE, USA). The measurement conditions were standardized as follows: atmospheric CO_2 concentration (C_a) of 400 μmol mol^{-1}, flow rate of 500 μmol s^{-1}, leaf chamber temperature maintained of 25 °C, and relative humidity of 60%. Key parameters recorded included the net photosynthetic rate (P_n), stomatal conductance (Cond), intercellular CO_2 concentration (C_i), and transpiration rate (T_r). Derived parameters—namely the stomatal limit values (LS), water use efficiency (WUE), and intrinsic water use efficiency (iWUE)—were calculated according to established methods (Condon et al. 2004), using the following formulas:

$$\mathrm{LS} = 1 - \frac{C_i}{C_a} \tag{1}$$

$$\mathrm{iWUE} = \frac{P_n}{Cond} \tag{2}$$

$$\mathrm{WUE} = \frac{P_n}{T_r} \tag{3}$$

Measurement of root characteristics

Root morphological analysis was conducted by carefully washing the root systems to remove soil residues under laboratory conditions. Surface moisture was then blotted with absorbent paper. The prepared samples were placed in transparent trays and scanned using a WinRHIZO root system analyzer (Regent Instruments Inc., Canada) to quantify five architectural parameters: root length (L, mm), root average diameter (D, mm), root surface area (A, mm^2), root volume (V, mm^3), and fractal dimension (FD). Based on these primary measurements, three functional root traits were derived: specific surface area (SSA, cm^2 cm^{-3}), specific root length (SRL, cm g^{-1}), and root fineness (RF, mm mm^{-3}). Following scanning, all plant materials were oven-dried at 80 °C for 24 h until constant mass was achieved to determine root biomass (B_r, g) and total biomass (B, g). The derived parameters were calculated as follows:

$$\mathrm{SSA} = \frac{A}{V} \tag{4}$$

$$\mathrm{SRL} = \frac{L}{B_r} \tag{5}$$

$$\mathrm{RF} = \frac{L}{V} \tag{6}$$

Measurement of the stress resistance index and leaf area index

Stress resistance index (SRI) was employed to quantify plant adaptive capacity under combined Cd and competition stress, calculated according to the following formula (Wang et al. 2024):

$$SRI = 1 - \frac{B_{ns} - B_s}{B_{ns}} \tag{7}$$

where B_s and B_{ns} represent the total biomass of species i under stressed and control conditions respectively, with higher SRI values indicating superior stress tolerance. SRI provides a standardized measure of relative tolerance, effectively eliminating baseline disparities caused by inherent growth rate of species and planting density.

The leaf area index (LAI) was determined by applying the following equation:

$$\mathrm{LAI} = \frac{A_{leaf}}{A} \tag{8}$$

where A_{leaf} represents the total leaf area of both species measured from scanned images (analyzed using ImageJ), and A is the corresponding ground soil area of experimental plots.

Statistical analysis

Statistical analyses were performed using SPSS statistics (version 27.0; IBM, Inc., NY, USA) to compute means and standard errors. Prior to analysis, all data were checked for normality (Shapiro–Wilk test) and homogeneity of variances (Levene's test), followed by two-way ANOVA to evaluate the interactive effects of Cd concentrations and planting densities on stress resistance indices (SRI) of *A. philoxeroides* and *T. repens*, with post-hoc Duncan tests ($p < 0.05$) identifying significant differences among treatments. Pearson correlation analysis was performed using Origin 2024 (OriginLab, Northampton, MA) to examine relationships between root architecture parameters, photosynthetic traits and SRI values, while dominance analysis was performed in Stata 17.0 (version 17.0; StataCrop, USA) to quantify the relative importance of these predictors. All graphical representations were generated using Origin 2024 (OriginLab, Northampton, MA).

Results

SRI responses to Cd concentration and planting density

Two-way ANOVA revealed significant effects of both Cd concentration and planting density on SRI of *A. philoxeroides* (under both monoculture and mixed culture)

and *T. repens* (under mixed culture) ($p < 0.001$; Table 1). Notably, a significant interaction between these two factors was observed only under mixed-culture conditions ($p < 0.001$). Under intraspecific competition, *A. philoxeroides* exhibited contrasting SRI reponses: it progressively declined with increasing Cd levels but gradually improved with higher planting density (Fig. 1). In mixed culture at Cd100, the SRI of *A. philoxeroides* and *T. repens* displayed divergent trends in response to increasing planting density: the SRI of *A. philoxeroides* declined gradually, whereas that of *T. repens* continued to rise. Overall, the highest SRI values across plants were recorded under Cd100 treatments, with the performance of *A. philoxeroides* differing between intra- and interspecific competition. Specifically, under intraspecific competition, the SRI of *A. philoxeroides* peaked at Cd100P9, while under interspecific competition, it reached its maximum at Cd100P5.

Root architecture responses to Cd concentration and planting density

Two-way ANOVA indicated that Cd concentration significantly affected root architecture ($p < 0.01$), while planting density and its interaction with Cd concentration notably influenced surface area ($p < 0.05$; Table 1). Under intraspecific competition, the root development of *A. philoxeroides* exhibited a significant and consistent trend: root length, surface area, and root volume decreased progressively with increasing competition intensity at all Cd stress concentrations (Fig. 2a, c, and d). Root average diameter increased continuously with increasing intensity of intraspecific competition under Cd stress, but significant difference in these changes were only observed at Cd100 treatment (Fig. 2b). The highest root surface area and volume occurred under Cd100P5 treatment, while the maximum root average diameter was recorded under Cd100P9.

Under interspecific competition, more complex responses were oberserved: Cd concentration and its interaction with planting density significantly affected all root structural parameters in both species ($p < 0.01$), whereas planting density alone only influenced surface area ($p < 0.001$). At low interspecific competition, root average diameter, surface area, and root volume in both species showed a tendency to increase initially and then decrease with rising Cd concentration. In contrast, under high interspecific competition, the structural responses differed between species: root surface area and volume of *A. philoxeroides* gradually decreased with the increase of Cd stress, whereas *T. repens* exhibited a "suppression-then-promotion" pattern in root length, average diameter, surface area, and volume. Overall, Cd stress combined with interspecific competition primarily promoted increases in root average diameter and root volume in *A. philoxeroides*, and enhanced root length and root average diameter in *T. repens*. In both species, the maximum root surface area and root volume were observed under Cd100P5 treatment.

