RESEARCH ARTICLE

Allelopathy and arbuscular mycorrhizal fungi interactions shape plant invasion outcomes

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Abstract

The novel weapon hypothesis suggests that allelopathy is an important mechanism for exotic plants to successfully invade native plant communities. Allelochemicals from exotic plants affect both native plants and arbuscular mycorrhizal fungi (AMF) in soil. To explore these effects, we conducted pot experiments using a native plant community comprising of *Chenopodium album* L., *Vitex negundo* L., *Rhus chinensis* Mill., and *Acer truncatum* Bunge. We incorporated AMF strains (*Funneliformis mosseae*, *Glomus versiforme*, and *Rhizophagus intraradices* in a 1:1:1 volume ratio) into a soil mixture comprising equal volumes of autoclaved field soil and grass ash at five concentrations (0 g L^{-1}, CK; 10 g L^{-1}, LRE; 20 g L^{-1}, NRE; 30 g L^{-1}, MRE; and 40 g L^{-1}, HRE) to investigate the allelopathy of *Rhus typhina* L. root and its interactions with AMF on the native plant community. Our results indicated that low concentrations of allelochemicals promoted the relative growth rate and leaf nitrogen content in the native plant community, which was attributed to the increased environmental stress that improved the degree of leaf photosynthetic capacity and organic synthesis rate in the native communities. Moreover, allelochemicals with toxicity decreased the colonization rates of AMF. Meanwhile, the presence of allelopathic effects induced a decrease in leaf nitrogen, and allelopathy altered the effects of AMF on the native community. Specifically, the high concentration of allelochemicals altered the positive effect of AMF on the total aboveground biomass of the native plant community to a negative effect, likely by decreasing colonization rates or affecting soil

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physicochemical properties and the composition of the mycorrhizal communities. Consequently, it is necessary to consider the effects of AMF when testing the roles of allelopathy or the novel weapons hypothesis in biological invasions.

Graphical abstract
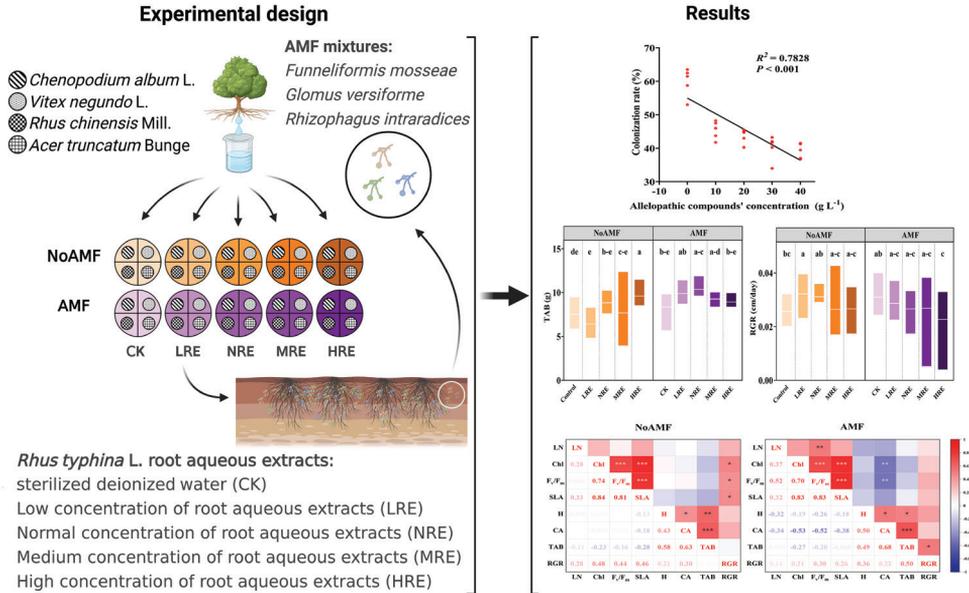
Keywords

Allelochemicals, mycorrhizal symbionts, photosynthetic acquisition capacity, physiological and growth parameters

Introduction

Exotic invaders are a worldwide problem, which can displace native species, causing significant changes in the diversity of native communities (Hassan and Mohamed 2020; Li et al. 2022; Wang et al. 2022a). Exotic plants can successfully establish communities due to their relatively strong allelopathic effects in the invaded habitats (Gruntman et al. 2016). The allelopathy of exotic plants can influence not only the growth and development of native communities but also the composition of mycorrhizal communities (Li et al. 2015; Liu et al. 2017; Hassan and Mohamed 2020). Therefore, comprehending how allelopathy affects native plant communities and mycorrhizal formation can provide valuable insights into invasion mechanisms (Callaway et al. 2011; Gruntman et al. 2016).

Allelopathic effects refer to the positive or negative interaction between plants mediated by chemical compounds (Gross 2003; Cheng and Cheng 2015; Qin et al. 2020). The novel weapons hypothesis posits that non-native species produce secondary chemicals to influence neighboring native species and reduce their competitive advantage (Callaway and Ridenour 2004; Yuan et al. 2021; Yuan et al. 2022). So far, various studies have found inhibitory effects of allelochemicals from exotic plants (Zhang et al. 2011; Hassan and Mohamed 2020; Zhang et al. 2020). For example, invasive plant extracts had negative effects on native seed germination (Yuan et al. 2021). *Centaurea maculosa* inhibits the growth and germination of indigenous species in field soils via the release of the phytotoxin (-)-catechin from its roots (Hierro and Callaway 2003). In addition, invasive plants' allelochemicals can target the mycorrhizal communities, and their outcomes may impact the ecosystem services of native plant communities (Kardol et al. 2006; Gruntman et al. 2016; Bennett and Klironomos 2019).

Arbuscular mycorrhizal fungi (AMF), a representative group of the mycorrhizal communities, can form symbiotic associations with approximately 70% of plant species (Callaway et al. 2011; Weremijewicz et al. 2016; Saia and Jansa 2022). Symbiotic fungi can enhance host plant growth by increasing nutrient absorption and utilization, improving disease resistance, and enhancing drought tolerance (Callaway et al. 2011; Delavaux et al. 2017; de Vries et al. 2020). In return, AMF can aquire carbohydrates derived from host photosynthesis (Sikes et al. 2009; Adomako et al. 2019). Although mycorrhizal symbionts are traditionally considered beneficial to the host (Antunes et al. 2008; Callaway et al. 2011), the association may sometimes have negative consequences (de Vries et al. 2020; Dong et al. 2021). For example, AMF can benefit the host under low phosphorus (P) conditions, whereas the opposite conclusion is drawn under high P conditions (Chen et al. 2020; Dong et al. 2021). Therefore, the effect of AMF on the host may vary depending on environmental conditions.

Invasive plants can produce distinct allelochemicals, which can disturb the structure of mycorrhizal communities in the rhizosphere and alter soil nutrient cycling patterns (Vogelsang and Bever 2009; de Vries et al. 2020). Typically, abundant allelopathic compounds, such as phenolics and flavonoids, are emitted into the surrounding environment through root exudates, volatile organic compounds, leaf leachates, and decomposition of plant materials (Inderjit et al. 2011; Inderjit et al. 2021; Yuan et al. 2022). Root exudates are one of the primary mechanisms to mediate these effects (Hassan and Mohamed 2020). They are released from the living root systems of invasive plants, directly or indirectly affecting the growth and production of native communities (Bennett and Klironomos 2019; Zhang et al. 2020; Dong et al. 2021). Specifically, root exudates from certain invasive species may harm some components of soil biota (Antunes et al. 2008; Vogelsang and Bever 2009). Previous research has demonstrated that invasive and native hosts differ considerably in their preferences for and reliance on AMF (Hawkes et al. 2006; Zhang et al. 2017; de Vries et al. 2020). The root exudates of invasive plants can selectively attract the most beneficial fungal species to facilitate their own growth (Vogelsang and Bever 2009; Zhang et al. 2019).

