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Nitrogen deposition enhances the competitive advantage of invasive plant species over common native species through improved resource acquisition and absorption

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Abstract

Background Previous studies into the interactions between native and invasive species under nitrogen (N) deposition have often overlooked the presence of co-occurring native species, a factor that could influence the outcomes of interspecific competition. Furthermore, publication bias may lead researchers to focus on rare native species with limited adaptability. In this study, we examined how two levels of N deposition affected the physiological and ecological traits and the interspecies interactions between three invasive and three common native species.

Results N deposition promoted the growth of both invasive and native species. The relative dominance index (RDI) of invasive species was consistently higher than that of native species. Invasive species had an advantage over common native species in using the increased N effectively. The biomass distribution of invasive species was biased toward the aboveground parts, indicating competition for light resources.

Conclusions N deposition conferred a stronger competitive advantage to invasive species than to native species, suggesting that the distribution range of invasive species may expand further under increased N deposition.

Keywords Nitrogen loading, Plant invasion, Interspecific relationship, Competition

Introduction

Over the past century, anthropogenic activities such as the burning of fossil fuels and the application of inorganic fertilizers have significantly increased global nitrogen (N) input (Galloway et al. 2008; Luo et al. 2014). The rise in atmospheric N deposition impacts plant morphology, physiology, and ecological performance as well as soil nutrients. Heightened atmospheric N can also alter how invasive species affect native species (Liu et al. 2018; Wang et al. 2022), leading to the degradation of local ecosystem structure and function, and thereby becoming a key driver of species declines in richness (Bobbink et al. 2010). Thus, it is essential to understand the mechanisms

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of plant growth responses to increased atmospheric N deposition. When atmospheric N deposition reaches a certain threshold, environmental damage can occur via a shift toward N eutrophication. With the increase of N deposition, the promotive effect on plants gradually weakens and finally turns to inhibition (Bobbink et al. 2010; Hu et al. 2019). Invasive species can take up and utilize N more effectively than most native species under a high N supply (Littschwager et al. 2010; Wang et al. 2019). Some studies have shown that N enrichment can enhance the competitive advantage of invasive species to the detriment of co-occurring native species, thus promoting the spread of invasive species (Ren et al. 2019; Sun et al. 2023; Wang et al. 2019). However, Luo et al. (2014) have shown that under N deposition, the promotive effect on the functional traits of invasive species gradually weakens, and the competition effect on native species is reduced. Consequently, the effects of N deposition on native and invasive species remain insufficiently characterized.

Invasive species, often grow faster than native species and allocate more resources to photosynthesis, and they may exhibit different strategies (Dawson et al. 2012b; van Kleunen et al. 2010). Invasive plants can quickly allocate resources to growth, and they generally possess higher rates of carbon assimilation relative to native species (Funk and Vitousek. 2007), a factor in successful invasion. According to the theory of fluctuating resource availability, an increase in a local community's resources tends to benefit invasive species more than native species (Davis et al. 2000). While several studies have focused on the effects of environmental treatments or resource levels on the biomass and/or photosynthesis of invasive and native species, comprehensive investigations encompassing multiple morphological and physiological parameters remain scarce (Wang et al. 2017b; Zeng et al. 2023). The mechanisms by which invasive and native species respond to N deposition through alterations in functional traits remain poorly understood.

Competition between native and invasive species plays a key role in the process of invasion (Bottollier-Curtet et al. 2013; Cuda et al. 2015). Extensive studies have focused on the interspecific competition between native and invasive species (Chen et al. 2024; Cooke et al. 2021; Liu et al. 2018), but few studies have considered the commonness and rarity of native species (Speißer et al. 2021; Zhang and van Kleunen 2019). Common species, those that can successfully spread and occupy large areas (Liu et al. 2017b), shape the environments of other species and are usually involved in diverse interactions, including competition (Gaston 2010). Common native species are usually constructive or dominant species in local communities, often playing key roles in driving the structure

and function of local ecosystems (Bottollier-Curtet et al. 2013; Dawson et al. 2012b). If invasive species successfully displace locally dominant common species, they may substantially alter ecosystem structure and function (Hejda et al. 2019). Hence, the competition outcomes between invasive species and common native species are likely to have a more profound impact on local ecosystems compared to situations involving rare native species. Furthermore, competition between invasive species and common native species is more likely than competition between invasive and rare native species. However, publication bias may incline researchers to choose rare native species with poor adaptability to obtain more significant results. Hence, it is imperative to investigate the interspecific interactions between invasive species and common native species, as well as the role of functional traits within these interspecies interactions.

Previous studies have compared the responses of invasive and native species with different degrees of commonness under environmental changes but often have not included competition treatments (Dawson et al. 2012a; Liu et al. 2022). Speißer et al. (2021) compared the competitive performances of native species against naturalized species under artificial light conditions. Some studies have explored the competitive dynamics between invasive and native species with varied commonness but without the inclusion of environmental treatments or resource levels (Feng et al. 2016; Ferenc et al. 2021; Zhang and van Kleunen 2019). As a result, the competitive interactions between invasive species and common native species under N deposition have yet to be fully explored.

Furthermore, the above-mentioned studies (Liu et al. 2022; Speißer et al. 2021; Zhang and van Kleunen 2019) were all conducted in Germany, with the commonness of invasive and native species determined by their distribution across the country. However, the commonness of native species could shift when considered on a larger scale, such as across Europe. Therefore, investigating on a broader spatial scale is necessary to ascertain the commonness of native species. Nitrogen deposition has increased nutrient availability in many parts of the world (Galloway et al. 2008) and may have affected the distribution of invasive and native plant species (Liu et al. 2017b). Nitrogen deposition is unevenly distributed in China (Chen et al. 2023), a factor that would likely have a broader impact on common species than on rare species (Xu et al. 2023). Therefore, invasive species and native species widely distributed in China were selected to study the effects of N deposition.

Invasive and native species may cohabit and encounter similar or even identical environmental selection pressures (Chen et al. 2024; Hulme and Bernard-Verdier 2018; Wang et al. 2021). Consequently, the functional

similarities and differences between these native and invasive species have been considered as important factors for successful invasion. In general, the preadaptation hypothesis holds that successful naturalization of invasive species in habitats comprising native species of the same genus is possible because they have similar characteristics as native species, making them better adapted to the local environment (Fan et al. 2023; Ricciardi and Mottiar. 2006). However, Darwin's naturalization hypothesis suggests that the native species in a regional flora could reduce the chances of naturalization for closely related aliens (Daehler 2003). This is because close relatives should compete more intensely and also because natural enemies of native species may also attack the closely related alien species (Daehler 2003). Previous studies have compared the similarity of functional traits between invasive species and native species but have not considered the universality of native species. Compared to rare species, invasive species have a higher probability of encountering common native species, and thus it is of practical significance to compare the similarity of functional traits between invasive species and common native species. It is unclear whether the functional traits of the invasive species would be more similar or different from those of the common native species.

Erigeron annuus, *Coryza canadensis* (also known as *Erigeron canadensis*), and *Amaranthus retroflexus* are highly invasive species in China that significantly reduce species diversity, causing substantial ecological harm and considerable economic losses (Feng and Zhu 2010; Hao and Ma. 2023). Dong et al. (2023) quantified the climatic suitability of cultivars in China using an ensemble forecast approach and found that *E. annuus*, *C. canadensis*, and *A. retroflexus* were highly suitable for the climate in China. As native analogs of these invasive taxa, *Artemisia argyi*, *Inula japonica*, and *Achyranthes bidentata* were selected for comparison in this study. These native species are very prevalent, inhabiting over 85% of Chinese regions (34 in total, including 23 provinces, five autonomous regions, four municipalities, and two special administrative regions) (Yuan et al. 2021). The invasive and native species that belong to the same families share a common phylogenetic history as well as similar morphological characteristics and habitats, thereby minimizing phylogenetic bias (van Kleunen et al. 2010).