Statistical analyses revealed significant effects of Cd concentration, planting density, and their interaction on SSA and RF of *A. philoxeroides* and *T. repens* ($p < 0.01$, Table 1). FD of *A. philoxeroides* in both monoculture and mixed culture decreased gradually with increasing Cd concentration under high planting density, whereas that of *T. repens* in mixed culture showed an opposite trend, increasing progressively. FD of both species in mixed culture increased gradually with increasing interspecific competition intensity under Cd stress-free condition. However, this trend reversed under Cd stress, with FD decreasing as competition intensified (Fig. 3a). It can be seen that SSA of both *A. philoxeroides* and *T. repens* decreased gradually with the increase of Cd concentration under high competitive intensities from the radar plots. Notably, density-dependent SSA responses diverged between species in mixed culture—*A. philoxeroides* showed decreasing SSA with density at low Cd but increasing trends under high Cd stress, while *T. repens* exhibited precisely inverse patterns (Fig. 3b).

SRL of *A. philoxeroides* increased gradually with intensifying intraspecific competition under Cd-free stress, but gradually decreased under Cd-stressed conditions. SRL of both *A. philoxeroides* and *T. repens* in mixed culture decreased gradually with planting density without Cd stress, while they increased gradually under low Cd stress conditions. Additionally, SRL of both species initially decreased then increased with rising Cd concentrations under low interspecific competition. Overall, SRL of *T. repens* was greater than that of *A. philoxeroides* (Fig. 3c). RF of both *A. philoxeroides* and *T. repens* followed a "decrease-then-increase" pattern with increasing Cd stress concentration. RF of *A. philoxeroides* in monoculture had the same tendency with SRL. However, that of *A. philoxeroides* and *T. repens* in mixed culture showed opposite trends at different Cd stress concentration. Specifically, their RF increased significantly with increasing planting density under Cd100 condition, while it decreased significantly under Cd200 condition (Fig. 3d).

Photosynthetic response to Cd concentration and planting density

ANOVA results revealed significant effects of Cd concentration, planting density, and their interactions on LAI of both *A. philoxeroides* and *T. repens* ($p < 0.05$, Table 1). Overall, LAI of both species decreased with increasing planting density under Cd stress, while the changes were not the same under Cd-free condition. Cd concentration

Table 1 Two-way ANOVA results for Cd concentration and planting density on root development and photosynthetic characteristics of *A. philoxeroides* and *T. repens*

Variables	Cd concentration	Planting density	Interaction	df_1, df_2	Cd concentration	Planting density	Interaction	df_1, df_2	Cd concentration	Planting density	Interaction	df_1, df_2
	F	*F*	*F*		*F*	*F*	*F*		*F*	*F*	*F*	
A. philoxeroides in monoculture					*A. philoxeroides* in mixed culture				*T. repens* in mixed culture			
SRI	179.88***	69.70***	0.06^{ns}	1, 16	108.48***	7.12***	105.33***	1, 16	27.26***	138.01***	51.41***	1, 16
L	38.266***	550.050***	11.378***	2, 24	14.45***	267.342***	495.436***	1, 24	126.995***	2.131^{ns}	142.578***	2, 24
D	7.413**	0.998^{ns}	6.586**	2, 24	10.971***	1.742^{ns}	5.914**	1, 24	5.779**	1.184^{ns}	12.532***	2, 24
A	8.004**	338.256***	3.812*	2, 24	97.943***	19.359***	89.841***	1, 24	29.435***	35.848***	146.337***	2, 24
V	4.003**	76.510***	1.267^{ns}	2, 24	18.491***	0.437^{ns}	47.467***	1, 24	5.779**	1.184^{ns}	12.532***	2, 24
FD	47.142***	1.929^{ns}	58.646***	2, 24	5.295*	5.118*	17.474***	1, 24	42.234***	13.904**	46.986***	2, 24
SSA	162.721***	237.129***	170.448***	2, 24	72.201***	57.866***	29.683***	1, 24	13.06***	5.72**	64.527***	2, 24
SRL	181.026	164.112***	70.97***	2, 24	120.178***	3.966^{ns}	300.842***	1, 24	133.48***	5.72^{ns}	47.996***	2, 24
RF	88.273***	170.47***	91.17***	2, 24	56.348***	9.089**	379.765***	1, 24	122.248***	157.445***	311.569***	2, 24
LAI	31.55***	45.265***	36.034***	2, 24	7.572**	8.078**	1.076^{ns}	1, 24	13.221***	4.259*	86.555***	2, 24
P_n	7.226**	403.596***	14.334**	2, 12	1.264^{ns}	117.326***	26.643***	1, 12	54.684***	24.943***	30.178***	2, 12
Cond	14.225**	13.762**	34.052***	2, 12	1.951^{ns}	107.529***	16.594***	1, 12	8.498**	2.913^{ns}	2.716^{ns}	2, 12
C_i	150.476***	639.014***	251.740***	2, 12	27.461***	15.970**	73.014***	1, 12	23.799***	6.183*	4.655*	2, 12
T_r	6.113*	12.979**	5.437*	2, 12	36.015***	574.224***	0.694^{ns}	1, 12	12.762**	85.077***	4.785*	2, 12
LS	1.013^{ns}	4.574^{ns}	4.399*	2, 12	2.213^{ns}	2.383^{ns}	3.677^{ns}	1, 12	2.542^{ns}	1.691^{ns}	1.065^{ns}	2, 12
iWUE	117.134***	113.115***	126.949***	2, 12	11.597**	13.931**	36.714***	1, 12	0.189^{ns}	14.671**	3.968*	2, 12
WUE	5.043*	2.320^{ns}	10.958**	2, 12	51.407***	89.829***	25.001***	1, 12	5.549*	300.955***	6.545*	2, 12

The significances are shown as follows: ns ($p > 0.05$)