Consequently, these root exudates may modify the composition of soil microbes. The alterations in mycorrhizal communities, which regulate nutrient availability in soil, may detrimentally affect the growth of native plants, potentially disrupting the symbiotic relationship between AMF and the native communities, thus impeding their access to resources and nutrients (Bennett and Klironomos 2019; Zhang et al. 2019). However, the majority of pertinent research has solely concentrated on the allelopathic impacts of invasive species (Zhang et al. 2011; Hassan and Mohamed 2020; Zhang et al. 2020), with limited emphasis placed on the effects of AMF when assessing the allelopathic effects of biological invasions (Antunes et al. 2008).

In this study, we selected four common plants of the warm temperate zone of China, namely *Chenopodium album* L., *Vitex negundo* L., *Rhus chinensis* Mill., and *Acer truncatum* Bunge, to simulate a native plant community. We used root aqueous extracts of *Rhus typhina* L. to simulate allelopathic effects of invasive plants, and inoculated AMF (*Funneliformis mosseae*, *Glomus versiforme*, *Rhizophagus intraradices*). We conducted a community-level greenhouse experiment to test the following hypotheses: 1) the allelopathic effects of *R. typhina* could negatively impact the growth of the native plant community, 2) the allelopathic effects of *R. typhina* could negatively impact the colonization rates of AMF, and 3) the allelopathic effects of *R. typhina* could alter the impact of AMF on the growth of the native plant community.

Materials and methods

Study species

Rhus typhina L., an exotic tree species indigenous to North America, was introduced to China as a horticultural and greening ornamental plant in 1959 (Hu et al. 2022). Due to its high ecological risk and potent reproductive capacity, it is now considered as one of the most destructive invasive tree species in China (Hu et al. 2022; Xu et al. 2023). To construct a native plant community, we selected four plant species from the warm temperate zone of China that commonly co-occur with *R. typhina*, including one herbaceous species (*Chenopodium album* L.), one shrub (*Vitex negundo* L.), and two trees (*Rhus chinensis* Mill. and *Acer truncatum* Bunge). Given the challenges of cultivating herbaceous plants with consistent growth and development, we dug up *C. album* seedlings with similar growth time directly after the other three plants (*V. negundo*, *R. chinensis*, and *A. truncatum*) had completed their seedling cultivation. Seeds of *V. negundo*, *R. chinensis*, and *A. truncatum* were collected from Mashan, Jimo, Qingdao, Shandong, China in the winter of 2020. We classified each species as invasive or native according to Alien Invasive Flora of China (Ma 2020) and the database Flora of China (www.efloras.org).

In mid-April 2021, we prepared sufficient quantities of seeds of the three selected plant species. The following treatments were performed to improve their germination rate. First, seeds of *R. chinensis* were treated with a baking soda solution at 70 °C for 10

minutes to remove their waxy skins and subsequently cleaning with sterile deionized water. Second, seeds of *A. truncatum* were subjected to a 4 °C treatment for 24 hours. Third, seeds of both *R. chinensis* and *A. truncatum*, as well as those of *V. negundo*, were soaked in fresh water for 24 hours, replacing the water every 12 hours. Soaked seeds were then evenly spread into trays with three layers of gauze on the bottom, and two layers of gauze were placed over the seed surface to improve germination. During this process, sterile deionized water was sprayed into the trays daily to maintain moisture levels. After approximately 30% of the seeds had germinated, we selected strong and uniform seedlings of each species and transferred them to cell trays for further culture. Finally, seedlings of *C. album* with 4–5 leaves were collected from the campus of Qingdao Agricultural University, Shandong, China, until three plant seedlings had developed 4–5 leaves.

Preparation of allelopathic solutions of *R. typhina*

There are two primary rationales for using the root aqueous extracts from *R. typhina* to study the allelopathic effects: (1) allelopathic effects of *R. typhina* are mainly mediated by phenolic substances, most of which, especially polyphenols, can be dissolved in water (Djurdjević et al. 2012; Xu et al. 2023), and (2) in nature, the root exudation pathway is one of the primary methods by which plants release allelochemicals (Hassan and Mohamed 2020; Inderjit et al. 2021). Fully mature *R. typhina* roots were randomly selected from Qingdao Agricultural University, Shandong, China, and gently washed before being cut into small fragments. We added 1000 ml of sterilized deionized water per 100 g of fresh roots at approximately 25 °C for 48 hours, stirring every six hours. The root residues were filtered out to obtain 100 g L^{-1} mother liquor of the *R. typhina* root aqueous extract. Sterilized deionized water was then added in various ratios to the mother liquor to achieve different concentrations of the root aqueous extract (10, 20, 30, and 40 g L^{-1}). The root extract concentration of 20 g L^{-1} represented the normal condition with *R. typhina*'s allelopathic effects (hereafter referred to as NRE) (Xu et al. 2023). Since the concentration of allelochemicals in the soil during the initial period of invasion was low (Zhang et al. 2020), 10 g L^{-1} was designated as the low concentration of the root extract treatment (hereafter referred to as LRE). During the establishment of *R. typhina*, allelochemicals in the soil gradually accumulated (Zhang et al. 2020), so 30 and 40 g L^{-1} were classified as medium and high concentration of the root extract treatments (hereafter referred to as MRE and HRE, respectively). The *R. typhina* root aqueous extracts were refrigerated at approximately 4 °C (for no more than one week), while sterilized deionized water served as the control (0 g L^{-1}; simulating conditions without allelopathic effects; hereafter referred to as CK).

Preparation of AMF

The AMF inoculum comprised a blend of three common AMF strains – *Funneliformis mosseae*, *Glomus versiforme*, and *Rhizophagus intraradices* – in a 1:1:1 volume ratio.

As different AMF types have varying colonization rates in diverse plant species, the AMF mixtures can ensure consistent colonization rates across diverse plant species. In the AMF treatments, each pot was inoculated with the AMF mixtures containing approximately 8×10^3 viable propagules. In the NoAMF treatments, an equivalent amount of sterilized AMF inoculum was added to prevent substrate effects.

Experimental design

The experiment was performed at Qingdao Agricultural University, situated in Qingdao, China (36°31'N, 120°39'E). The region has a temperate monsoon climate with an annual temperature of approximately 12.7 °C, mean annual precipitation of around 821.8 mm, and average yearly sunshine duration of about 2,541.1 h. In the summer of 2021, we conducted a 70-day experiment in an artificially-controlled greenhouse maintained at an average temperature of 29.4 °C and a relative humidity of 77%, using a digital display humidity thermometer, DL-WS20 (Hangzhou Gsome Technology Co., China). The plastic pots used in this study were 20.0 cm in height and 20.0 cm in diameter, and were filled with soil materials consisting of autoclaved field soil and grass ash mixed at a 1:1 volume ratio.

In each plastic pot, we planted four different species of seedlings (*C. album*, *V. negundo*, *R. chinensis*, and *A. truncatum*), with four to five leaves per seedling. One seedling for each plant species was transplanted into one of the four equal sections of the cross lines past the center of the circle within each pot, resulting in a total of four plants per pot. The control treatment consisted of no AMF and root aqueous extracts of *R. typhina*. Overall, we established 100 experimental pots, including two AMF treatments (with and without AMF) and five concentrations (0 g L^{-1}, CK; 10 g L^{-1}, LRE; 20 g L^{-1}, NRE; 30 g L^{-1}, MRE; and 40 g L^{-1}, HRE). Each treatment had ten replicates ($n = 10$), and all individuals of each species and treatments were randomly distributed. Over the entire experiment, we added 50 ml of the appropriate concentration solution of the root aqueous extracts from *R. typhina* once every two days in the five concentration treatments, for a total of thirty times. Weeding and pest control measures were implemented as usual and the greenhouse was adequately ventilated. All pots were placed randomly within the greenhouse and rotated normally to minimize any potential effects of environmental differences during the experiment.