China is one of the top three global hotspots for nitrogen (N) deposition (Chen et al. 2023; Vet et al. 2014; Zhou et al. 2023). The elevated N deposition could potentially shift the dynamics of interspecific competition between invasive species and their co-occurring native counterparts. To investigate the effects of N deposition on the growth dynamics of invasive and common native plant species, as well as their interspecies interactions,

we conducted a multi-species experiment that comprised three invasive species and three common co-occurring native species with two levels of N deposition. We tested the following three hypotheses: (1) N deposition improves the growth performance of invasive and common native species, (2) invasive species exhibit superior competitive ability compared to common native species, and (3) N deposition amplifies the competitive advantage of invasive species over common native species.

Materials and methods

Experimental materials

We used three pairs of native and invasive species from two families that naturally co-occur in the field in China (Table S1). They are widely distributed in China, covering more than 85% of China's regions (Table S2). We used the distribution of species across China as a measure of prevalence. In April 2021, *A. bidentata* seeds were purchased from Huinong Seed Industry, Suqian City, Jiangsu Province, China. The seeds were soaked in distilled water at 30–50 °C for 24 h and stored in damp gauze trays to promote germination. Seedlings were transplanted into 12-cm-high and 14-cm-diameter plastic pots once two true leaves were observed. In June 2021, healthy and similar-sized (with *A. bidentata*) saplings of *A. argyi*, *I. japonica*, *E. annuus*, *C. canadensis*, and *A. retroflexus* were collected from the campus of Qingdao Agricultural University. Later, in June 2021, two healthy and uniform saplings of each species were selected and transplanted into 12-cm-high and 14-cm-diameter plastic pots. Each pot was filled with 1.314 kg of a loam and peat mixture in a 2:1 (v/v) ratio after passing through a 2-mm mesh to remove debris. The loam was obtained from a grassy wasteland in the Qingdao Agricultural University campus. Throughout the experiment, the pots were watered every 2 days to maintain soil saturation and control weed and insect infestation.

Experimental design

The experiment was conducted at 36° 31' N, 120° 3' E in Qingdao, Shandong Province, China. Qingdao features a warm temperate monsoon climate with an average annual precipitation ranging from 525.6 to 672.5 mm. To ensure a controlled and consistent environment, the experiment was conducted in a greenhouse. The greenhouse was situated at an altitude of approximately 100 m above sea level. The temperature in the greenhouse was kept at about 25–30 °C, while the relative humidity ranged between 70 and 80%.

Three planting methods were used in this study: (1) native vs native, (2) invasive vs invasive, and (3) invasive vs native. There were two plants in each pot, and each group was divided into an N treatment group (N1) and

a control group (N0), with 10 replicates per group for a total of 180 pots. The N0 and N1 groups were applied with N levels of 0 and 12 g m⁻² year⁻¹, respectively, in the form of NH₄NO₃. The N1 treatment simulated elevated deposition levels anticipated in the future (Chen et al. 2023; Kanakidou et al. 2016; Zhang et al. 2011). For the N1 treatment, 200 ml of 0.0014 mol/l NH₄NO₃ solution was added to each pot, and for the N0 treatment, the same volume of water was added. Pots were arranged randomly and reassigned at seven-day intervals throughout the experiment. Starting on July 4th, N fertilizer treatments were applied once per week for a total of ten times, concluding on September 5th.

Measurements and calculations

Measurements of sapling height (H), defined as the distance from ground level to the terminal bud, and crown area (CA) were taken at the end of the N treatment. The CA of the plant was calculated according to the diamond area, $CA = 0.5 \times a \times b$ (Guo et al. 2013), where the crown length (*a*) was measured at the maximum spread of each seedling, and the crown width (*b*) was measured in the vertical direction of the plane. The maximum root length (MRL) was measured with a ruler.

Leaf morphological characteristics were recorded 90 days after treatment. The third or fourth fully expanded leaves from the top of plants in each treatment (one leaf per pot for monocultures and one leaf per species per pot for mixed culture) were scanned and photographed. The average leaf area (ALA) per plant was measured through image analysis using Image-Pro Plus Version 4.5 (Media Cybernetic Inc., Silver Spring, MD, USA). We measured the leaf number of each plant. The total leaf area (TLA) was defined as the ALA multiplied by the leaf number. We also chose another fully expanded and healthy leaf (the third or fourth leaf from the tip) from each plant to measure the chlorophyll fluorescence parameters using a Pocket PEA (Hansatech Instruments Ltd, King's Lynn, Norfolk, UK). The maximum photochemical efficiency (F_v/F_m) of photosystem II was obtained. Following scanning, the leaves were subjected to enzyme deactivation by drying in an oven at 105 °C for 30 min, followed by oven-drying at 85 °C for 48 h to obtain the leaf dry weight. The leaf water content (LWC) was calculated as the ratio of the difference between fresh leaf weight and dry leaf weight to dry leaf weight. Specific leaf area (SLA) was then calculated as the ratio of leaf area to leaf dry weight.

After 100 days of treatment, ethanol was utilized to extract and determine the concentrations of chlorophyll a and b. Approximately 0.2 g of freshly sheared leaf tissue from the second or third leaf of the uppermost shoot was immersed in 10 ml of 95% ethanol for each treatment,

with 10 replicates per treatment. After 24 h incubation in darkness, the absorbance of the supernatant at 649 nm (D649) and 665 nm (D665) was measured using a Hitachi UH5300 UV/VIS spectrophotometer (Hitachi, Inc., Tokyo, Japan). From these measurements, the contents of chlorophyll a (Chl a), chlorophyll b (Chl b), and leaf chlorophyll content (Chl) were calculated separately:

$$\text{Chl a} = (13.95 \times D665 - 6.88 \times D649) \times 0.01 / \text{dry weight of leaf tissue},$$

$$\text{Chl b} = (24.96 \times D649 - 7.32 \times D665) \times 0.01 / \text{dry weight of leaf tissue},$$

$$\text{Chl} = \text{Chl a} + \text{Chl b}.$$

At the end of the experiment, all saplings were harvested, and their roots were thoroughly washed with tap water. Subsequently, each sapling was divided into leaf, stem, root and flower and fruit sections.

All sections of each sapling were oven-dried twice: first at 105 °C for 30 min to deactivate enzymes and then at 85 °C for 48 h. After drying, the sections were weighed. The total biomass (TB) and biomass allocation were calculated as follows:

$$\begin{aligned} \text{TB} = & \text{leaf biomass(LB)} + \text{stem biomass} \\ & + \text{root biomass(RB)} \\ & + \text{flower and fruit biomass(FB)}, \end{aligned}$$

$$\begin{aligned} \text{Shoot biomass(SB)} = & \text{leaf biomass(LB)} \\ & + \text{stem biomass} \\ & + \text{flower and fruit biomass(FB)}, \end{aligned}$$

$$\begin{aligned} \text{Root-to-shoot ratio(RSR)} = & \text{root biomass(RB)} \\ & / \text{shoot biomass(SB)}. \end{aligned}$$

When grown individually, the TB of two individuals in a single pot was averaged for this study.

Soil samples (one-third of the soil) were collected from each pot, and used for determining soil N (SN) and phosphorus (SP) concentrations through the Kjeldahl method and the Molybdenum antimony-D-isoascorbic-acid colorimetry method, respectively. The SN/SP was subsequently calculated.

The relative dominance index (RDI) was used to assess the dominance of invasive species and native species in mixed culture (Yuan et al. 2013).

$\text{RDI} = \text{biomass of one species} / \text{total biomass of two species in a pot}.$

We employed the relative competition intensity index (RCI) (Grace 1995) to gauge the impacts of interaction

on target species' performance. The RCI was calculated using the equation $RCI = (\text{total biomass of target species grown in intraspecific competition} - \text{total biomass of target species grown in interspecific competition}) / \text{total biomass of target species grown in intraspecific competition}$.