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

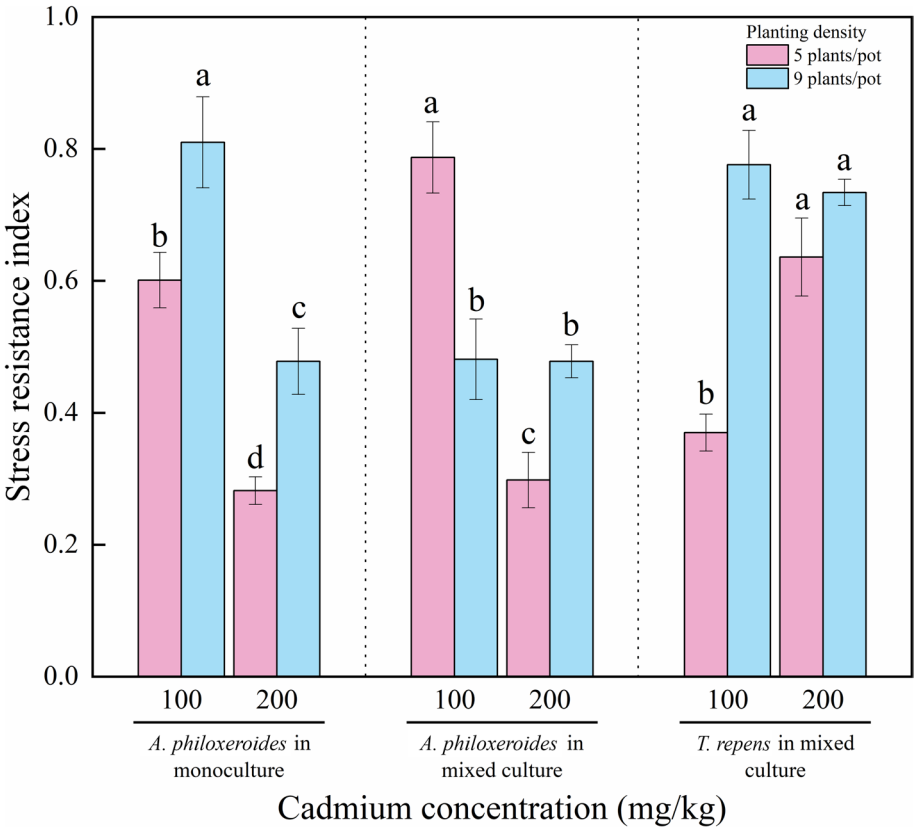


Fig. 1 SRI of *A. philoxeroides* and *T. repens* among different treatments. SRI was analyzed in three groups, *A. philoxeroides* in monoculture, *A. philoxeroides* in mixed culture, and *T. repens* in mixed culture, respectively. Bars represent mean and standard error ($n = 5$). Different lowercase letters in each group indicate statistically significant differences among different Cd concentrations and planting densities ($p < 0.05$, Duncan's test). The same below

and planting density enhanced LAI of *A. philoxeroides* in monoculture, and showed a tendency to increase and then decrease with increasing Cd stress concentration at low planting density. LAI of *A. philoxeroides* and *T. repens* in mixed culture showed opposite trends at low planting density: *A. philoxeroides* showed a decreasing and then increasing trend in LAI with increasing Cd concentration, whereas *T. repens* showed an increasing and then decreasing trend. Both species exhibited a gradually decrease in LAI with increasing Cd stress at high planting density (Fig. 4). *A. philoxeroides* achieved peak LAI under intraspecific competition at intermediate Cd stress (Cd100P5), whereas both species exhibited maximal LAI values without Cd contamination in interspecific competition. Notably, *T. repens* consistently maintained superior LAI compared to *A. philoxeroides*.

ANOVA results revealed that Cd concentration, planting density, and their interactions significant influenced the gas exchange parameters of *A. philoxeroides* in monoculture, while these factors only significantly affected C_i of *A. philoxeroides* and *T. repens* in mixed culture ($p < 0.05$, Table 1). P_n and Cond of *A. philoxeroides* in monoculture exhibited a "first suppression-then-increase" trend with increasing Cd concentration at low planting density, while these parameters followed a "first increase-then-decrease" trend at high planting density (Fig. 5a, b). Both P_n and Cond increased progressively with planting density under Cd stress. C_i and T_r of *A. philoxeroides* in mixed culture both showed a "decrease-then-increase" trend with increasing Cd stress concentration at low competitive intensity, whereas different trends were shown at high competitive intensity (Fig. 5c, d). P_n, Cond, and T_r of *A. philoxeroides* in mixed culture gradually increased with planting density at all Cd concentrations, whereas C_i trends were differed between Cd-free and Cd-stressed. P_n, C_i, and T_r of *T. repens* in mixed culture all exhibited a "decrease-then-increase" trend with increasing Cd concentration at low planting density, whereas P_n, Cond, and T_r gradually increased with Cd concentration at high planting densities. Moreover, Cond and C_i of *T. repens* increased with planting density at the same Cd concentration. Overall, P_n, Cond, and T_r of *T. repens* were significantly higher than those of *A. philoxeroides* in mixed culture.

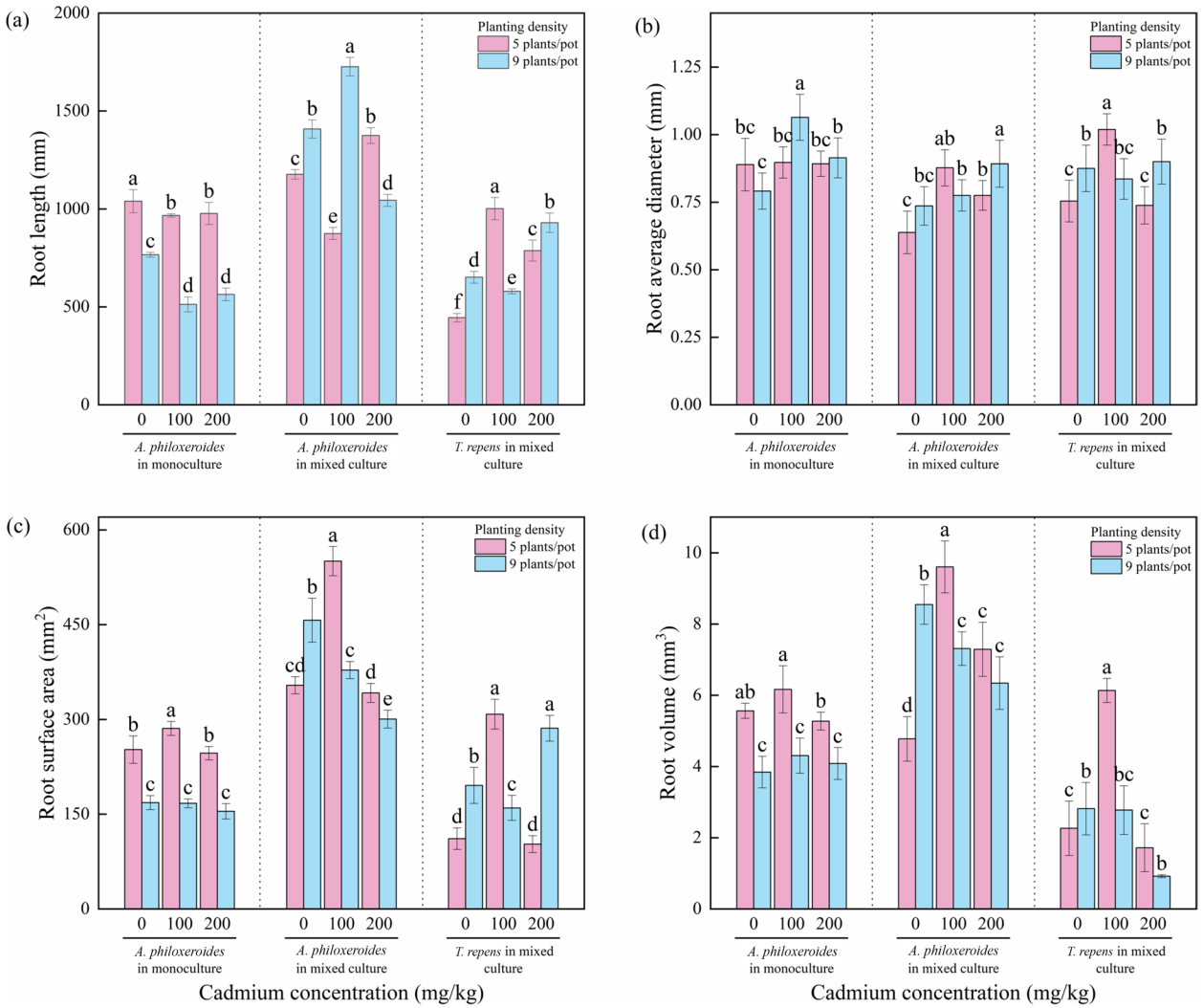


Fig. 2 Responses of root length (**a**), root average diameter (**b**), root surface area (**c**), and root volume (**d**) in *A. philoxeroides* and *T. repens* to Cd concentration and planting density

