

Allelopathic effects of *Robinia pseudoacacia* and *Quercus acutissima* on the exotic plant *Rhus typhina* in Shandong Peninsula

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ABSTRACT

We compared the allelopathic effects of *Robinia pseudoacacia* and *Quercus acutissima* on the exotic plant *Rhus typhina* in Shandong Peninsula, China. We identified the phenolic acids in *R. pseudoacacia* and *Q. acutissima* soils to explore the allelopathic mechanism of community resistance to invasion. The Petri dish filter paper bioassay was done to test the allelopathic effects of aqueous litter leachates of *R. pseudoacacia* and *Q. acutissima*. High-performance liquid chromatography (HPLC) was used to determine the composition and concentrations of phenolic acids in the *R. pseudoacacia* and *Q. acutissima* soil. Only *Q. acutissima* litter leachates significantly inhibited the seed germination and seedling growth of *Lactuca sativa*. *Q. acutissima* litter leachates at high concentrations, significantly inhibited the seed germination and seedling growth of *R. typhina*. While, *R. pseudoacacia* litter leachates had no inhibitory effect on *L. sativa*, but reduced the germination speed index of *R. typhina*. HPLC analysis showed that the phenolic acids concentration (except salicylic acid) in the *Q. acutissima* soil was higher than in *R. pseudoacacia* soil. It may be hypothesized that the native species *Q. acutissima* produced more allelochemicals than the introduced species *R. pseudoacacia* (American origin), thereby inhibiting the growth and development of exotic *R. typhina* plant and improving the invasion resistance of plant community. Therefore, we could use some native dominant species such as *Q. acutissima*, for local afforestation to control invasion of exotic plants.

Key words: Allelochemicals, allelopathy, germination, introduced spp., invasion resistance, leachates, native spp., phenolics acids, *Quercus acutissima*, *Rhus typhina*, *Robinia pseudoacacia*, seedling growth.

INTRODUCTION

Natural resources are limited, and the survival of plants under limited resources depends on the competitive efficiency of species in adverse environments (23). Allelopathy is the most common pathway in plant-plant competition, affecting numerous ecosystem processes, including community composition and function (21,25). Allelopathy also plays an important role in biological invasion (3,6,35). One of the reasons for the successful invasion of exotic species is that they exhibit strong allelopathic effects on native species (4,6). Allelochemicals released by invasive plants are novel and toxic to native species, and native species cannot adapt to this change in a short period of time due to the lack of co-evolution (2,31). They gradually develop a disadvantage in resource competition; the exotic species can successfully invade and reduce the biodiversity. Alternatively, many native

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plants, especially dominant trees in forests, also produce allelochemicals (6,26,29,32). However, the allelopathic effects of native plants on exotic species have been largely ignored (9,17,26,27). As invasive plants can secrete allelochemicals to help them successfully invade and some dominant species in invaded areas secrete allelochemicals to help them resist the invasion.

Allelochemicals are plant secondary metabolites that influence cell micro- and ultra-structure, cell division and elongation, membrane permeability, oxidative and antioxidant systems, growth regulation systems, respiration, enzyme synthesis and metabolism, photosynthesis, mineral ion uptake, and protein and nucleic acid synthesis (7). Under natural conditions, plants release allelochemicals into the environment through root secretion, stem and leaf leaching and volatilization, and leaf litter decomposition (30). Most of these allelochemicals eventually returns to the soil and affects the surrounding plants using the soil as medium (20). Phenolic acids are important allelochemicals in the soil (19,26). They not only affect the movement of nutrients in the ecosystem but also combine with Al, Fe, and Mn ions, and organic nitrogen and phosphorus in the soil to affect the rate of nutrients returning to the soil (18). These are also correlated with the distribution and growth of rhizosphere microorganisms (1). Microorganisms use the phenolic acids as carbon source and for energy and the effects of phenolic acids on plants can be increased or reduced by the microorganisms (22). However it is unclear, whether there is higher contents of phenolic acids in the rhizosphere soil of some native plants that resist invasive plants.

In this study, we examined the allelopathic effects of *Robinia pseudoacacia* L. (*R. pseudoacacia*) and *Quercus acutissima* Carruth. (*Q. acutissima*), two common dominant species in the hilly habitats of Shandong Peninsula. *Lactuca sativa* is a common vegetable, which highly sensitive to allelochemicals, and *Rhus typhina* (*R. typhina*), an exotic invasive plant, were selected as target species. The Petri dish filter paper bioassay was done to find the allelopathic effects. In addition, high-performance liquid chromatography (HPLC) was used to determine the composition and concentrations of phenolic acids in the soil of *R. pseudoacacia* and *Q. acutissima* forests. The research will deepen our understanding of the mechanisms underlying the community resistance to invasion and provide a scientific guidance to prevent and control the exotic plants invasion.

METHODS AND MATERIALS

I. Study Site

Zhenshan Mountain (Yantai, Shandong) is located along the coast of Yellow Sea, Northern Shandong Peninsula, China. It has continental monsoon climate (mean annual rainfall: 740.3 mm) and daily mean annual temperature: 12°C. The mean height above sea level of Zhenshan Mountain (N37°30'-37°32', E121°19'-121°21') is 230-250 m. Due to frequent human activities, the original vegetation has been destroyed, and the existing vegetation mainly comprises of secondary types. In 2005, *R. typhina* was planted on the roadsides of Zhenshan Mountain for ornamental purposes. Since then, *R. typhina* has rapidly

spread and invaded the surrounding habitats, even forming a single dominant species in some habitats (16).