An RCI value of 0 suggests no impact of interspecific interaction on the target species; $RCI < 0$ indicates the facilitative effect of interspecific interaction on the target species, while $RCI > 0$ signifies a negative outcome of interspecific interaction on the target species (Grace 1995).

We examined the relative significance of interspecific versus intraspecific competition using the relative yield (RY):

$$RY = Y_{\text{mixture}} / Y_{\text{monoculture}}$$

where Y_{mixture} is the average biomass of an individual of one species when grown with another and $Y_{\text{monoculture}}$ is the average biomass of an individual of the species when grown in monoculture (Vila and Weiner. 2004). If $RY = 1$ interspecific competition is not significantly different from intraspecific competition, if $RY > 1$, interspecific competition is less than intraspecific competition and if $RY < 1$ interspecific competition is greater than intraspecific competition.

Data analysis

A three-way analysis of variance (ANOVA) was conducted to investigate the effects of N addition, species, cultivation, and their interaction on plant growth, functional traits and soil chemical properties (Table 1 and Tables S3–5). Simple effect tests were used after three-way ANOVAs. The results of the simple effect tests include figures (Figs. 1, 2 and 4) and tables (Tables S6–57). The competition index and soil chemical properties were analyzed by one-way ANOVA. The growth and physiological indexes of the three species were analyzed respectively (Figs. S1–12). The significance level was set at $P \leq 0.05$. Before conducting ANOVA, the data were checked for normality and homogeneity of variance. The data for flower and fruit biomass were logarithmically transformed. After the three-way analysis of variance, simple-effect tests were used. A MANOVA was performed for each trait category (growth, morphology, and physiology) (Table S58). The three-way ANOVAs was performed for growth, morphology, and physiology (Figs. S13–15). To determine which functional traits had significant variation and influenced the performance of invasive and native species, we performed a principal component analysis (PCA) using Origin 2021 software (OriginLab Co., MA, USA). Traits that explained at least 30% of

Table 1 Results of three-way ANOVA for the effects of nitrogen (N), species (S), cultivation (C), and their interactions on performance and functional traits of the species

Parameters	N	S	C	N×S	N×C	S×C	N×C×S
Height (cm)	4.273*	29.414**	0.498	0.451	0.063	4.135*	0.203
Crown area (cm ²)	34.007**	11.842**	6.388*	2.526	0.019	11.935**	0.046
Leaf number	4.957*	35.958**	0.124	0.600	0.690	2.151	1.899
Maximum root length (cm)	2.032	13.833**	0.002	7.228**	7.050**	9.980**	0.009
Average leaf area (cm ²)	0.536	9.197**	27.650**	2.572	0.773	2.330	2.178
Total leaf area (cm ²)	10.561**	29.115**	14.308**	8.222**	0.055	4.675*	4.517*
Total biomass (g)	23.075**	22.406**	1.130	3.776	2.090	17.096**	1.286
Root biomass (g)	11.124**	1.686	0.714	7.841**	4.064*	12.053**	1.715
Leaf biomass (g)	16.262**	50.824**	2.318	3.244	0.002	12.742**	2.160
Flower and fruit biomass (g)	22.835**	3.387	1.124	0.019	0.031	3.926*	0.004
Shoot biomass (g)	19.280**	54.823**	18.338**	0.001	0.543	8.418**	1.822
Root-to-shoot ratio (g g ⁻¹)	1.120	33.565**	3.476	5.359*	5.091*	0.658	1.547
Maximal quantum yield (F_v/F_m)	1.799	0.001	1.345	0.004	3.009	0.090	1.498
Total chlorophyll (mg g ⁻¹)	26.966**	8.792**	0.009	1.356	0.051	0.001	0.619
Specific leaf area (cm ² g ⁻¹)	0.592	4.297*	3.300*	0.848	2.036	0.017	0.096
Leaf water content (g g ⁻¹)	0.163	1.973	5.415*	1.374	1.832	1.647	0.101
Soil available N (%)	0.660	1.518	3.646	0.802	0.014	1.518	0.802
Soil available P (%)	0.012	0.897	0.001	0.788	0.133	0.897	0.788
Soil N:P ratio	0.015	2.405	1.717	1.394	0.486	2.405	1.394

The numbers in the table represent *F* values. Asterisks indicate significant effects: ** $P \leq 0.01$, * $0.01 < P \leq 0.05$

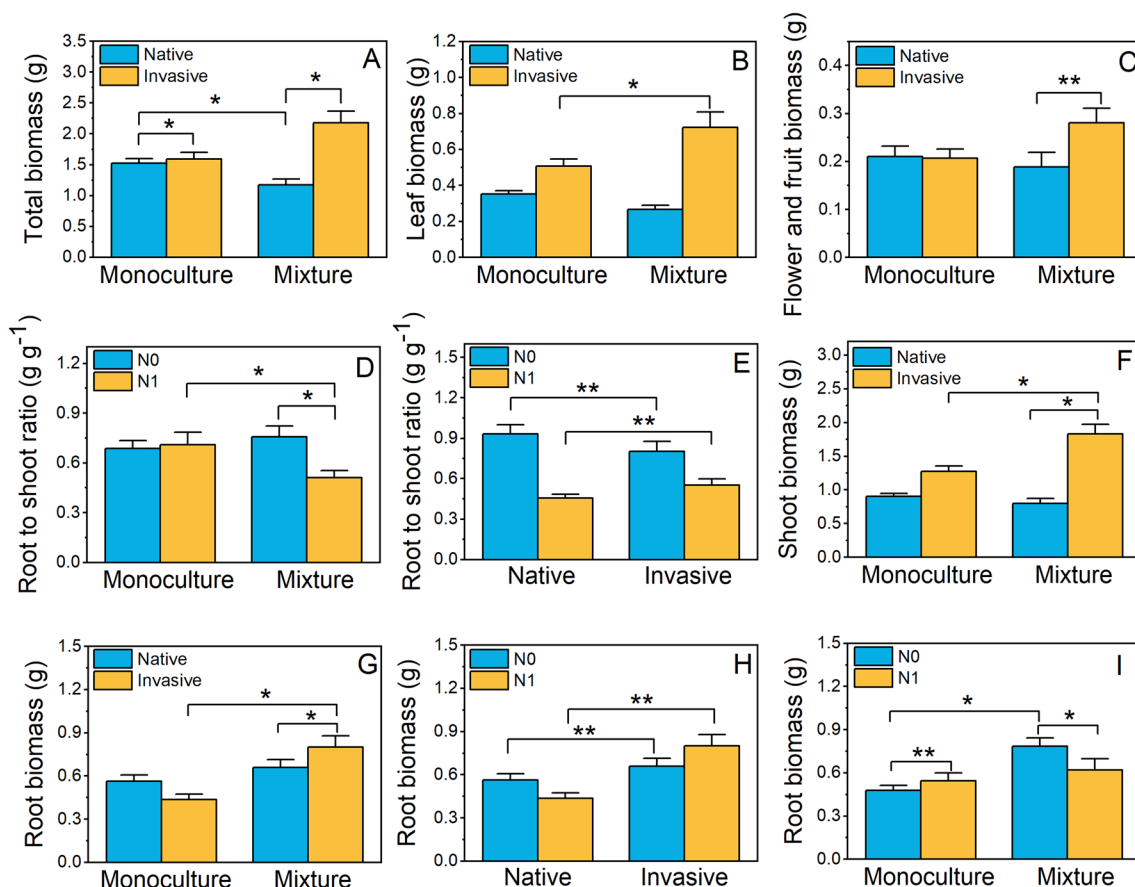


Fig. 1 Total biomass (TB) (A), leaf biomass (LB) (B), flower and fruit biomass (FB) (C), root-to-shoot ratio (RSR) (D, E), shoot biomass (SB) (F), and root biomass (RB) (G–I) of invasive and native species under different N deposition and cultivation. Values are shown as mean \pm standard error (SE) ($n=8-10$). Symbol shapes represent different N levels. N0: 0 g N m⁻² year⁻¹; N1: 12 g N m⁻² year⁻¹. Different symbols indicate a significant difference in simple effect tests. ** $P \leq 0.01$, * $P \leq 0.05$

the variance in PC1 or PC2 were considered as main influencing factors. Pearson's product-moment correlation coefficients were calculated among the main functional traits to evaluate the level of phenotypic integration for each species. All statistical analyses were performed using SPSS Statistics software (version 25.0; SPSS Inc., Chicago, USA). The figures were created using Origin 2021 software (OriginLab Co., MA, USA).