Two-way ANOVA results indicated that Cd concentration, planting density, and their interaction significantly affected iWUE of *A. philoxeroides* in monoculture ($p < 0.001$), whereas they had a significant effect on WUE of *A. philoxeroides* and *T. repens* in mixed culture ($p < 0.05$, Table 1). The LS of *A. philoxeroides* and *T. repens* in mixed culture exhibited an "increase-then-decrease" with rising Cd concentration at low planting density. LS of *A. philoxeroides* increased with planting density without Cd stress under both intra- and interspecific competition, but showed the opposite trend under Cd stress. That is, LS of *A. philoxeroides* under intraspecific competition gradually enhanced with planting density, while it gradually decreased with planting density under interspecific competition. LS of *T. repens* in mixed culture decreased gradually with planting density at low Cd concentrations (0 and 100 mg/kg) and increased gradually with planting density at high Cd concentration (200 mg/kg, Fig. 6a). WUE and iWUE of *A. philoxeroides* and *T. repens* in mixed culture followed similar trend at the same Cd concentration, decreasing progressively with planting density under Cd stress. Maximum WUE and iWUE of *A. philoxeroides* in mixed culture occurred under Cd100P5 treatment (Fig. 6b, c).

Analysis of the influence factors of changes in SRI

Pearson correlation analysis revealed that SRI of *A. philoxeroides* in monoculture showed significant positive correlations with FD and IWUE, but negative correlations with SRI, LAI, and C_i (Table 2). To quantify

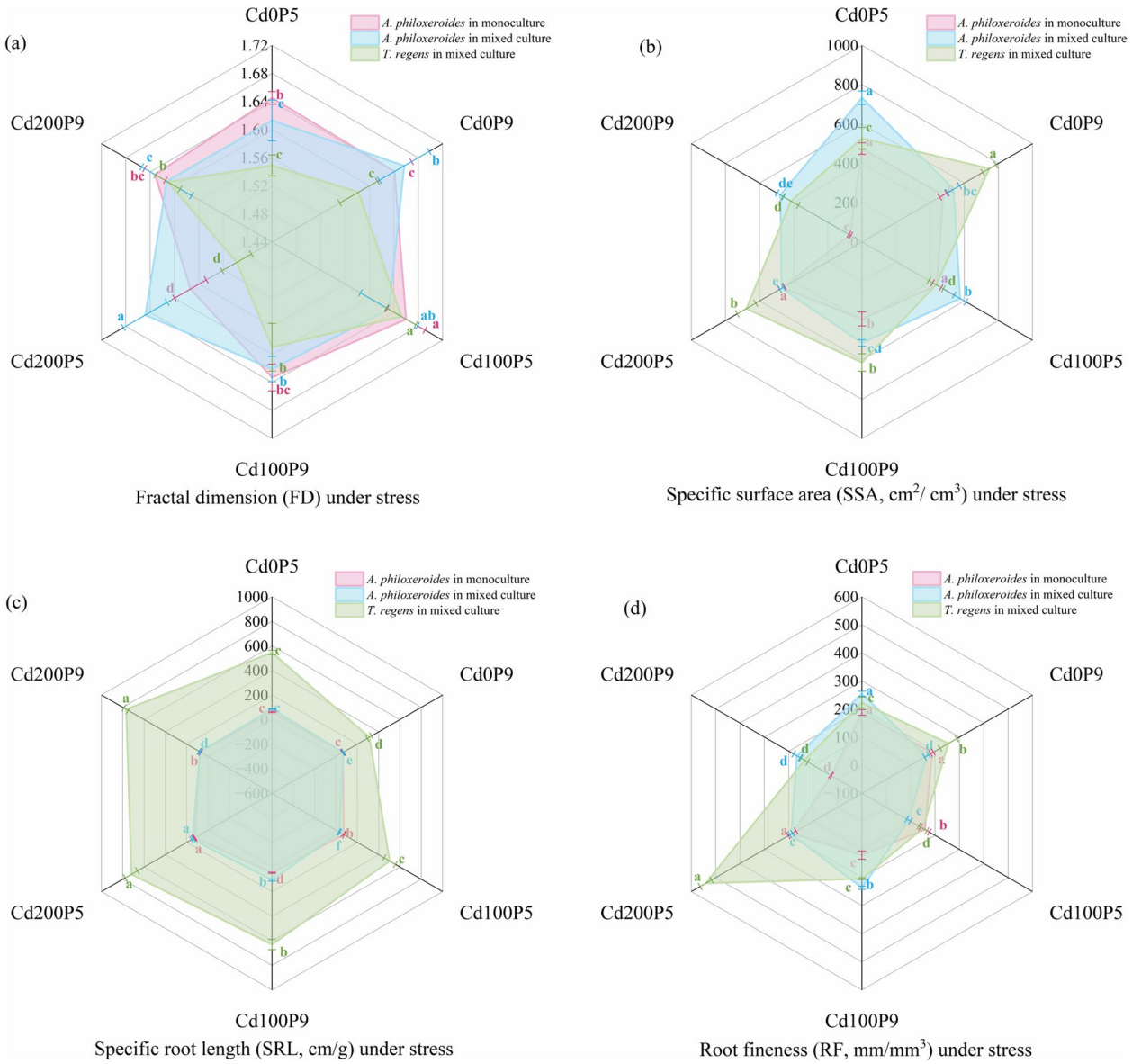


Fig. 3 Responses of root system geometric features and complexity to Cd concentration and planting density. **a**–**d** represent the differences in FD, SSA, SRL, and RF of *A. philoxeroides* and *T. repens* among different treatments, respectively

the relative contributions of various factors to stress resistance, we employed dominance analysis. All indicators influenced the SRI of *A. philoxeroides* in monoculture, among which SRL, LAI, FD, IWUE, and C_i had the greatest relative impact on it, at 28.82%, 15.49%, 10.71%, 8.94%, and 6.10%, respectively (Fig. 7a). The Pearson correlation analysis showed that SRI of *A. philoxeroides* and *T. repens* in mixed culture were significantly correlated with root average diameter and root surface area (Table 2). The results of relative importance analysis showed that SSA, SRL, root average diameter, WUE, and Cond had the greatest relative impact on SRI of *A. philoxeroides* in mixed culture, at 21.37%, 15.93%, 12.08%, 7.05%, and 5.66%, respectively. But among them, only root surface area, SSA, and Cond were significantly correlated with SRI (Fig. 7b). Similarly, root length, root volume, SRL, root surface area, and WUE had the greatest relative impact on SRI of *T. repens* with 26.39%, 10.97%, 9.65%, 7.4%, and 6.67%, respectively. Among them, root length, root surface area, root volume, and WUE were significantly negatively correlated with SRI (Fig. 7c).