Harvest and measurements

Physiological parameters measured in the native plant community included specific leaf area (*SLA*), total chlorophyll concentration (*Chl*), F_v/F_m, and leaf nitrogen (*LN*), which can characterize the degree of leaf photosynthetic capacity (Wang et al. 2020). Growth parameters included plant height, crown area (*CA*), relative growth rate (*RGR*), and total aboveground biomass (*TAB*). Plant height and *CA* characterize the ability of the native plant community to acquire light (Wang et al. 2020; Wang et al. 2022b). *RGR* describes the rate of plant growth. At the conclusion of the experiment, the

intertwining of root systems in each plastic pot prevented the measurement of below-ground biomass for each plant. Consequently, we measured the total aboveground biomass (*TAB*) of all four plants to represent the community's growth. Additionally, the AMF colonization rate was used to characterize the quantity of mycorrhizal symbiont formation under different conditions.

Prior to the treatment, the aboveground component of five seedlings from each indigenous species with 4–5 true leaves were oven-dried at 105 °C for 0.5 h to inactivate them. The drying process was continued for an additional 48 h at 80 °C, and then the weight was measured. The mean value was regarded as the initial biomass for each species.

After 60 days, when the herbaceous flora had reached the reproductive stage, the maximum growth index of all native plants was determined. The vertical height of the plant from the base to the terminal bud was gauged as the plant height. The *CA* was calculated using the diamond-shaped area formula (Wang et al. 2022b; Guo et al. 2023b).

$$CA = 0.5 \times a \times b$$

where *a* indicates the length of the plant's maximum horizontal extension, and *b* signifies the length perpendicular to *a* on the plant's maximum horizontal extension plane.

For each plant, chlorophyll fluorescence parameters were evaluated during sunny and cloudless weather conditions from 8:30 to 11:30 using Pocket PEA (Hansatech Instruments Ltd., UK). The top-to-bottom first fully developed leaf was selected, and after undergoing dark treatment for 0.5 h, the maximum fluorescence value (F_m) and variable fluorescence value (F_v) were evaluated. The maximum photochemical efficiency (F_v/F_m) of PSII was then calculated (Hu et al. 2022; Xing et al. 2022).

The second or third fully expanded and healthy leaf from the apical meristem of each plant was selected, cleaned with sterilized deionized water, and the leaf area was measured using a portable leaf area meter (Yaxin-1241, Yaxin Inc., Beijing, China). The leaves were inactivated to inactivation at 105 °C for 0.5 h and dried at 85 °C for 24 h in a drying oven until they reached constant weight to obtain their dry weights. The *SLA* was calculated using the formula (Wang et al. 2022b; Guo et al. 2023a).

$$SLA = leaf\ area \div dry\ weight$$

The total chlorophyll content was determined using the ethanol extraction method. Four fully mature leaves near the top of each plant (one leaf per plant) were collected for each treatment and chopped to approximately 0.2 g fresh weight. The leaves were then submerged in 10 ml of 95% alcohol until completely whitened. The absorbance of chlorophyll in the solution at 665 nm and 649 nm wavelengths was measured using a UH5300 UV/VIS spectrophotometer (Hitachi, Inc., Tokyo, Japan). The concentrations of chlorophyll *a*, *b*, and total chlorophyll were calculated using the following formulas (Wang et al. 2022b; Guo et al. 2023a):

$$Chlorophyll\ a\ concentration = 13.95 \times A_{665} - 6.88 \times A_{649}$$

$$Chlorophyll\ b\ concentration = 24.96 \times A_{649} - 7.32 \times A_{665}$$

$$Chlorophyll\ content \\ = Chlorophyll\ concentration \\ \times volume\ of\ extraction\ solution\ /\ fresh\ weight\ of\ sample$$

$$Chl = Chlorophyll\ a\ content + Chlorophyll\ b\ content$$

The aboveground parts of the plants were harvested, washed, classified according to species, inactivated at 105 °C for 0.5 h in the oven, and dried in the oven at 80 °C for 48 h. The total aboveground biomass of all species in the same pot was measured and the *RGR* of native plants was calculated using the formula (Wang et al. 2022b).

$$RGR = (ln\ X_1 - ln\ X_2) \div \varDelta T$$

where X_2 and X_1 denote the final and initial biomass, respectively, and $\varDelta T$ is the duration of the experiment.

For *LN* measurements, dried leaves of each species were ground and weighed to 0.5 g using the Kai-style digestion method (K9860, Hanon, Shandong, China).

Roots were collected from 70-day plants. Fine roots (15 g) were excised from each plant, washed, and stained with acid fuchsin to determine the percentage of mycorrhizal colonization by the method of Biermann and Linderman using a BX50 Olympus microscope (Olympus Optical Co., Ltd., Tokyo, Japan) (Biermann and Linderman 1981).

Data analyses

The Community-Weighted Trait (*CWT*) method was utilized to evaluate the relevant physiological parameters (leaf nitrogen, total chlorophyll concentration, F_v/F_m, and specific leaf area) and growth parameters (height, crown area, and relative growth rate) of the native plant community in this study (Wang et al. 2020). *CWT* was calculated according to the following formula:

$$CWT = \sum_{i=1}^{S} P_i \times X_i$$

where *S* is the total number of species and P_i represents the relative abundance of species i in the native community. $P_i = n_i \div N$, n_i and *N* represent the plant number of species *i* and the number of plants of all species in the native plant community, separately. X_i denotes the average value of morphological and physiological characteristics of species i.

To assess differences in growth and physiological traits among different treatments, we conducted a two-way analysis of variance (*ANOVA*). Prior to the *ANOVA*, we performed variance homogeneity tests for each group of data and transformed unevenly

distributed data. We used Duncan's test with a significance level of $\alpha \leq 0.05$. For each concentration of allelochemicals, we performed linear regressions to determine the relationship between AMF colonization rates and the concentration of root aqueous extracts from *R. typhina*. To evaluate the correlation level of the main traits for the native plant community, we generated Pearson product-moment correlation coefficients among the physiological and growth parameters. We used the IBM SPSS Statistics 25.0 software package (IBM Corporation, Armonk, NY, USA) to conduct all analyses. We created all figures using Origin 2021 (OriginLab Co., Northampton, MA, USA).

To gain an understanding of how growth and physiological parameters of the native plant community were influenced by allelopathy and AMF, and how these parameters were moderated, structural equation modeling (*SEM*) was utilized. A conceptual model, based on theoretical interactions among variables, was established to serve as our formal hypothesis. To test our hypotheses statistically, the variance-covariance matrix implied by the conceptual model was compared with the observed variance-covariance matrix, and maximum likelihood estimation was employed to estimate model coefficients. Model fit was considered acceptable if the χ^2 test was non-significant, the root mean square error of approximation (*RMSEA*) was low (*RMSEA* < 0.01), and the comparative fit index (*CFI*) was high (*CFI* > 0.90). *SEM* was conducted using the *lavaan* and *semPlot* package in R 4.2.3 (R Core Team 2023).

Results

Plant physiology

Physiological parameters such as *LN* and *Chl* were significantly affected by allelopathy ($p < 0.001$, Table 1). In detail, *LN* values were improved by the NRE and MRE treatments, increasing by 32% and 28% respectively compared to the control (Table 1, Fig. 2A), whereas *Chl* was higher in the NRE treatment than the LRE, MRE, and HRE treatments ($p = 0.037$, Table 1, Fig. 2B), which resulted in a 34%, 46%, and 57% advance respectively. Furthermore, the allelopathic effects had negligible effect on F_v/F_m and *SLA* (Table 1, Fig. 2C, D).