We conducted path analysis to assess the direct and indirect effects of N deposition and cultivation on the performance of invasive and native plants. An initial a priori conceptual model including all possible pathways was constructed, and maximum likelihood was used to estimate model coefficients. The conceptual model was compared to the observed variance-covariance matrix, and non-significant pathways were eliminated to obtain the final model. Model adequacy was assessed using the χ^2 test, with low root mean square

error of approximation (RMSEA < 0.10) and high comparative fit index (CFI > 0.90) indicating goodness of fit. Path analysis was conducted using AMOS version 24.0 (Amos Development, Spring House, USA).

Results

Accumulation and allocation of biomass

Nitrogen deposition and species significantly affected TB, and the interaction of species and cultivation had a significant effect on TB (Table 1). The MANOVAs indicated that N deposition had significant effects on TB, LB, FB, SB and RSR (Table S58). In monocultures, plants under N1 had significantly greater TB than N0. In mixed pots, the biomass of the invasive species was significantly higher than that of the native species (Fig. 1A, Fig. S13A). Specifically, the TB of invasive species treated with N was significantly greater than that of invasive species treated without N addition (Table 1, Fig. S1A). The leaf biomass of the invasive species was

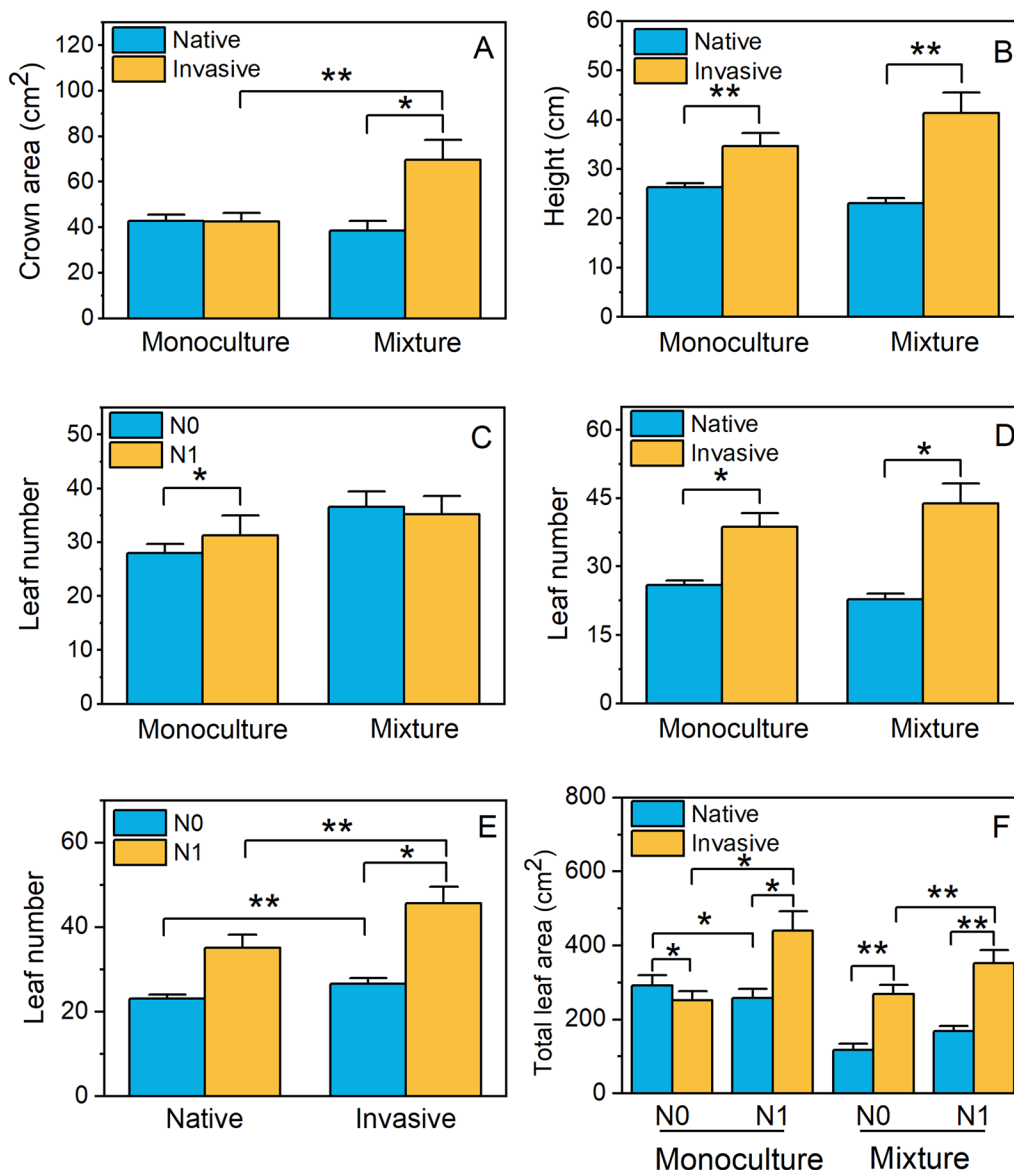


Fig. 2 Crown area (CA) (A), height (H) (B), leaf number (C–E), and total leaf area (TLA) (F) of invasive and native species under different N deposition and cultivation. The values shown are the mean \pm SE ($n=8-10$). Different symbols indicate a significant difference in simple effect tests. ** $P \leq 0.01$, * $P \leq 0.05$

consistently greater than that of the native species in all cases, including when the species were mixed. Furthermore, LB increased with N addition for all plants, and N deposition and species significantly affected the LB (Table 1, Fig. 1B). Nitrogen addition significantly increased FB, and the FB of the invasive species was significantly higher than that of the native species in the mixed culture (Table 1, Fig. 1C). The RB of invasive species in N1 was the highest in the mixed pots (Fig. 1G–I). Species had a significant influence on RSR (Table 1). However, RSR decreased significantly after

adding N to mixed pots, indicating that N supplementation significantly reduced the RSR of the native species (Fig. 1D). In N0, the RSR of the native species was significantly higher than that of the invasive species. In N1, the RSR of the invasive species was significantly higher than that of the native species (Fig. 1E).

Plant morphology

The invasive species had a significantly larger CA than the native species in the mixed treatment, and N deposition promoted canopy width in both species. However,

this effect was more pronounced among invasive species, with a 63.9% increase (Fig. 2A, Fig. S14). Nitrogen deposition, species and cultivation significantly affected the CA (Table 1). In all cases, the H of the invasive species was greater than that of the native species (Fig. 2B). Nitrogen deposition and species significantly influenced H (Table 1). In the MANOVAs, species had significant effects on H, CA, MRL, ALA, and TLA (Table S58).