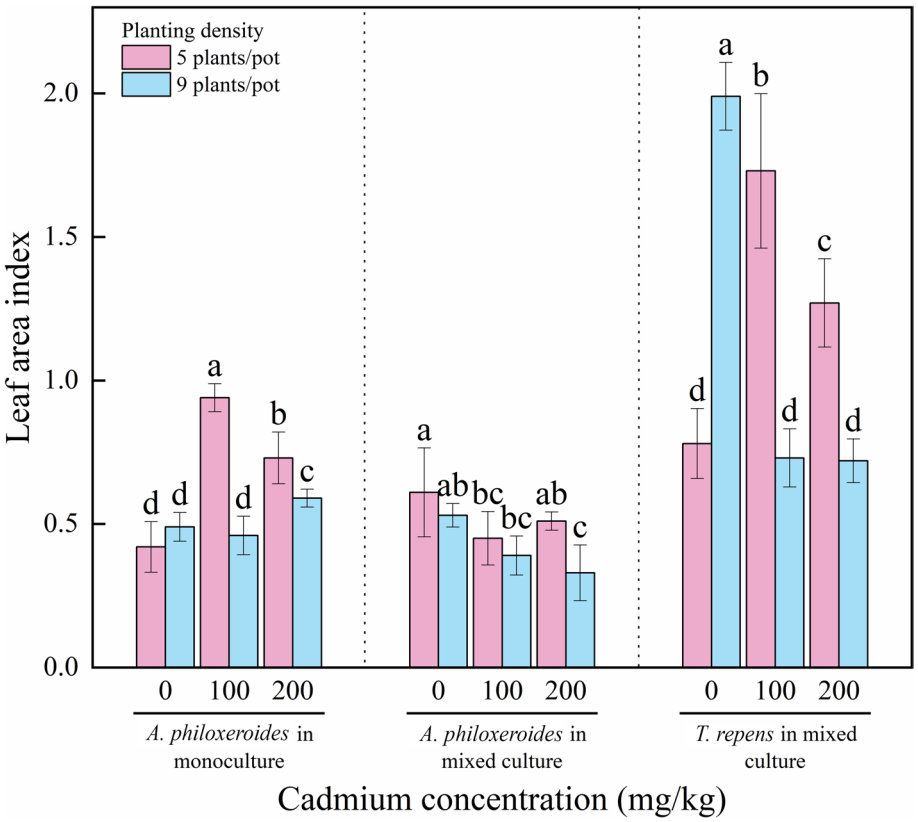


Fig. 4 Responses of LAI of *A. philoxeroides* and *T. repens* to Cd concentration and planting density

Discussion

The stress resistance index (SRI) is a simplified and quantitatively precise system proposed for assessing and measuring stress resistance in plants (Wang et al. 2024). This method enables consistent and equitable comparison of inherent plant stress resistance across different treatments, thereby servesing as a reliable indicator for assessing adaptive strategies under multiple stresses. Under Cd100 stress, the SRI of *A. philoxeroides* under intra- and interspecific competition did not follow the same trend with increasing planting density, indicating that competition type influences its resistance to Cd. In contrast, under Cd200 stress, the SRI of *A. philoxeroides* under both competition types followed similar trends, with values significantly lower than those under Cd100, indicating that high Cd stress diminishes resistance capacity. Under combined Cd stress and competition, the SRI of *A. philoxeroides* in monoculture and *T. repens* in mixed culture showed clear density dependence (Zhang and Tielbörger 2020), with SRI increasing with planting density across all Cd stress concentrations. For *T. repens*, SRI was influenced by both interspecific competition with *A. philoxeroides* and intraspecific competition, reflecting density-dependent regulatory patterns. Density dependence plays a critical role in modulating the impact of stress on plant performance (Murphy and Burns 2019), driving adaptive shifts in competitive strategies. Positive density dependence was observed in *A. philoxeroides* under monoculture and in *T. repens* under mixed culture. In contrast, *A. philoxeroides* in mixed culture shifted from negative to positive density dependence with increasing Cd stress, indicating that the alleviation of Cd toxicity by *T. repens* enabled plants to achieve greater biomass at higher densities under severe stress. Positive density dependence generally inhibits species coexistence, as the most competitive species tend to reach high densities and benefit most from such effects (De Silva and Jang 2015). The higher SRI of *T. repens* compared to *A. philoxeroides* under high Cd stress confirms its greater benefit from positive density dependence. This also suggests that smaller plants may respond more actively to stress mitigation than larger ones (Zhang and Tielbörger 2020).

Root architectural adaptations and stress resistance in *A. philoxeroides* and *T. repens*

The root system architecture of plants reflects their self-regulation ability and survival strategies (Yang et al.