The AMF inoculation significantly affected only *LN*, which was depressed within the LRE, NRE, MRE, and HRE treatments ($p < 0.001$, Table 1, Fig. 1A), leading to a 15%, 35%, 28%, and 29% reduction compared to the corresponding NoAMF treatments respectively. According to the results of the two-way ANOVA, inoculating AMF did not significantly affect *Chl* (Table 1), while multiple comparisons showed that *Chl* was reduced by 31% in the NRE treatment compared to the corresponding NoAMF treatments (Fig. 2B). Additionally, all other physiological parameters, including *SLA* and F_v/F_m, were not impacted by AMF (Table 1, Fig. 2C, D).

Most physiological trait values were not influenced by the interaction between allelopathic effects and AMF treatments, such as *Chl*, F_v/F_m, and *SLA* (Table 1, Fig.2B–D). Nevertheless, the interaction between allelopathic effects and AMF had a significant

Table 1. Results of two-way *ANOVA* for the effects of allelopathy, AMF and their interaction on growth and physiological parameters of native plant community. *CA*, crown area; *RGR*, relative growth rate; *TAB*, total aboveground biomass; *LN*, leaf nitrogen; *Chl*, total chlorophyll concentration; *SLA*, specific leaf area. Data are presented with *F* value (*n* = 10). Significant effects are indicated by bold font ($p \leq 0.05$).

	Growth parameters				Physiological parameters			
	CA	**Height**	*RGR*	*TAB*	*LN*	*Chl*	F_v/F_m	*SLA*
Allelopathy	1.274	2.109	**2.567**	2.183	**34.661**	**2.671**	0.257	1.208
AMF	1.011	2.259	1.041	**3.589**	**241.722**	1.921	3.662	0.004
Allelopathy × AMF	0.283	2.288	2.254	**4.716**	**24.352**	1.667	1.172	0.702
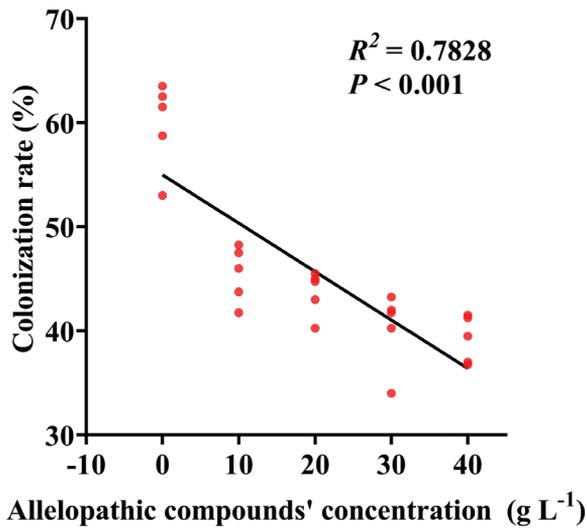
Figure 1. Responses of AMF colonization rate to the different concentrations of allelochemicals (*n* = 5). Five different concentrations of *Rhus typhina* L. root aqueous extracts were used, which were 0, 10, 20, 30, and 40 g L⁻¹, respectively. The proportion of variance is explained by R^2. The regression line was significant at the $p < 0.05$ level.

effect on *LN* of the native plant community (Table 1). The LRE, NRE, and HRE treatments decreased *LN* by 13%, 14%, and 30% respectively, compared to the control ($p <$ 0.001, Fig. 2A).

Plant growth

The two-way ANOVA indicated that only *RGR* was altered by allelopathic effects ($p =$ 0.043, Table 1). Specifically, the LRE treatments raised *RGR* by 25% compared to the control (Table 1, Fig. 3D). The allelopathic effects had no significant effects on plant height, *CA*, and *TAB* (Table 1, Fig. 3A–C). However, according to the multiple comparisons, *TAB* was significantly improved by the HRE treatment, increasing 40% by compared to the control (Table 1, Fig. 3C). Further analysis of four individual species
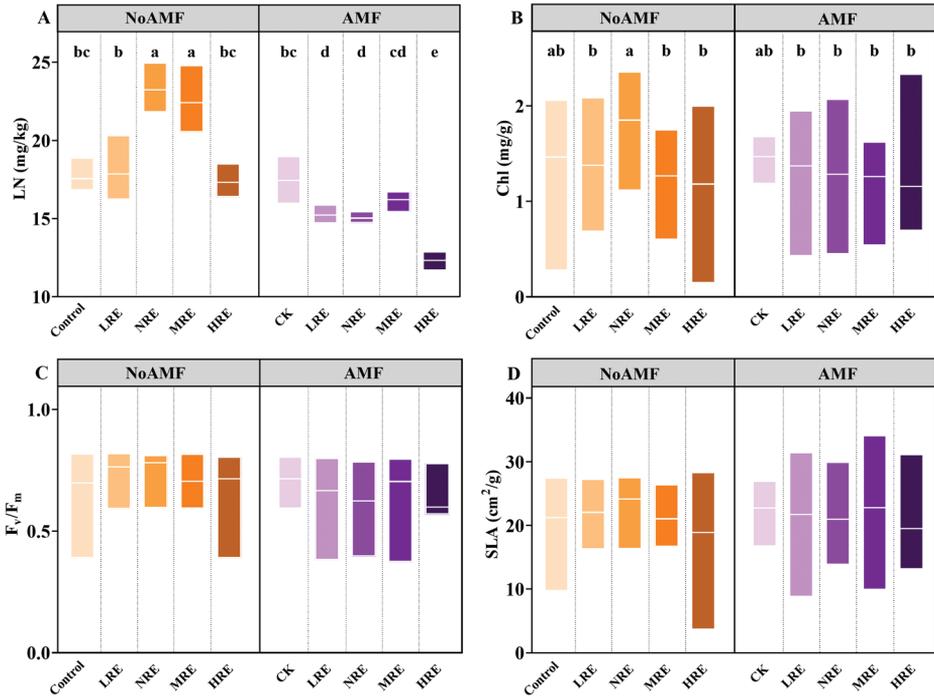
Figure 2. Responses of physiological parameters of native plant community to the allelopathy and its interactions with AMF ($n = 10$). The boxes represent the range of maximum and minimum values, with a bold horizontal line indicating the average value. Colors indicate different AMF treatments (orange, AMF; purple, NoAMF). The physiological parameters include leaf nitrogen (*LN*) (**A**) total chlorophyll concentration (*Chl*) (**B**) F_v/F_m (**C**) and specific leaf area (*SLA*) (**D**). There were five different concentrations of the root aqueous extracts of *Rhus typhina* including 0 g L^{-1} (CK), 10 g L^{-1} (LRE), 20 g L^{-1} (NRE), 30 g L^{-1} (MRE), and 40 g L^{-1} (HRE). The different letters indicate a significant difference ($p \leq 0.05$) with Duncan's test.

found that the HRE treatment significantly improved the aboveground biomass of only *C. album* (Suppl. material 1: fig. S1A).

Inoculation with AMF increased *TAB* by 57% in the LRE treatment and decreased it by 29% in the HRE treatment compared to the NoAMF treatment ($p = 0.006$, Table 1, Fig. 3C). Overall, plant height was not influenced by AMF while the LRE treatment increased plant height by 34% compared to the corresponding NoAMF treatments (Table 1, Fig. 3A). Moreover, AMF treatments did not significantly change all other growth parameters, including *CA* and *RGR* (Table 1, Fig. 3B, D).