Species had a significant effect on the MRL, and the interaction between N deposition and cultivation had a significant effect on MRL (Table 1). The leaf number of invasive species was significantly greater than that of native species, and the leaf number of invasive species was significantly increased after N was added (Fig. 2C–E). Nitrogen deposition, species, and cultivation had significant effects on the ALA and TLA (Table 1). The TLA was significantly affected by N deposition and the interaction between N deposition and species (Table 1). In the MANOVAs, the three-way interaction among N deposition, species, and cultivation had a significant effect on TLA (Table S58). In monoculture, under the N1 treatment, the invasive species had a larger leaf area index than the native species (Fig. S14D–E). The TLA of the invasive species increased with N addition, which was different from that of the native species. In the mixed culture, the invasive species had a larger TLA than the native species (Fig. 2F).

Physiological parameters

Nitrogen deposition and species had significant effects on Chl and LWC (Table 1). The cultivation had a significant influence on LWC (Table 1). In MANOVAs, species had significant effects on SLA, Chl and LWC (Table S58). The Chl of the native species was higher than that of the invasive species (Fig. S15).

Soil N and phosphorus concentrations

The SP in N1 was significantly higher than that in N0. The SP of N1 was lower than that under monoculture, and the highest concentration occurred in native species monoculture (Fig. 3A). The maximum SP was observed in invasive species monoculture, but there was no significant difference between treatments (Fig. 3B). The SN/SP under the N0 treatment was significantly higher under native species and mixed culture than under invasive monoculture, but there was no significant difference between native species and mixed culture treatments (Fig. 3C). There were no significant effects of N deposition, species, or cultivation on the SP, SN, or SN/SP (Table 1).

Competitive effects of invasive species against native species

In all N deposition treatments, the invasive species had a significantly greater RDI than the native species, and this dominance was further exacerbated by N addition

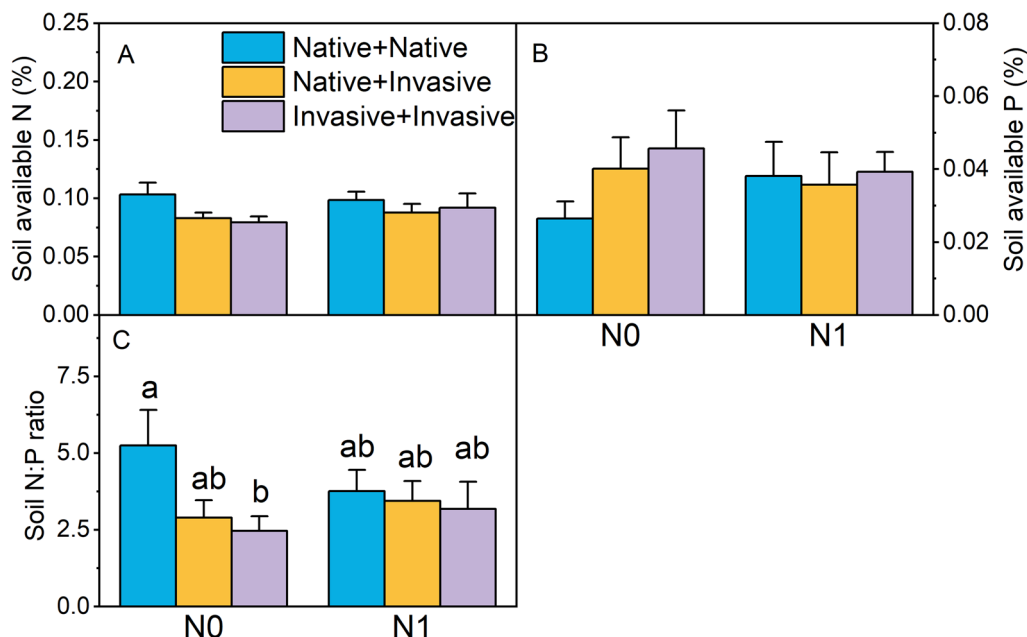


Fig. 3 Soil available N (SN) (A), soil available P (SP) (B), and soil nitrogen to phosphorus ratio (SN/SP) (C) of invasive and native species under different N deposition and cultivation. The values shown are the mean \pm SE ($n=3-5$). Different letters indicate a significant difference ($P \leq 0.05$) with Duncan's multiple range test

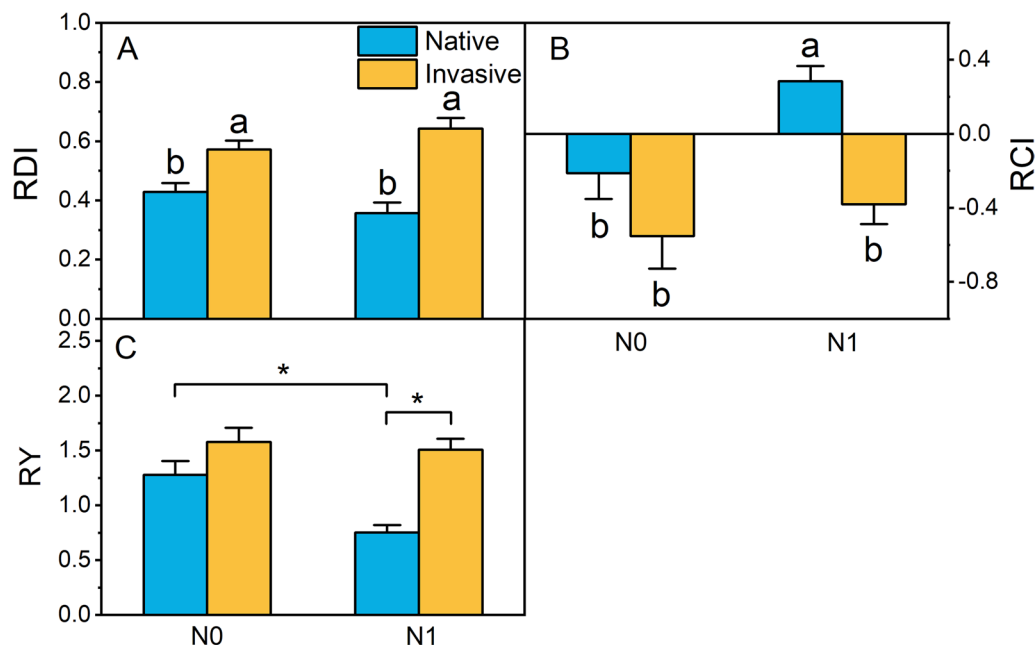


Fig. 4 Relative dominance index (RDI) (A) of invasive and native species under different N deposition and cultivation. Relative competition intensity index (RCI) (B) and the relative yield (RY) (C) of invasive and native species under different N deposition and cultivation. The values are shown as mean \pm SE ($n=8-10$). ** $P \leq 0.01$, * $P \leq 0.05$

(Fig. 4A). The RDI values of *E. annuus* and *C. canadensis* were significantly higher than those of *A. argyi* and *I. japonica* (Figs. S4, S8). Nitrogen deposition significantly influenced the RCI of native species, being increased with the amount of N deposition. In the N0 treatment, the RCI of both native and invasive species was negative, and there was no significant difference. In the N1 treatment, the RCI of the native species was positive and significantly greater than that of the invasive species. This result suggested that the TB under interspecific competition was lower than that under intraspecific competition (Fig. 4B). When no N was applied (N0 treatment), the RY values for both native and invasive species were greater than 1, suggesting that interspecific competition was less intense than intraspecific competition. However, in the N1 treatment, the RY values for native species were less than 1, indicating that interspecific competition surpassed intraspecific competition (Fig. 4C).

Principal component analysis

The first two PCA axes explained 50.4% of the variation in growth traits and physiological traits between invasive and native plants (Fig. 5). The first axis (that explained 26.9% of the variation) was associated with RSR and ALA. The second axis, accounting for 23.5% of the variation, was affected by H, CA, and Chl (Table 1; Fig. 5). The functional traits of invasive and native species were separated along the PC2 axis (Fig. 5).