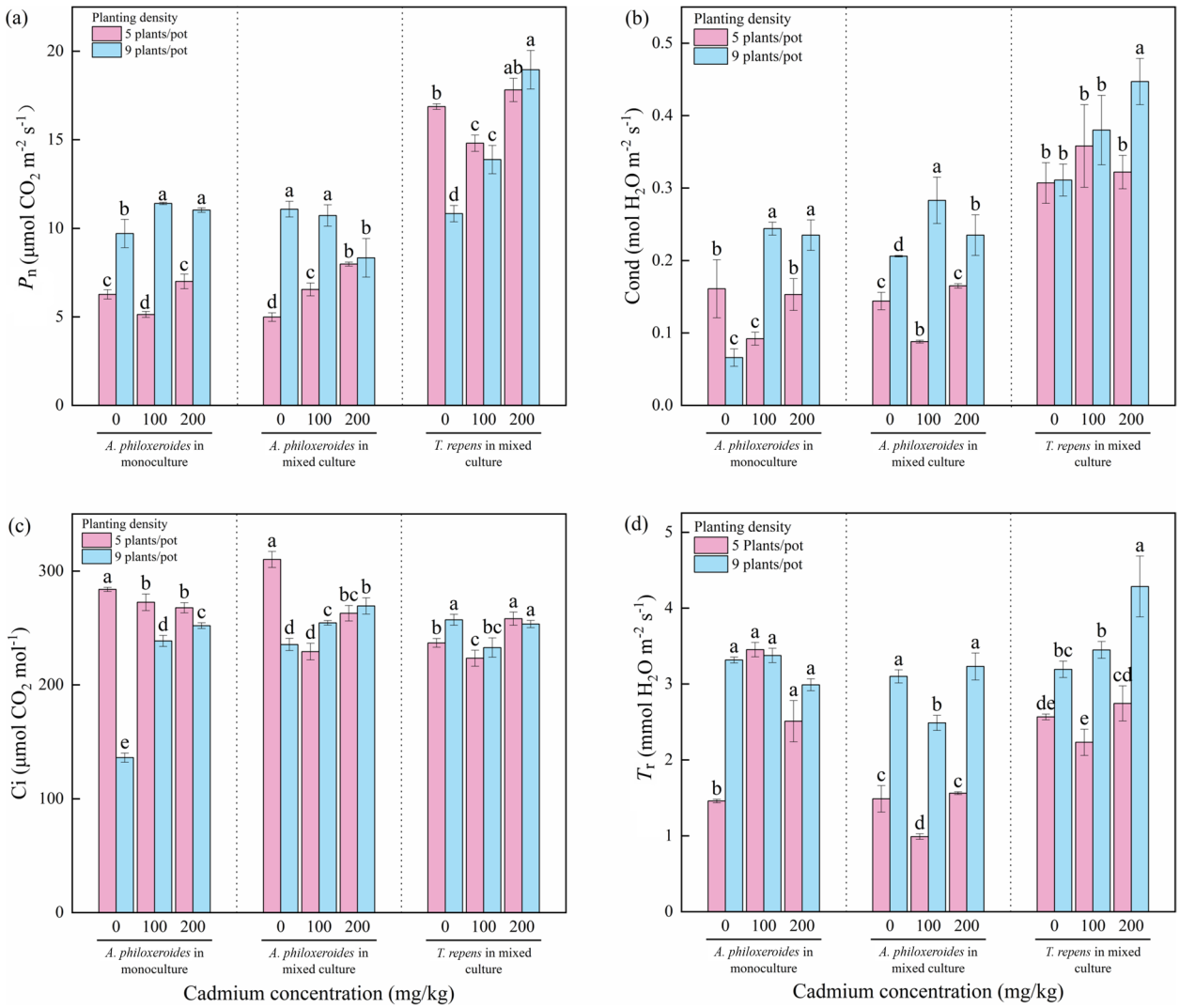


Fig. 5 Photosynthetic responses to Cd concentration and planting density in *A. philoxeroides* and *T. repens*: **a** P_n, **b** Cond, **c** C_i, and **d** T_r of *A. philoxeroides* in monoculture, *A. philoxeroides* and *T. repens* on mixed culture, respectively

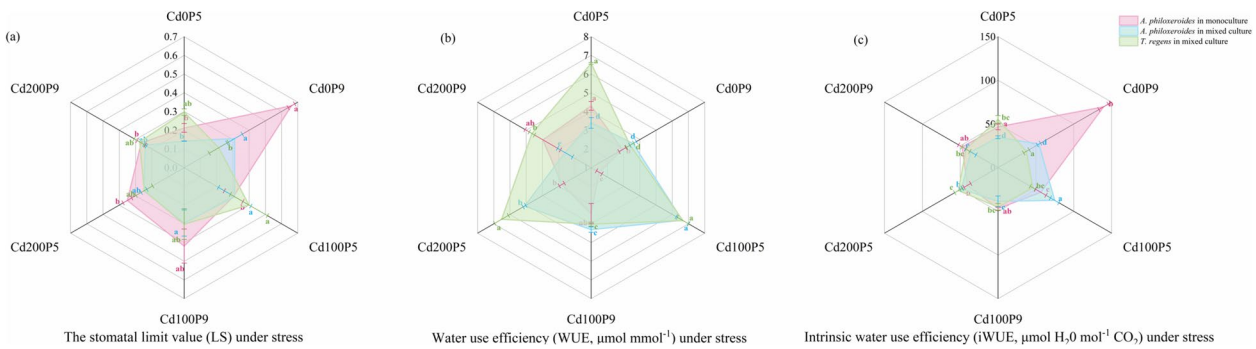


Fig. 6 Responses of LS, WUE, and iWUE to Cd concentration and planting density

Table 2 Correlations between SRI of *A. philoxeroides* and *T. repens* and the values of the plants' functional traits, and the photosynthetic characteristics

Indicators	SRI		
	***A. philoxeroides* in monoculture**	***A. philoxeroides* in mixed culture**	***T. repens* in mixed culture**
Root length	− 0.021	− 0.227	− 0.764***
Root average diameter	− 0.057	0.466**	− 0.471**
Root surface area	− 0.150	− 0.374*	− 0.363*
Root volume	− 0.117	− 0.057	− 0.576***
FD	0.380*	0.030	− 0.425*
SSA	0.174	0.444*	0.023
SRL	− 0.719***	0.010	− 0.290
RF	0.084	0.138	− 0.017
LAI	− 0.570***	0.362*	− 0.180
P_n	0.089	− 0.182	− 0.206
Cond	− 0.204	− 0.376*	− 0.033
C_i	− 0.416*	0.069	0.404*
T_r	− 0.194	− 0.062	0.274
LS	0.343	− 0.143	− 0.396*
iWUE	0.505**	0.216	− 0.005
WUE	0.317	− 0.087	− 0.425*

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

2011), with morphological traits often being interrelated and coordinated during environmental adaptation, thereby optimizing resource allocation and improving resource-use efficiency (Niu et al. 2022). SRI of *A. philoxeroides* in monoculture exhibited a strong negative correlation with SRL ($p < 0.001$) and a positive association with FD ($p < 0.05$), both of which contributed significantly to SRI. FD reflects the developmental extent and branching ability of root system under environmental influence, characterizing the complexity of root configuration (Liu et al. 2021). A high FD indicates a more developed root system with relatively complex branching (Cui et al. 2023; Ji 2010), thereby enhancing the efficiency of soil resource absorption and utilization. SRL, which quantifies root length per unit biomass, serves as a measure of root construction cost and benefit (Sun et al. 2023). A high SRL indicates greater metabolic costs for root construction but also enhanced soil exploration capacity.

An inverse relationship was observed between SRL and root average diameter, consistent with findings by Yang et al. (2020) and Jiang et al. (2024), and in line with the "root economic spectrum" hypothesis. This hypothesis suggests a trade-off between SRL, associated with rapid resource acquisition, and root average diameter, linked to resource conservation (Reich 2014). The negative correlation between SRL and root average diameter suggests that under Cd stress, in *A. philoxeroides* in monoculture sacrifices root diameter to expand spatial exploration for resource acquisition. Conversely, thicker roots generally correspond to less developed cortical tissues, resulting in reduced absorption and transport capacity (Liu et al. 2016). Under the Cd100P9 treatment, roots exhibited the lowest SRL and the largest average root diameter, indicating minimized resource acquisition capacity. This reduction consequently limited Cd uptake and transport, ultimately contributing to the highest SRI observed in *A. philoxeroides* under monoculture at this treatment level.