The interaction between allelopathic effects and AMF significantly affected on *TAB* and the LRE and NRE treatments increased *TAB* by 48% and 45% respectively, compared to the control ($p = 0.005$, Table 1, Fig. 3C). Meanwhile, the LRE treatment resulted in a 27% advance in plant height compared to the control (Fig. 3A). Nevertheless, the *CA* and *RGR* were not influenced by the interaction between allelopathic effects and AMF treatments (Table 1, Fig. 3B, D).
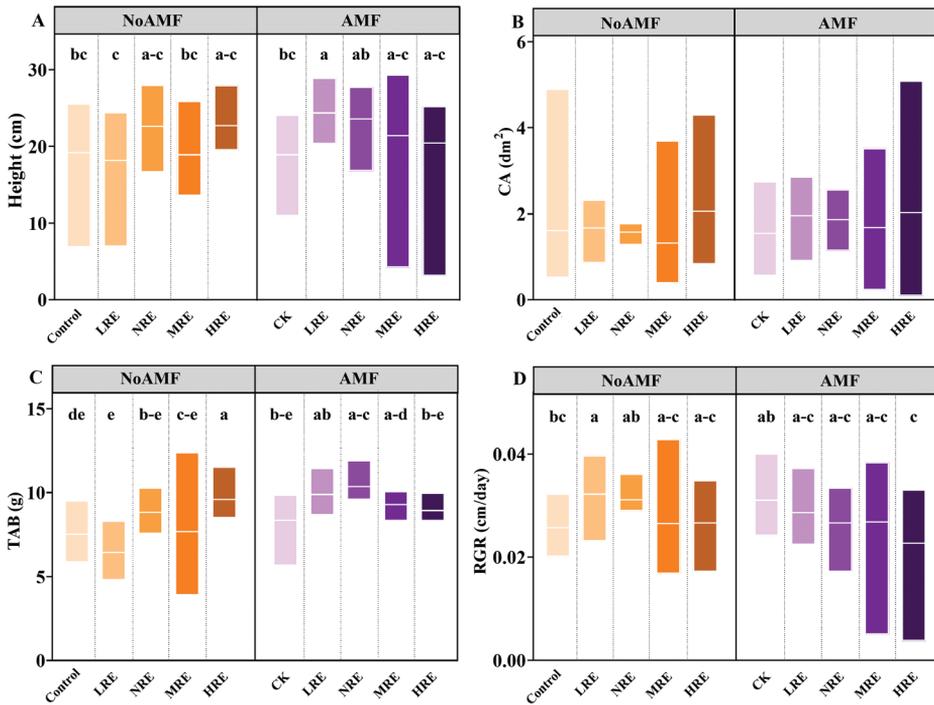
Figure 3. Responses of the growth parameters of native plant community to the allelopathy and its interactions with AMF (*n* = 10). The boxes represent the range of maximum and minimum values, with a bold horizontal line indicating the average value. Colors indicate different AMF treatments (orange, AMF; purple, without AMF). The growth parameters include height (**A**) crown area (*CA*) (**B**) total aboveground biomass (*TAB*) (**C**) and relative growth rate (*RGR*) (**D**). There were five different concentrations of the root aqueous extracts of *Rhus typhina* including 0 g L^{-1} (CK), 10 g L^{-1} (LRE), 20 g L^{-1} (NRE), 30 g L^{-1} (MRE), and 40 g L^{-1} (HRE). The different letters indicate a significant difference (*p* ≤ 0.05) with Duncan's test.

Trait correlation

We examined 28 pairs of growth and physiological traits in the native community using a Pearson correlation test. Nine pairs for the NoAMF treatments and 10 pairs for the AMF treatments were significantly correlated at *p* ≤ 0.05 (Fig. 4). The six correlated pairs of the NoAMF treatments were also correlated in the AMF treatments. The different three correlated pairs of the NoAMF treatments were *RGR* and *SLA*, *RGR* and *Chl*, *RGR* and F_v/F_m, which were positively correlated (Fig. 4). The different four correlated pairs of the AMF treatments were *CA* and *Chl*, *CA* and F_v/F_m, which were negatively correlated, while *LN* and F_v/F_m, *RGR* and *TAB* were positively correlated (Fig. 4).

The *SEM*s were well-ftted to the data (χ^2 = 4.507, *df* = 11, *P* = 0.953, *CFI* = 1.000, *RMSEA* = 0.000). Allelopathy had direct negative associations with relative growth rate, total chlorophyll concentration, specific leaf area, leaf nitrogen and F_v/F_m but positive associations with height, crown area and total aboveground biomass (Fig. 5). AMF had a negative direct association with all plant traits except height and total
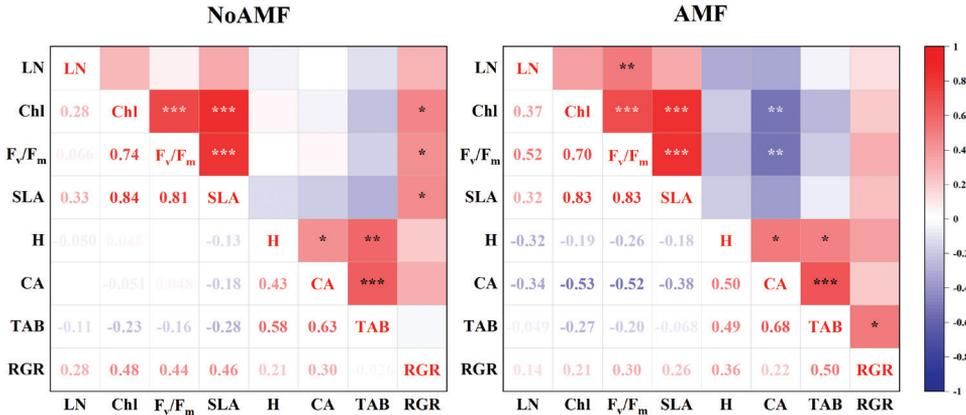
Figure 4. Matrix of Pearson product-moment correlation coefficients for the growth and physiological traits of the native community across different AMF treatments ($n = 10$). Traits include leaf nitrogen (*LN*), total chlorophyll concentration (*Chl*), F_v/F_m, specific leaf area (*SLA*), plant height (*H*), crown area (*CA*), total aboveground biomass (*TAB*), and relative growth rate (*RGR*). Significant correlations are denoted by bold font and asterisks: *** $P \le 0.001$, ** $P \le 0.01$, and * $P \le 0.05$.
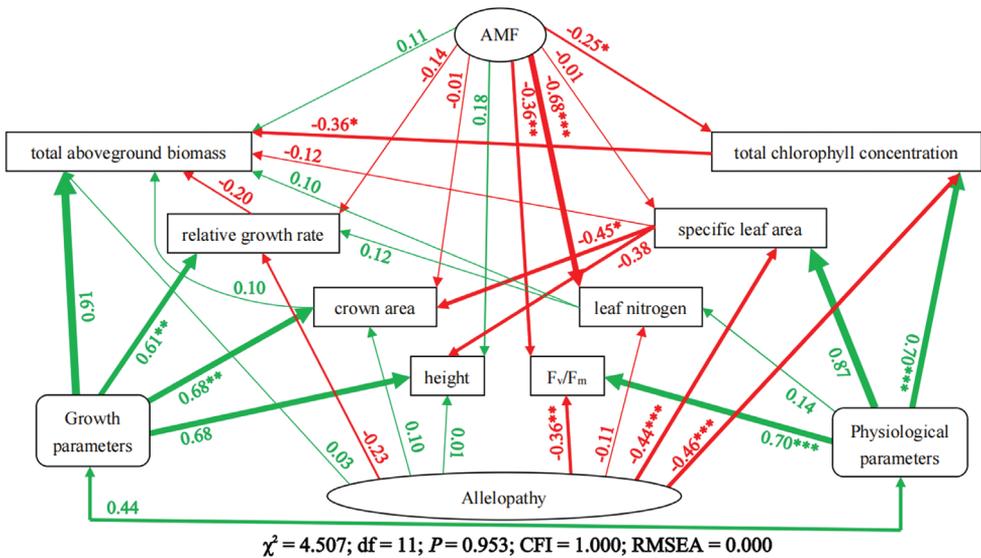
Figure 5. The structural equation models relating the growth and physiological parameters of the native plant community. Green lines indicate positive relationships while red lines indicate negative relationships. Line thickness depicts the magnitude of path coefficients. Significant effects are indicated by asterisks: *** $P \le 0.001$, ** $P \le 0.01$, and * $P \le 0.05$.

aboveground biomass (Fig. 5). Although leaf nitrogen had a positive association with relative growth rate and total aboveground biomass, the association was not statistically signifcant ($p = 0.455$; $p = 0.470$, Fig. 5). Further, AMF had a negative direct association with all plant traits except height and total aboveground biomass (Fig. 5). Total

aboveground biomass was also positively linked to relative growth rate, total chlorophyll concentration and specific leaf area, but negatively related to crown area and leaf nitrogen. Also, growth parameters had a strong and positive relationship with height, crown area, relative growth rate and total aboveground biomass. In turn, physiological parameters had direct positive associations with total chlorophyll concentration, specific leaf area, leaf nitrogen and F_v/F_m (Fig. 5). Finally, growth parameters had a direct association with physiological parameters (Fig. 5).