Path analysis

χ^2 tests indicated that there was a nonsignificant discrepancy between the model-implied covariance matrix and the original covariance matrix ($P > 0.05$), and thus our model was deemed plausible. Nitrogen deposition had direct positive associations with CA, Chl, SLA, and TB of invasive plants and direct negative associations with the ALA of invasive plants (Fig. 6A). Nitrogen deposition indirectly affected the TB of invasive plants by influencing H and SNC (Fig. 6A). Cultivation directly affected ALA and SPC negatively and SLA, CA, Chl and TB positively (Fig. 6A). The TB of invasive plants was indirectly, positively affected by cultivation through affecting RSR (Fig. 6A).

Nitrogen deposition had direct positive associations with CA, Chl, SPC, and H of native plants and direct negative associations with the ALA and RSR of native plants (Fig. 6B). The RSR, CA, and H directly affected the TB of native plants (Fig. 6B). Cultivation directly and negatively affected the TB, ALA, Chl, H, and SPC (Fig. 6B). The TB of native plants was indirectly and positively affected by cultivation through H and CA (Fig. 6B).

Trait correlations

For each species, 36 pairs of functional traits were examined by Pearson's correlation. Among these traits, nine pairs of traits for invasive plants and 14 pairs of traits for native plants were significantly correlated at the 0.05

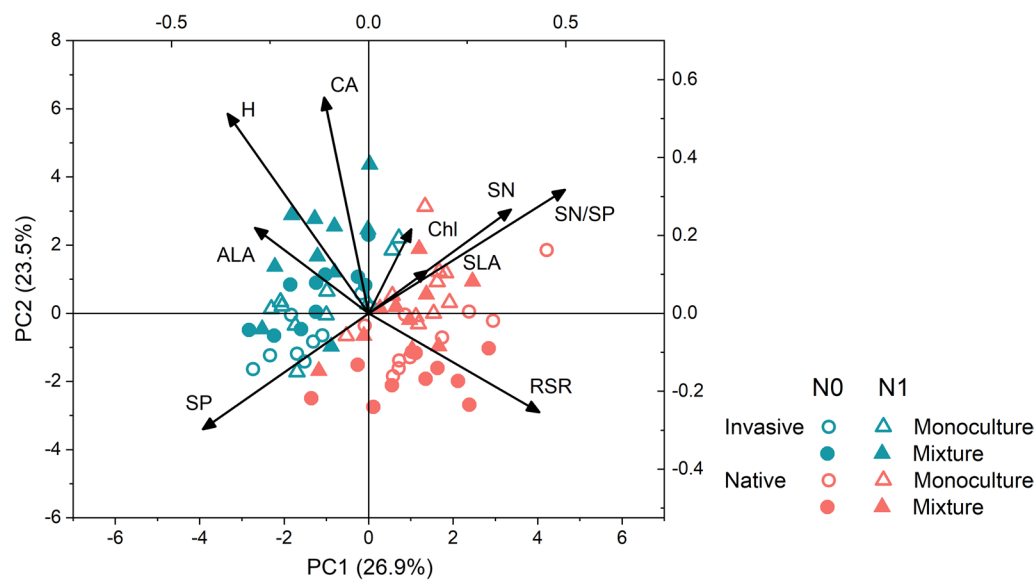


Fig. 5 Principal component analysis of invasive and native species across three levels of N deposition and two cultivation types based on nine functional traits. H, height; CA, crown area; ALA, average leaf area; RSR, root-to-shoot ratio; Chl, leaf chlorophyll content; SLA, specific leaf area; SN, soil nitrogen content; SP, soil phosphorus content; SN/SP, soil nitrogen to phosphorus ratio

level (Fig. 7). The seven functional traits were correlated in both invasive plants and native plants. These were TB and CA were positively correlated with Chl, SLA, and H. ALA was negatively correlated with H in invasive species (Fig. 7A). Native species' TB was positively correlated with ALA, Chl, H, and CA (Fig. 7B).

Discussion

Our investigation into the interplay between N deposition and interspecific competition has revealed enhanced productivity in both invasive species and common native species under conditions of increased N. Notably, invasive species exhibited superior performance relative to native species, with N deposition further magnifying this discrepancy. Overall, our results imply that while N deposition may provide limited benefits to common native species, it tends to offer a more substantial advantage to invasive species, potentially facilitating their invasion. This finding corroborates the theory of fluctuating resource availability, positing that an upsurge in available nutrients within a native plant community disproportionately benefits invasive species (Davis et al. 2000).

Nitrogen deposition contributes to plant growth

Nitrogen deposition increased the biomass (TB, LB, RB and SB) and the H and CA of invasive and native species, which is a common response among native and invasive species (van Kleunen et al. 2010). Therefore, the first hypothesis that N deposition would improve the growth performance of both invasive and native species

was confirmed. The TB of the native species after N deposition in the mixed culture was lower than that in the monoculture, while under monoculture, N deposition increased the TB of native species. This confirmed that N deposition was beneficial to native species, but this benefit could be sustained when the invasive species coexisted with the native species. The LB of the invasive species was consistently greater than that of the native species across various N loading and cultivation conditions, conferring the invasive species an advantage in competition for light energy above ground. In mixed culture, the H, CA, TLA, and SB values of the invasive species were greater than those of the common native species. The taller invasive species can intercept and preempt light, making it unavailable to low-growing common native species. Competition for light is likely to be highly size-asymmetric (Hautier et al. 2018; Zhang et al. 2020). When the species were mixed, the decrease in the RB of native species was likely caused by light competition, as this necessitates greater allocation of biomass to aboveground structures. Additionally, in mixed culture, the increased SN concentration reduced the need for native species to invest in their root systems. The biomass allocation to above-ground parts of the plant is generally higher than to roots under low light (Freschet et al. 2018; Poorter et al. 2015). This enables the plants to capture more light resources. As in the present case, the N deposition relieved the N limitation in the soil, and with the greater biomass allocated to the aboveground, parts led to the greater competition for light. In mixture,