SRI of *A. philoxeroides* in mixed culture showed contrasting correlations: it was positively associated with root average diameter and SSA, but negatively correlated with root surface area. Among these traits, only SSA and root average diameter contributed most significantly to SRI, indicating that the root morphology characteristics are crucial for the adaptation of *A. philoxeroides* to the stressful environments as well as for the dominance of the interspecific competition. Under combined Cd stress and interspecific competition, *A. philoxeroides* developed thicker roots (increased average diameter) and reduced SSA—a morphological adaptation that limits heavy metal uptake by minimizing root-soil contact interfaces (Lu et al. 2023). This may also result from the enlargement of parenchyma cells and expansion of cortical tissue, which

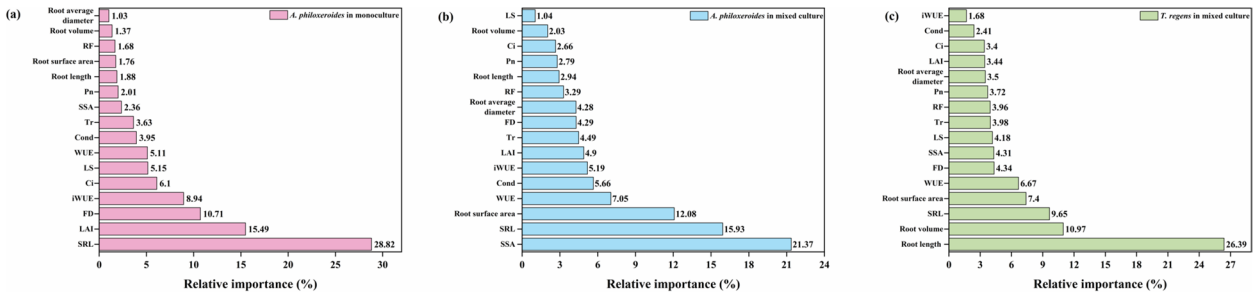


Fig. 7 The relative importance of factors affecting SRI of *A. philoxeroides* and *T. repens*

collectively increase hydraulic resistance and reduce Cd influx (Lux et al. 2010). Notably, fine roots exhibit greater Cd sensitivity and accumulation capacity than coarse roots, serving as primary sites for metal uptake and translocation (Xiao et al. 2023). Accordingly, the highest SRI of *A. philoxeroides* was observed under Cd100P5 treatment, characterized by a relatively short and thick root system.

The decrease in root length and SRL, along with the increase in root average diameter in mixed culture, indicated that Cd treatment reduced the plant's resource acquisition capacity and lowered its Cd transport efficiency (Staňová et al. 2012). Thicker roots contain more cortical cells and exhibit longer lateral transport pathways than fine roots (Liu et al. 2016), which reduces Cd retention in root cells and decreases the efficiency of Cd translocation to shoots. Under Cd stress, increased interspecific competition led to reductions in root surface area, root volume (Fig. 2c, d), and FD (Fig. 3a) in *A. philoxeroides*, reflecting strategic adjustments in resource-limited environments. The synchronous decrease in root surface area and root volume suggests a coordinated downregulation of root expansion, which may mitigate direct competition with *T. repens* roots and conserve energy and resources (Li et al. 2022). This is further supported by the reduction in root FD, indicating reduced root branching complexity, which lowers construction and maintenance costs and improves survival efficiency under competition. From an economic perspective, limiting lateral root development to alleviate intra-root competition and allocating more resources to primary root growth represent a cost-efficient adaptive strategy (Gao and Lynch 2016; Yang et al. 2023). Therefore, under interspecific competition, *A. philoxeroides* enhances its SRI primarily by developing short, thick roots and suppressing lateral root formation, thereby constraining Cd transport capacity.

In *T. repens*, SRI showed significant negative correlations with key root architectural traits—including root length, diameter, surface area, volume, and FD—all of which contributed substantially to SRI variation. These findings underscore the central role of root system architecture in the ecological adaptation of *T. repens,* enhancing both competitive ability and resource acquisition efficiency. The consistently higher SRI observed at high planting densitie was mainly associated with increased FD and SRL, along with decreased SSA and RF. A higher SSL reflects a low-investment, high-yield ecological strategy that extends the depth and breadth of root distribution, thereby maximizing soil exploration and utilization (Bergmann et al. 2020; Freschet et al. 2021). Under competitive conditions, elevated FD enhances soil uptake and resource extraction capacity (Hodge 2004), thereby supporting plant competitiveness and sustaining normal growth. The observed reduction in RF further aligns with improved nutrient capture efficiency, as finer roots and higher SRL generally correlate with superior resource acquisition functionality (Ma et al. 2018). SSA, a key morphological determinant of water and nutrient uptake, decreased under high planting densities in this study, indicating a strategic reduction in growth-related investment. Moreover, a decline in SSA represents a common plant response to heavy metal stress, serving to limit metal uptake (Li et al. 2009). Therefore, *T. repens* mainly increases its SRI by increasing root complexity and expanding the nutrient foraging range, thereby raising nutrient uptake efficiency while reducing growth investment cost and heavy metal absorption.

Photosynthetic adaptations and stress resistance in *A. philoxeroides* and *T. repens*

Photosynthesis is a fundamental process for energy conversion in nature and for maintaining atmospheric balance. Its efficiency directly reflects plant vitality and growth (Ma et al. 2020), making it a crucial indicator of plant physiological status. Moreover, photosynthesis is among the most sensitive physiological process to Cd stress, with photosynthetic gas exchange parameters serving as key adaptive traits under such conditions (Hu et al. 2023). In this study, the SRI of *A. philoxeroides* in monoculture exhibited a significant negative correlation with LAI and C_i values, but a positive correction with iWUE. Among these parameters, LAI, iWUE, and C_i contributed most significantly to SRI, suggesting that *A. philoxeroides* primarily maintains photosynthetic performance by regulating stomatal behavior. Notably, LAI exhibited an inverse relationship with SRI, where larger LAI corresponded to lower SRI, indicating that leaf expansion inhibited dry matter accumulation under intraspecific competition. Furthermore, the trend of LAI with increasing Cd concentration was opposite to that of P_n across varying intensities of intraspecific competition, indicating that although higher LAI enhances light capture, it may lead to overlapping leaves in confined potting conditions, thereby impairing ventilation and light penetration for lower leaves (Chen et al. 2021) and ultimately limiting photosynthetic efficiency.