Mycorrhizal colonization

The colonization rates of mycorrhizal in the native plant community were negatively correlated with the concentrations of root aqueous extracts from *R. typhina* ($p < 0.001$; $R^2 = 0.7828$, Fig. 1). The AMF colonization rates in the LRE, NRE, MRE, and HRE treatments were significantly reduced by 25%, 27%, 33%, and 35% respectively compared to the control (Fig. 1).

Discussion

The allelopathy and its interactions with AMF affected the physiological and growth parameters of the native plant community. In general, the low concentration of allelochemicals promoted *RGR* and *LN* in the native plant community, while the present of allelochemicals altered AMF effects on the native community.

Responses of native plant community to allelopathy

Allelopathy, as a plants' defense mechanism, could alter the physical and chemical properties of the soil conditions (Lorenzo et al. 2013). The normal concentration of allelochemicals can produce stress on the growth of native plants. In response to the stress, the native plant community allocated or produced more *LN* and *Chl* to improve the degree of leaf photosynthetic capacity and organic synthesis rate. This observation was consistent with previous studies that compared the photosynthetic properties of native plant species in plots invaded and non-invaded by alien species (Wang et al. 2020). As reported, the ability of sunlight acquisition and the degree of leaf photosynthetic capacity of native plant species were prominently improved under invasion by *Solidago canadensis* and *Erigeron annuus* (Wang et al. 2020). In our experiments, when the concentration of allelopathic compounds was above a certain threshold value, the stress no longer influenced the native plant community.

Allelochemicals have long been considered as a mechanism by which invasive species eliminate natives (Bais et al. 2003; Gruntman et al. 2016; Hassan and Mohamed 2020). Nevertheless, few studies have found that allelochemicals of invasive plants have neutral or positive effects on native plants (Gross 2003; Zhang et al. 2020). Moreover, it is important to note that the source heterogeneity of allelochemicals can affect the

allelopathic effects (Zhang et al. 2020). In this study, we investigated the allelopathic effects of root aqueous extracts of *R. typhina* on native plant communities. In conclusion, the low concentrations of allelochemicals promoted *RGR*, whereas the medium and normal concentrations of allelochemicals fostered *LN* in native plant communities, contradicting our first hypothesis. In another study, the leaf aqueous extracts of *R. typhina* decreased all seed germination indices and radicle length of the native plant *Lactuca sativa* L. (Xu et al. 2023). Although disturbances from competition among plants were excluded when using the extracts to explore the allelopathic effects of invasive plants, the different simulating ways might make the conclusions inconsistent (Callaway et al. 2008; Zhang et al. 2020). Since the allelopathic effects of *R. typhina* were simulated only by the root aqueous extracts in our study, it is reasonable that our findings differed from those of experiments involving individual plants of *R. typhina* or using other simulations.

Additionally, we found that the total aboveground biomass of the native plant community was significantly higher in the HRE treatment than in the other extract treatments. We analyzed the allelopathic effects on the aboveground biomass of four species (*C. album*, *A. truncatum*, *R. chinensis*, and *V. negundo*) that constituted the native plant community separately. Only the aboveground biomass of *C. album* increased significantly with the HRE treatment, while the aboveground biomass of the remaining three plants remained unchanged statistically. A previous study suggests that under the presence of allelopathic compounds, distinct plant species exhibited varying germination and growth rates (McEwan et al. 2010). Therefore, we speculate that these results might be due to a superior defense of *C. album* against allelochemicals.

Responses of the native plant community to AMF and allelopathy

AMF can facilitate host plants growth and provide them with competitive advantages (Antunes et al. 2008; Delavaux et al. 2017; Adomako et al. 2019). However, our results suggest that AMF induced *LN* decline of the native community under the influence of allelopathic effects of *R. typhina*. The presence of allelopathic effects was considered as an environmental stress. In response to this stress, the degree of leaf photosynthetic capacity of the native plant community was reduced when AMF existed. Furthermore, under allelopathic effects alone on the native plant community, the response of *LN* was inconsistent with the results obtained from the combined effects of allelopathy and AMF. The Pearson product-moment correlation coefficients among the growth and physiological traits indicated that *CA* and F_v/F_m had a negative correlation, while *LN* and F_v/F_m, *CA* and *TAB* positively correlated. In the presence of AMF, low concentrations of allelochemicals hindered *LN* but promoted *TAB* in the native plant community. This suggests that native plants prioritize absorbing a greater amount of resources from the soil to resist environmental stress rather than enhancing the degree of leaf photosynthetic capacity in response to mild allelopathy. Based on the resource optimization hypothesis (Agren and Franklin 2003), we speculate that the host plant allocates more available resources to promote the growth of belowground parts. The

inoculated AMF can combine with the host plant roots to generate mycorrhizal symbionts that can obtain additional water and nutrients from the soil, contributing to the growth and development of the native plant community (Agren and Franklin 2003).

While the significance of AMF alone in soil has long been recognized in relation to plant invasions, few studies have examined the influence of AMF on allelopathic effects in the context of communities (Pellegrino et al. 2015; Bennett and Klironomos 2019). Our results showed that the *TAB* was differently affected by the AMF treatment among the growth parameters treated with different strengths of the allelopathic effects. Specifically, AMF treatments significantly promoted *TAB* of the native plant community in the LRE treatment. Although few empirical experiments have investigated the effects of soil microbes on plant allelopathy, available experiments have found that soil microbes can counteract allelopathy by degrading the secondary metabolites secreted by the plants, which could reduce or completely eliminate allelopathy (Saia and Jansa 2022). This function might have mitigated the negative effects of allelopathy on AMF.

The high concentration of allelochemicals transformed the promotive effect of AMF on *TAB* into the inhibitory effect. Our results suggest that the high concentration of allelochemicals had a neutral impact on the native plant community. Therefore, this phenomenon can be attributed to two plausible reasons: (1) the allelopathic effects from invasive plants can influence patterns of soil nutrient cycling and the soil nutrient environment, altering the effect of AMF on the host (Zhang et al. 2017; de Vries et al. 2020); (2) allelopathy can decline the AMF colonization rates, influencing the mycorrhizal beneficial symbiosis and reducing the uptake and utilization of water and nutrients from the soil by native plants (Zhang et al. 2017; de Vries et al. 2020). Invasive and native hosts have different preferences for AMF and high concentrations of allelochemicals from *R. typhina* with strong toxicity may filter the AMF in the soil and accumulate beneficial fungal species to promote their own growth (Antunes et al. 2008; Inderjit and van der Putten 2010; Inderjit et al. 2021), which could also explain the reduction of AMF colonization rates. The filtering could result in a reduction of mycorrhizal communities helpful for the growth of native plant communities (Antunes et al. 2008).