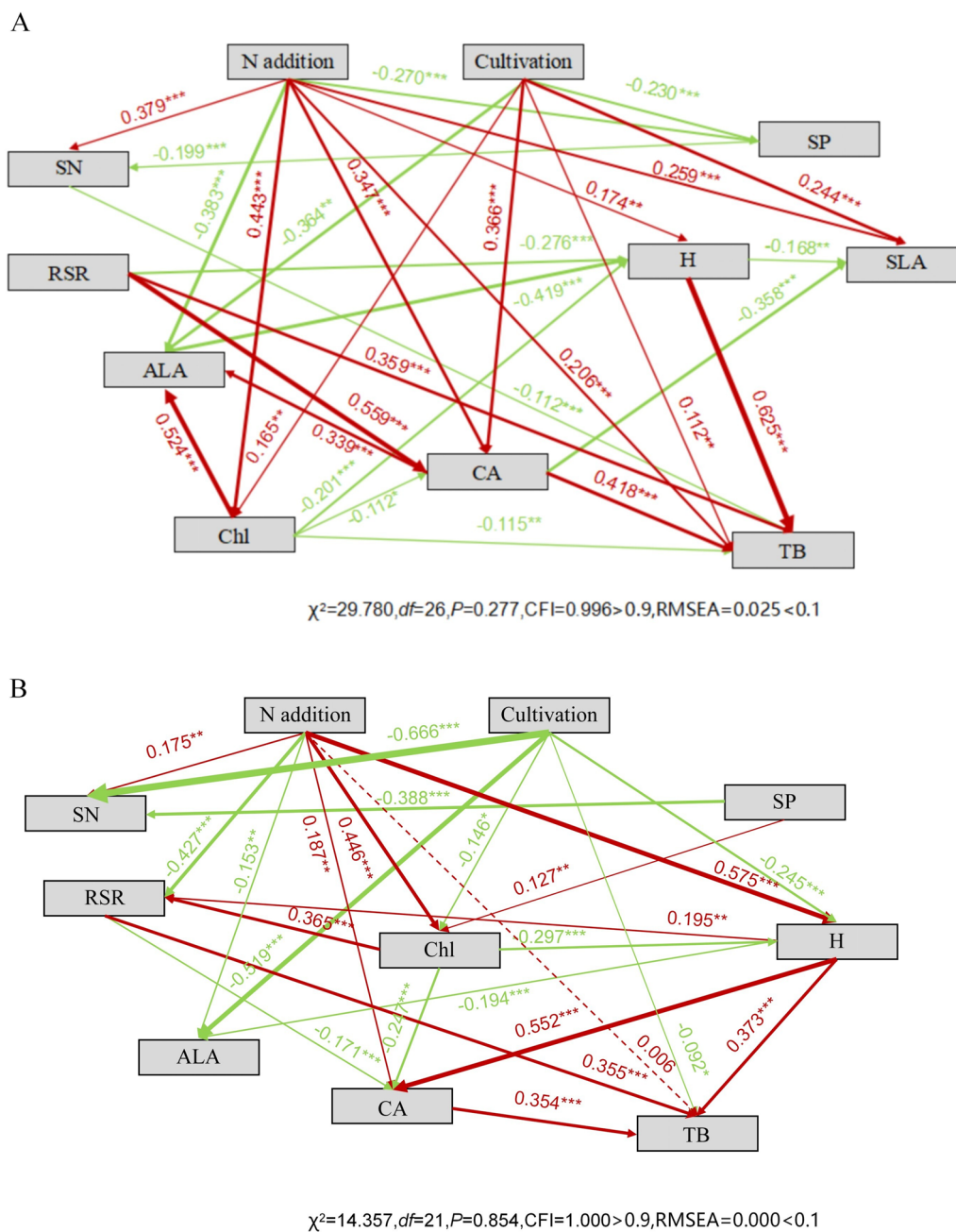


Fig. 6 Path analysis showing the direct and indirect effects of N deposition and cultivation on soil nutrient content and performance of invasive (A) and native plants (B). Red and green arrows reflect positive and negative pathways, respectively. Dotted lines indicate hypothesized relationships whose path coefficients were not statistically significant. Numbers along the arrows, as well as the thickness of the arrows, indicate standardized path coefficients. H, height; CA, crown area; ALA, average leaf area; RSR, root-to-shoot ratio; TB, total biomass; Chl, leaf chlorophyll content; SLA, specific leaf area; SN, soil available N; SP, soil available P; *** $P \leq 0.001$, ** $0.001 < P \leq 0.01$, * $0.01 < P \leq 0.05$

light, rather than N, was the most limiting resource for the native species.

The growth (TB and H) of common native species was promoted by N deposition. Although the SN was not significantly different among treatments, when native species were planted in monoculture, the SN was always

higher than that under mixed culture and monoculture of invasive species, regardless of N deposition. This suggests that the common native species possessed a low N absorption capacity compared to invasive species under low and high levels of N deposition. The low N absorption capacity of native species is probably one of the

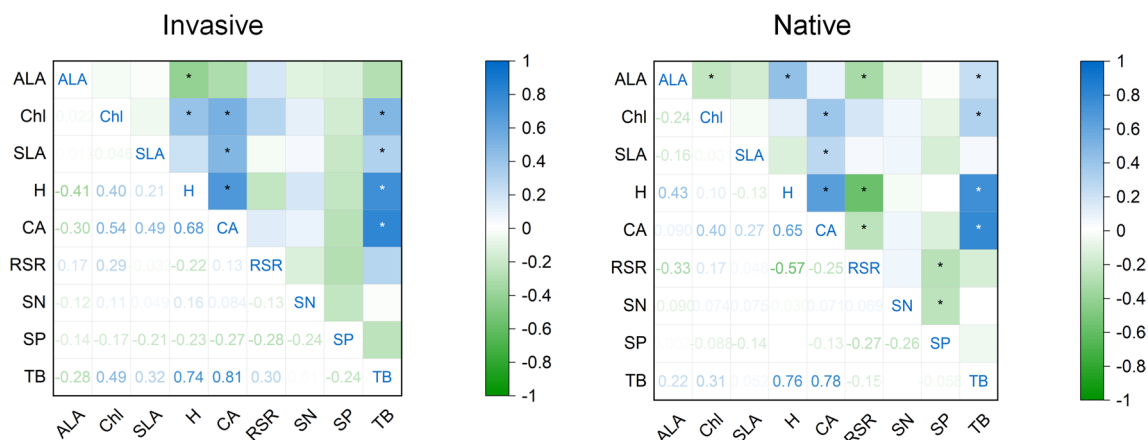


Fig. 7 Matrix of Pearson's product-moment correlation coefficients for functional traits of invasive and native across different treatments. ALA, average leaf area; Chl, leaf chlorophyll content; SLA, specific leaf area; H, height; CA, crown area; RSR, root-to-shoot ratio; SN, soil available N; SP, soil available P; TB, total biomass. Significant correlations are denoted by bold font and asterisks: * $P \leq 0.05$

reasons why the biomass of the common native species under mixed culture did not increase when N was added. In contrast, as the invasive species benefited more from the increased N content (Liu et al. 2017a), the soil N in mixed pots was similarly low under N0 and N1. This means that the native species were less competitive than the invasive species under N addition and that they were resource conservative (Daehler 2003). Meanwhile, under N0, although the common native species absorbed less N from the soil than invasive species under monoculture, they still accumulated similar TB, possibly due to a higher N use efficiency in native species than in the invasive species (Amanda et al. 2021; Daehler 2003). This high N use efficiency in native species should be one of the reasons why the native species under mixed culture promoted the growth of invasive species, especially under N0, as the invasive species accumulated more biomass in mixed culture compared to that under monoculture.

The present study has several limitations, primarily because it focuses on only two plant families. While Compositaceae and Amaranthaceae represent approximately 21% of all invasive species in China, species from other families might exhibit distinct responses to N deposition. It has been suggested that N addition can affect the allelopathic potential of invasive species by altering their secondary metabolism. The impact of N application on allelopathy seems to be dual: some evidence suggests that N supplementation can mitigate the negative effects of environmental stressors on plant growth and potentially decrease the allelopathic potential of invasive species (Wang et al. 2017a, 2020). However, other studies have not observed such effects (Clemensen et al. 2017; Hofland-Zijlstra and Berendse. 2009), indicating

that outcomes may vary according to the plant family or the specific amounts of N added. Therefore, a consensus on the impact of N deposition on allelopathy has not yet been reached, and further research is needed to clarify the role of allelopathy in competition between native and invasive species, as well as the effect of N deposition on this role.

Different biomass allocation and acquisition strategies between invasive and common native species

In some studies, invasive species exhibited higher SLA than native species, leading to more rapid returns on resource investment and increased growth rates (Colesie et al. 2020; Feng et al. 2008; van Kleunen et al. 2010). Nonetheless, in our experiment, the invasive species had a lower SLA compared to the common native species. One possible explanation is that previous studies often did not consider the prevalence of native species, they compared the overall average SLA of all native species with the mean SLA of invasive species instead (Colesie et al. 2020; Feng et al. 2008; van Kleunen et al. 2010). Another possible explanation is that earlier research did not address the competition between native and invasive species (Adler et al. 2014; Colesie et al. 2020). In this study, native species were located directly beneath and shaded by the invasive species, leading the native species to increase their leaf SLA to adapt to the lower light intensity. In contrast, the invasive species had lower SLA leaves that were more robust and longer lived, enabling them to utilize high irradiance more efficiently (Fonseca et al. 2000). In our experiment, the H, CA, and TB of the native species tended to be lower in the mixed culture than in the monoculture, while the opposite was true for

the invasive species, indicating that the invasive species inhibited the growth of the native species. The RDI of the invasive species exceeded that of the native species, indicating that the invasive species was dominant under coexistence. This confirms the second hypothesis that invasive species exhibit superior competitive ability compared to native species.