At low Cd stress (100 mg/kg), the trends of P_n and Cond aligned with that of C_i, suggesting that stomatal limitation was the main factor affecting photosynthesis. Changes in stomatal conductance affected CO_2 diffusion into leaves, thereby impacting photosynthetic carbon assimilation. Conversely, at high Cd stress (200 mg/kg), the opposite trends suggested the dominance of non-stomatal factors—likely involving impaired chloroplast function and reduced carbon assimilation capacity.

Overall, under combined Cd stress and high intraspecific competition, *A. philoxeroides* exhibited a distinctive adaptive strategy characterized by coordinated enhancement of WUE and P_n. This synchronization reflects this species' unique capacity to synergistically optimize light energy conversion, hydraulic regulation, and carbon metabolism under dual stressors. Specifically, increased P_n directly enhanced CO_2 fixation and promoted the synthesis of photosynthetic products (Zhang et al. 2020), while improved WUE reduced water consumption, allowing reallocation of conserved energy to essential metabolic processes such as antioxidant defense and osmotic adjustment (Jiang et al. 2022). This integrated strategy not only supported sustainable biomass accumulation but also improved SRI under intense intraspecific competition.

In mixed culture, the SRI of *A. philoxeroides* showed a significant positive correlation with LAI and a negative correlation with Cond, though WUE and iWUE were the parameters that contributed most substantially to SRI. In contrast, *T. repens* exhibited positive correlations between SRI and intercellular CO_2 concentration (C_i), but negative correlations with both WUE parameters, with only WUE making a significant contribution to its stress adaptation. Overall, *T. repens* demonstrated significantly higher values in LAI, P_n, Cond, and WUE than *A. philoxeroides*, indicating a clear competitive advantage in light energy capture. Under low interspecific competition, P_n of *A. philoxeroides* continued to increase with increasing Cd stress, suggesting the effective maintenance of carbon assimilation efficiency via non-stomatal mechanisms (Gao et al. 2018). The coordinated trends in Cond, C_i, and T_r further support the dominance of non-stomatal regulation, which may involved Cd-induced activation of protective responses such as increased leaf mesophyll conductance or enhanced Rubisco activity (Aguiló-Nicolau et al. 2024). Under high interspecific competition, however, P_n of *A. philoxeroides* was significantly higher than under low competition but decreased progressively with increasing Cd concentration. This suggests that combined Cd and competition stress damaged the photosystem and reduced carbon assimilation. The concurrent decrease in iWUE reflected an imbalance in the "energy cost–benefit" of stomatal regulation, where the metabolic cost of operating stomata exceeded the photosynthetic gain (Takaragawa and Wakayama 2024). In *T. repens*, leaf acclimatization under dual stresses from interspecific competition and Cd was mediated through changes in LAI. Under low competition, LAI initially increased then decreased with rising Cd levels, suggesting that the species initially compensated for photosynthetic losses through leaf thickening or expansion. Under higher Cd stress, however, resources were likely redirected from leaf growth to resistance mechanisms such as proline synthesis (Rouphael et al. 2021), thereby improving resilience. At high planting densities, *T. repens* faced both intra- and interspecific competition, driving it to maintain high Cond and T_r to compete for carbon dioxide and water. This resulted in higher P_n with increasing Cd concentration, alongside inconsistent trends in C_i and stomatal limitation values, suggesting that photosynthesis in *T. repens* is co-regulated by both stomatal and non-stomatal factors.

However, this study inferred the resistance mechanisms of *A. philoxeroides* and *T. repens* based on phenotypic and physiological responses without quantifying Cd uptake and accumulation. Therefore, future studies should measure Cd absorption and translocation in different plant tissues to determine whether the resistance of *A. philoxeroides* is attributed to exclusion or tolerance mechanisms, thereby providing a more comprehensive understanding of its adaptive strategy and resistance mechanism.

Conclusion

The present study revealed that distinct competitive strategies employed by *A. philoxeroide*s and *T. repens* to enhance their SRI under Cd stress and competition. Under interspecific competition, *A. philoxeroides* developed shorter and thicker roots by increasing average root diameter while reducing SSA and FD, thereby decreasing lateral root branching, limiting Cd uptake and transport, and improving survival efficiency. In addition, it reduced LAI to minimize excessive leaf overlap and increased CO_2 fixation through stomatal regulation, which accelerated photosynthate synthesis and increased SRI. In contrast, *T. repens* decreased RF and SSA but increased SRL, facilitating efficient resource acquisition while reducing heavy metal uptake. It also maintained high P_n by adjusting LAI and maintaining high Cond and T_r, thereby improving competitiveness for CO_2 and water resources and enhancing stress resistance. Overall, the root plasticity of *A. philoxeroides* was more effective than that of *T. repens* in conferring Cd resistance under competitive stress, while *T. repens* was more efficient in light resource utilization. Moreover, *T. repens* showed stronger stress resistance under high Cd stress and intense interspecific competition. Under intraspecific competition, *A. philoxeroides* primarily reduced SRL while increasing root average diameter and FD, forming a more complex root system that restricted heavy metal uptake and transport, thereby improving SRI. In terms of light competition, it mainly optimized photosynthetic efficiency through non-stomatal mechanisms, though this strategy was challenged under high

competition combined with high Cd stress. Notably, density-dependent responses were observed in both *A. philoxeroides* under intraspecific competition and *T. repens* under interspecific competition. These findings elucidate the adaptive strategies of *A. philoxeroides* during invasion in heavy metal-contaminated environments, offering insights into plant invasion mechanisms and providing a theoretical and technical basis for ecological restoration and invasion management in polluted environments.

Abbreviations

Cd	Cadmium
SRI	Stress resistance index
LAI	Leaf area index
Cond	Stomatal conductance
T_r	Transpiration rate
P_n	Net photosynthetic rate
FD	Fractal dimension
SSA	Specific surface area
SRL	Specific root length
RF	Root fineness
LS	Stomatal limit value
WUE	Water use efficiency
iWUE	Intrinsic water use efficiency

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Author contributions
Yuanyuan Cui: writing–original draft, data curation, formal analysis, visualization, investigation. Qiaoying Zhang: supervision, project administration, funding acquisition, writing–review and editing. Peng Liu: resources, investigation, data curation. Chang He: investigation, visualization. Tiantian Xie: investigation, resources. Jing Wan: resources, visualization. Lin Zhang: methodology, supervision. Yunchun Zhang: methodology, supervision, project administration, funding acquisition, writing–review and editing.

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Availability of data and materials
The data that support the findings of this study are available on reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

Author details
[1]College of Environmental Science and Engineering, China West Normal University, Nanchong 637009, China. [2]Agronomy College, Gansu Agricultural University, Lanzhou 730000, China. [3]School of Geographical Sciences, China West Normal University, Nanchong 637009, China. [4]Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu 610041, China.

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