Conclusion

As biological invasions continue to worsen, it is increasingly necessary to explore the mechanisms behind successful species invasions (Zhang et al. 2020). In this study, we conducted experiments and found that the growth and physiological parameters of the native plant community were affected by allelopathy and its interactions with AMF. Our results indicated that the *RGR* and *LN* of the native plant community were increased by the low concentration of allelochemicals, promoting leaf photosynthetic capacity and organic synthesis rate. Meanwhile, due to allelopathic stress from exotic plants, AMF inhibited *LN* in the native community. The high concentration of allelochemicals turned the positive effect of AMF on the native plant community into a negative effect, which was probably caused by a decrease in the colonization rates

of AMF or by affecting soil physicochemical properties and mycorrhizal community composition. Our findings offer additional theoretical support for managing the invasion of exotic plants in temperate China. For the management and control of invasive plants, we propose planting native plants tolerant to the allelopathic effects of *R. typhina* around invaded areas to establish native communities. This measure may reduce the impact of *R. typhina* on native communities and slow down the rate of invasion. Nevertheless, further experiments are necessary to verify their feasibility.

Acknowledgements

References

Adomako MO, Ning L, Tang M, Du DL, van Kleunen M, Yu FH (2019) Diversity- and density-mediated allelopathic effects of resident plant communities on invasion by an exotic plant. Plant and Soil 440(1–2): 581–592. https://doi.org/10.1007/s11104-019-04123-9

Agren GI, Franklin O (2003) Root: Shoot ratios, optimization and nitrogen productivity. Annals of Botany 92(6): 795–800. https://doi.org/10.1093/aob/mcg203

Antunes PM, Miller J, Carvalho LM, Klironomos JN, Newman JA (2008) Even after death the endophytic fungus of *Schedonorus phoenixreduces* the arbuscular mycorrhizas of other plants. Functional Ecology 22(5): 912–918. https://doi.org/10.1111/j.1365-2435.2008.01432.x

Bais HP, Vepachedu R, Gilroy S, Callaway RM, Vivanco JM (2003) Allelopathy and exotic plant invasion: From molecules and genes to species interactions. Science 301(5638): 1377–1380. https://doi.org/10.1126/science.1083245

Bennett JA, Klironomos J (2019) Mechanisms of plant-soil feedback: Interactions among biotic and abiotic drivers. The New Phytologist 222(1): 91–96. https://doi.org/10.1111/nph.15603

Biermann B, Linderman RG (1981) Quantifying vesicular-arbuscular Mycorrhizae: A proposed method towards standardization. The New Phytologist 87(1): 63–67. https://doi.org/10.1111/j.1469-8137.1981.tb01690.x

Callaway RM, Ridenour WM (2004) Novel weapons: Invasive success and the evolution of increased competitive ability. Frontiers in Ecology and the Environment 2(8): 436–443. https://doi.org/10.1890/1540-9295(2004)002[0436:NWISAT]2.0.CO;2

Callaway RM, Cipollini D, Barto K, Thelen GC, Hallett SG, Prati D, Stinson K, Klironomos J (2008) Novel weapons: Invasive plant suppresses fungal mutualists in America but not in its native Europe. Ecology 89(4): 1043–1055. https://doi.org/10.1890/07-0370.1

Callaway RM, Bedmar EJ, Reinhart KO, Silvan CG, Klironomos J (2011) Effects of soil biota from different ranges on *Robinia* invasion: Acquiring mutualists and escaping pathogens. Ecology 92(5): 1027–1035. https://doi.org/10.1890/10-0089.1

Chen E, Liao H, Chen B, Peng S (2020) Arbuscular mycorrhizal fungi are a double-edged sword in plant invasion controlled by phosphorus concentration. The New Phytologist 226(2): 295–300. https://doi.org/10.1111/nph.16359

Cheng F, Cheng Z (2015) Research Progress on the use of Plant Allelopathy in Agriculture and the Physiological and Ecological Mechanisms of Allelopathy. Frontiers in Plant Science 6: 1020. https://doi.org/10.3389/fpls.2015.01020

de Vries FT, Griffiths RI, Knight CG, Nicolitch O, Williams A (2020) Harnessing rhizosphere microbiomes fordrought-resilient crop production. Science 368(6488): 270–274. https://doi.org/10.1126/science.aaz5192

Delavaux CS, Smith-Ramesh LM, Kuebbing SE (2017) Beyond nutrients: A meta-analysis of the diverse effects of arbuscular mycorrhizal fungi on plants and soils. Ecology 98(8): 2111–2119. https://doi.org/10.1002/ecy.1892

Djurdjević L, Gajić G, Kostić O, Jarić S, Pavlović M, Mitrović M, Pavlović P (2012) Seasonal dynamics of allelopathically significant phenolic compounds in globally successful invader *Conyza canadensis* L. plants and associated sandy soil. Flora – Morphology, Distribution. Flora (Jena) 207(11): 812–820. https://doi.org/10.1016/j.flora.2012.09.006

Dong LJ, Ma LN, He WM (2021) Arbuscular mycorrhizal fungi help explain invasion success of *Solidago canadensis*. Applied Soil Ecology 157: 103763. https://doi.org/10.1016/j.apsoil.2020.103763

Gross EM (2003) Allelopathy of aquatic autotrophs. Critical Reviews in Plant Sciences 22(3–4): 313–339. https://doi.org/10.1080/713610859

Gruntman M, Zieger S, Tielbörger K (2016) Invasive success and the evolution of enhanced weaponry. Oikos 125(1): 59–65. https://doi.org/10.1111/oik.02109

Guo X, Hu Y, Ma J-Y, Wang H, Wang K-L, Wang T, Jiang S-Y, Jiao JB, Sun Y-K, Jiang X-L, Li M-Y (2023a) Nitrogen Deposition Effects on Invasive and Native Plant Competition: Implications for Future Invasions. Ecotoxicology and Environmental Safety 259: 115029. https://doi.org/10.1016/j.ecoenv.2023.115029

Guo X, Ma J-Y, Liu L-L, Li M-Y, Wang H, Sun Y-K, Wang T, Wang K-L, Meyerson LA (2023b) Effects of salt stress on interspecific competition between an invasive alien plant *Oenothera biennis* and three native species. Frontiers in Plant Science 14: 1144511. https://doi.org/10.3389/fpls.2023.1144511

Hassan MO, Mohamed HY (2020) Allelopathic interference of the exotic naturalized *Paspalum dilatatum* Poir. threatens diversity of native plants in urban gardens. Flora (Jena) 266: 151593. https://doi.org/10.1016/j.flora.2020.151593

Hawkes CV, Belnap J, D'Antonio C, Firestone MK (2006) Arbuscular Mycorrhizal Assemblages in Native Plant Roots Change in the Presence of Invasive Exotic Grasses. Plant and Soil 281(1–2): 369–380. https://doi.org/10.1007/s11104-005-4826-3

Hierro JL, Callaway RM (2003) Allelopathy and exotic plant invasion. Plant and Soil 256(1): 29–39. https://doi.org/10.1023/A:1026208327014

Hu Y, Xu Z-W, Li M-Y, Croy JR, Zhang Z-Y, Li H-M, Guo W-H, Jiang X-L, Lu H-C, Guo X (2022) Increasing soil heterogeneity strengthens the inhibition of a native woody plant by an invasive congener. Plant and Soil 481(1–2): 677–690. https://doi.org/10.1007/s11104-022-05666-0

Inderjit SD, Kaur H, Kalisz S, Bezemer TM (2021) Novel chemicals engender myriad invasion mechanisms. The New Phytologist 232(3): 1184–1200. https://doi.org/10.1111/nph.17685