The RSR of the invasive species remained consistent under different N deposition and cultivation conditions, and thus its allocation to roots and shoots seemed to be consistent under various nutrient conditions, and there was weak plasticity of allometry (Niklas 2004; Yu et al. 2023). Unlike invasive species, the common native species had less RSR under N1 when grown in mixed culture compared to monoculture and thus higher light absorption, probably because the taller invasive species had a larger crown area and intercepted more of the light resources. The common native species allocated more biomass to organs (e.g., shoots) that make the best use of a particular resource (e.g., light) to help individuals survive under conditions of stress (Liu et al. 2021; McCarthy and Enquist 2007), indicating a more economical strategy for biomass allocation.

Leaf chlorophyll content generally increases in the presence of increased N for native and invasive species, and thus the application of N probably promoted photosynthesis in the plants (Wang et al. 2022, 2023). Without additional N, the Chl of the invasive species and that of the common native species in this experiment were basically the same, suggesting that photosynthetic capacity did not account for the competitive advantage of the invasive species. Furthermore, there was no significant difference in F_v/F_m values, indicating that the potential maximum photosynthetic capacity was similar between the invasive and native species across different treatments.

Intensity of competition between invasive and native species

Our findings indicate that N deposition enhances the competitive interactions between invasive and native species. Consistent with previous studies, the competitive advantage of invasive species over native species increased with the nitrogen level (He et al. 2012, 2011). Following N deposition, the RCI for native species was positive, indicating that interspecific competition suppressed the growth of native species. Additionally, the RY outcomes revealed that interspecific competition was markedly intensified post-N addition. The RDI of invasive species over native species increased after N addition. This confirmed our third hypothesis that N loading amplifies the competitive advantage of invasive species over native species, mainly via enhancing

interspecific competition that inhibits the growth of native species.

Our results tended to support Darwin's naturalization hypothesis (Daehler 2001; Durand and Goldstein. 2001). Utilizing PCA, we discovered that the invasive species and the common native species exhibited distinct separation in morphology, physiology, and biomass allocation. Therefore, the common native species and the invasive species had different strategies of growth and tended to diverge in functional traits. Our research findings are consistent with several previous studies (Chen et al. 2022; Luo et al. 2015; Wang et al. 2022) but diverge from the results reported by Fan et al. (2023). This contradiction may be attributed to the fact that environmental filtering holds greater significance at the regional scale (Fan et al. 2023). In contrast, at the local community scale, intense interactions with predators and competitors are more common, often leading to trait divergence (Cadotte et al. 2018; Wang et al. 2021). When the invasive species has the greater competitive ability, the trait separation between invasive and native species favors successful invasion (Chen et al. 2024; Feng et al. 2016). The invasive species in mixed culture exhibited a greater response to N deposition, with its competitive capacity increasing along with the increases in H, CA, LB, RB, SB and TB. In contrast, the growth of common native species was relatively insensitive to N deposition, as demonstrated by the accumulation of dry mass.

In this study, we estimated the magnitude of phenotypic integration by assessing the number of significant correlations among functional traits. Several studies have demonstrated that phenotypic integration tends to increase with environmental stress (Matesanz et al. 2021; Zimmermann et al. 2016). Our results showed that common native species exhibited higher levels of phenotypic integration than invasive species, a factor that may enable them to adapt to the adverse environments created by invasive competitors. Although high phenotypic integration is considered an important determinant of invasiveness (Buru et al. 2019; Zimmermann et al. 2016), our findings indicate that the phenotypic integration of invasive species is not necessarily stronger than that of native species, particularly the common species. Some studies have demonstrated that invasive species show higher trait integration than non-invasive species (Osunkoya et al. 2010, 2014; Wang et al. 2022), contrary to our findings. This may be due to previous studies not accounting for the prevalence of both native and invasive species. Our research further emphasizes the necessity of considering the commonness of native species in future studies, as the differences in functional traits (e.g., SLA) and phenotypic integration between common native species and invasive species are distinct from those observed

between rare native species and invasive species. This difference may also be due to the relative importance of the trait mean values of invasive species to adaptation compared to phenotypic integration (Godoy et al. 2012). When N was added, the invasive species had a higher average character, and the biomass of the invasive species was higher than that of the native species under the mixed culture. The high correlation of TB with H, Chl and CA of both common native species and invasive species may indicate that these traits respond consistently to plant growth, allowing the plants to better utilize the increase in N resources and resulting in higher biomass accumulation. This follows the principle of phenotypic integration: an integrated phenotype may better adapt to environmental changes through the coordinated variation of functional traits and thus acquire more resources (Luo et al. 2015; Van Kleunen and Fischer 2005).

Conclusion

Nitrogen deposition enhanced the growth of both invasive and common native species when grown in monoculture settings. However, a more pronounced increase in TB was noted in invasive species compared to native species when the species were grown in mixed culture. This indicates that N deposition bolsters the suppressive influence of invasive species on native counterparts and facilitates their invasion. The invasive species exhibited a marked dominance and robust competitive edge by adopting a rapid growth strategy. Conversely, native species opted for a more conservative approach toward N deposition and interspecific competition. Our investigation explored the combined effects of N deposition and interspecific relationships on the growth, physiology, and morphology of multiple invasive and common native species, shedding light on the complex ecological dynamics of plant invasion. Anticipated future increments in N deposition are likely to further accelerate the spread of exotic species. Consequently, managing N deposition levels may slow the invasion process but may not substantially change the current trends of invasive species dominance. In regions experiencing high N deposition, strategically introducing a diverse array of native species with high N use efficiency in proximity to invasive species could potentially mitigate the pace of invasion. Further greenhouse and field studies are essential to validate the effectiveness of this management strategy. Moreover, managing invasive species should be prioritized in areas with high N deposition rates over those with low N deposition rates.

Abbreviations

ALA	Average leaf area
CA	Crown area
Chl	Chlorophyll content

FB	Flower and fruit biomass
F_v/F_m	The maximum photochemical efficiency
H	Height
LB	Leaf biomass
LWC	Leaf water content
MRL	Maximum root length
N	Nitrogen
P	Phosphorus
RB	Root biomass
RCI	Relative competition intensity index
RDI	Relative dominance index
RY	Relative yield
RSR	Root-to-shoot ratio
SB	Shoot biomass
SLA	Specific leaf area
SN	Soil available nitrogen
SN/SP	Soil nitrogen to phosphorus ratio
SP	Soil available phosphorus
TB	Total biomass
TLA	Total leaf area

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-024-00541-5>.

Supplementary Material 1. These include Tables S1–58 and Figs. S1–15.

Acknowledgements

We thank Jinye Ma, Jiayuan Liang, Fan Li, Zheyu Sun and Wenyao Zhang for their assistance in the laboratory. We thank LetPub (www.letpub.com.cn) for its linguistic assistance during the preparation of this manuscript.

Author contributions

XG proposed the idea, guided the study, and edited the manuscript. CX conducted experiments, data collection, and wrote the manuscript under the supervision of XG. XW carried out data interpretation and reviewed and edited the manuscript. LLL, MYL, YKS, and TW reviewed and edited the manuscript. YNC helped in the analysis of data and edited the manuscript. HML provided resources. All authors have read and approved the final manuscript.

Funding

This research was supported by the National Natural Science Foundation of China (32271588 and 31971718), Qingdao Agricultural University Doctoral Start-Up Fund (6631120094), and the Talent Introduction Program for Youth Innovation Team of Shandong Higher Learning (018-1622001).

Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Received: 14 January 2024 Accepted: 18 August 2024

Published online: 28 August 2024

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