Inderjit SD, van der Putten WH (2010) Impacts of soil microbial communities on exotic plant invasions. Trends in Ecology and Evolution 25: 512–519. https://doi.org/10.1016/j.tree.2010.06.006

Inderjit SD, Wardle DA, Karban R, Callaway RM (2011) The ecosystem and evolutionary contexts of allelopathy. Trends in Ecology and Evolution 26: 655–662. https://doi.org/10.1016/j.tree.2011.08.003

Kardol P, Bezemer TM, van der Putten WH (2006) Temporal variation in plant-soil feedback controls succession. Ecology Letters 9(9): 1080–1088. https://doi.org/10.1111/j.1461-0248.2006.00953.x

Li Y-P, Feng Y-L, Chen Y-J, Tian Y-H (2015) Soil microbes alleviate allelopathy of invasive plants. Science Bulletin 60(12): 1083–1091. https://doi.org/10.1007/s11434-015-0819-7

Li S-P, Jia P, Fan S-Y, Wu Y, Liu X, Meng Y, Li Y, Shu W-S, Li J-T, Jiang L (2022) Functional traits explain the consistent resistance of biodiversity to plant invasion under nitrogen enrichment. Ecology Letters 25(4): 778–789. https://doi.org/10.1111/ele.13951

Liu Y, Kleunen M, Cornelissen H (2017) Responses of common and rare aliens and natives to nutrient availability and fluctuations. Journal of Ecology 105(4): 1111–1122. https://doi.org/10.1111/1365-2745.12733

Lorenzo P, Pereira CS, Rodríguez-Echeverría S (2013) Differential impact on soil microbes of allelopathic compounds released by the invasive *Acacia dealbata* Link. Soil Biology & Biochemistry 57: 156–163. https://doi.org/10.1016/j.soilbio.2012.08.018

Ma J (2020) Alien invasive flora of China. Shanghai Jiao Tong University Press, Shanghai, China.

McEwan RW, Arthur-Paratley LG, Rieske LK, Arthur MA (2010) A multi-assay comparison of seed germination inhibition by *Lonicera maackii* and co-occurring native shrubs. Flora – Morphology, Distribution. Flora (Jena) 205(7): 475–483. https://doi.org/10.1016/j.flora.2009.12.031

Pellegrino E, Öpik M, Bonari E, Ercoli L (2015) Responses of wheat to arbuscular mycorrhizal fungi: A meta-analysis of field studies from 1975 to 2013. Soil Biology & Biochemistry 84: 210–217. https://doi.org/10.1016/j.soilbio.2015.02.020

Qin TJ, Zhou J, Sun Y, Muller-Scharer H, Luo FL, Dong BC, Li HL, Yu FH (2020) Phylogenetic diversity is a better predictor of wetland community resistance to Alternanthera philoxeroides invasion than species richness. Plant Biology 22(4): 591–599. https://doi.org/10.1111/plb.13101

Saia S, Jansa J (2022) Editorial: Arbuscular Mycorrhizal Fungi: The Bridge Between Plants, Soils, and Humans. Frontiers in Plant Science 13: 875958. https://doi.org/10.3389/fpls.2022.875958

Sikes BA, Cottenie K, Klironomos JN (2009) Plant and fungal identity determines pathogen protection of plant roots by arbuscular mycorrhizas. Journal of Ecology 97(6): 1274–1280. https://doi.org/10.1111/j.1365-2745.2009.01557.x

Vogelsang KM, Bever JD (2009) Mycorrhizal densities decline in association with non-native plants and contribute to plant invasion. Ecology 90(2): 399–407. https://doi.org/10.1890/07-2144.1

Wang C, Wei M, Wang S, Wu B, Cheng H (2020) *Erigeron annuus* (L.) Pers. and *Solidago canadensis* L. antagonistically affect community stability and community invasibility under the co-invasion condition. The Science of the Total Environment 716: 137128. https://doi.org/10.1016/j.scitotenv.2020.137128

Wang J, Li SP, Ge Y, Wang XY, Gao S, Chen T, Yu FH (2022a) Darwin's naturalization conundrum reconciled by changes of species interactions. Ecology 104(1): e3850. https://doi.org/10.1002/ecy.3850

Wang Q, Li MY, Eller F, Luo YJ, Nong YL, Xing LJ, Xu ZW, Li HM, Lu HC, Guo X (2022b) Trait value and phenotypic integration contribute to the response of exotic *Rhus typhina* to heterogeneous nitrogen deposition: A comparison with native *Rhus chinensis*. The Science of the Total Environment 844: 157199. https://doi.org/10.1016/j.scitotenv.2022.157199

Weremijewicz J, Sternberg LSLOR, Janos DP (2016) Common mycorrhizal networks amplify competition by preferential mineral nutrient allocation to large host plants. The New Phytologist 212(2): 461–471. https://doi.org/10.1111/nph.14041

Xing L-J, Li M-Y, Jiang S-Y, Li W, Guo S-X, Li H-M, Guo X (2022) Comparison between the exotic *Coreopsis grandiflora* and native *Dendranthema indicum* across variable nitrogen deposition conditions. Acta Physiologiae Plantarum 44(8): 82. https://doi.org/10.1007/s11738-022-03417-3

Xu Z, Zhong S, Yu Y, Wang Y, Cheng H, Du D, Wang C (2023) *Rhus typhina* L. triggered greater allelopathic effects than *Koelreuteria paniculata* Laxm under ammonium fertilization. Scientia Horticulturae 309: 111703. https://doi.org/10.1016/j.scienta.2022.111703

Yuan L, Li J-M, Yu F-H, Oduor AMO, van Kleunen M (2021) Allelopathic and competitive interactions between native and alien plants. Biological Invasions 23(10): 3077–3090. https://doi.org/10.1007/s10530-021-02565-w

Yuan L, Li J, van Kleunen M (2022) Competition induces negative conspecific allelopathic effects on seedling recruitment. Annals of Botany 130(6): 917–926. https://doi.org/10.1093/aob/mcac127

Zhang S, Zhu W, Wang B, Tang J, Chen X (2011) Secondary metabolites from the invasive *Solidago canadensis* L. accumulation in soil and contribution to inhibition of soil pathogen *Pythium ultimum*. Applied Soil Ecology 48(3): 280–286. https://doi.org/10.1016/j.apsoil.2011.04.011

Zhang F-J, Li Q, Chen F-X, Xu H-Y, Inderjit, Wan F-H (2017) Arbuscular mycorrhizal fungi facilitate growth and competitive ability of an exotic species *Flaveria bidentis*. Soil Biology & Biochemistry 115: 275–284. https://doi.org/10.1016/j.soilbio.2017.08.019

Zhang P, Li B, Wu J, Hu S (2019) Invasive plants differentially affect soil biota through litter and rhizosphere pathways: A meta-analysis. Ecology Letters 22(1): 200–210. https://doi.org/10.1111/ele.13181

Zhang Z, Liu Y, Yuan L, Weber E, van Kleunen M, Gurevitch J (2020) Effect of allelopathy on plant performance: A meta-analysis. Ecology Letters 24(2): 348–362. https://doi.org/10.1111/ele.13627

Supplementary material 1

Responses of the aboveground biomass of native plant species to the allelopathy ($n = 10$)

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Data type: tif

Explanation note: The boxes represent the range of maximum and minimum values, with a bold horizontal line indicating the average value. The plant species include *Chenopodium album* L. (A), *Vitex negundo* L. (B), *Rhus chinensis* Mill. (C), and *Acer truncatum* Bunge (D). There were five different concentrations of the root aqueous extracts of *R. typhina* including 0 g L^{-1} (CK), 10 g^{-1} (LRE), 20 g L^{-1} (NRE), 30 g L^{-1} (MRE), and 40 g L^{-1} (HRE). The asterisk (*) indicates a significant difference ($p \leq 0.05$) with Duncan's test.

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