R. pseudoacacia and *Q. acutissima* are the most common dominant broad-leaf tree species on Zhenshan Mountain (33). *R. pseudoacacia* (Fabaceae family) is native to North America and is widely distributed in Europe, Turkey, China, South Africa, Argentina, Chile and Australian coastal regions (12). It is used for windbreaks, erosion control and the reclamation of disturbed sites (10). *Q. acutissima* (Fagaceae family) is dominant native broadleaf tree species in the deciduous forests of Northern China (24). It prefers the moist, well-drained, acidic soils of moderate fertility, but adapts well to relatively poor dry soils of neutral or slightly alkaline pH (11). The *Quercus* species are used for fuel or bioenergy, charcoal, timber, bed logs to grow mushrooms and raw material for tannin extraction (11).

II. Materials

The fresh falling litter of *R. pseudoacacia* and *Q. acutissima* was collected from Zhenshan Mountain and air-dried on craft paper naturally. Plant samples (25 g) were weighed and immersed in 500 mL distilled water at room temperature for 24 h. The leachate was filtered through filter paper and used as the stock solution ($0.05 \text{ g}\cdot\text{mL}^{-1}$). Two concentrations ($0.05 \text{ g}\cdot\text{mL}^{-1}$ and $0.01 \text{ g}\cdot\text{mL}^{-1}$) of aqueous leachates were prepared from the stock solution using distilled water. All the solutions, were stored in refrigerator until use.

L. sativa seeds without dormancy were bought from a seed company. *R. typhina* seeds were collected from Zhenshan Mountain and their dormancy was broken before use. The seeds of *R. typhina* were kept in hot water ($70\text{-}90^\circ\text{C}$) for 0.5 h. The seeds were naturally cooled and immersed in water for 24 h (32). All seeds were disinfected with 0.3% potassium permanganate for 2 h and washed with distilled water.

III. Bioassays

Laboratory bioassays were done to determine the allelopathic effects of aqueous litter extracts of *Q. acutissima* and *R. pseudoacacia* on the seed germination and seedling growth of *L. sativa* and *R. typhina*. The uniform size seeds were spread on 9-cm dia Petri dishes lined with 2 layers of filter paper. Twenty seeds were sown per Petri dish and 5 mL leachates were added. Five mL distilled water was added to control group. The experiment had five replications. The Petri dishes were kept in an artificial climate incubator [light 12 h (28°C)/dark 12 h (25°C) and relative humidity (65%)]. During the period of the laboratory bioassay, equal amount of extract was added to each Petri dish as needed to prevent drying of seeds or seedlings. The number of germinated seeds were recorded at 24 h intervals till 10-days. A seed was considered to have germinated when $> 2 \text{ mm}$ long radicle broke through the seed coat.

The allelopathic effects on the receptor seeds were expressed by three indices: Seed germination rate (SGR), Germination speed index (GSI) and Root length (RL).

$$\text{SGR} = (\text{Number of shoots at the end of germination}) / 20 \times 100\%$$

$\text{GSI} = 2 \times \{nX_1 + (n-1)X_2 + (n-2)X_3 + \dots + X_n\}$ (X : Number of germinations every 24 h; X_1 : Germination number at 24 h; X_2 : Germination number at 48 h, and so on in a similar fashion, n is the total number of days)

$$\text{RL} = (\text{RL}_1 + \text{RL}_2 + \dots + \text{RL}_n) / n \text{ (RL: Root length; n as the number of germinations)}$$

IV. Detection of phenolic acids in *R. pseudoacacia* and *Q. acutissima* soil

Soil samples were collected from a *R. pseudoacacia* forest and *Q. acutissima* forest during April 2018. The distance between the two plant communities was > 100 m. The two communities had similar site conditions, including slope aspect and elevation. In addition, soil samples were collected from an adjacent non-forested land where only grass grew were used as control. Soil samples were collected from the top 10 cm soil layer. Every 6 sampling points were mixed into one soil sample and there were total of 3 soil samples for each plant community. The soils were sieved through a 2-mm sieve. All soils were stored in refrigerator until use.

The extraction method was modification of Hartley and Buchan (15) method. Briefly, 25 g fresh soil was added to 25 mL 1 mol·L⁻¹ NaOH solution. It was incubated overnight and agitated for 30 min with shaker. The soil suspension was centrifuged and the supernatant was filtered through filter paper. It was acidified to pH 2.5 with 12 mol·L⁻¹ HCL. After 2 h, the humic acid was removed by centrifugation, and the supernatant was filtered through a 0.22- μ m filter. The final extracts were analysed using high-performance liquid chromatography, and the results were converted to dry weight of soil.

Liquid chromatography was done in Waters HPLC system (Waters, e2695, USA) with a diode array detector using a Uranus C18 column (250 \times 4.6 mm, 5 μ m) and a guard column (20 \times 4.6 mm, 5 μ m). Phenolic compound standards were purchased from Sigma. Detection was performed at 280 nm. Different phenolic acids were identified by their retention times compared to authentic standards (Figure 1). The chromatographic data were recorded and processed using a Waters Empower workstation. Standards of nine phenolic acids were prepared in different concentrations. The standard curve equations of the nine phenolic acids were obtained by taking the peak area of the liquid chromatogram as Y and the sample concentration as X. The concentrations of each compound in the soil samples were obtained based on peak areas using external standards.

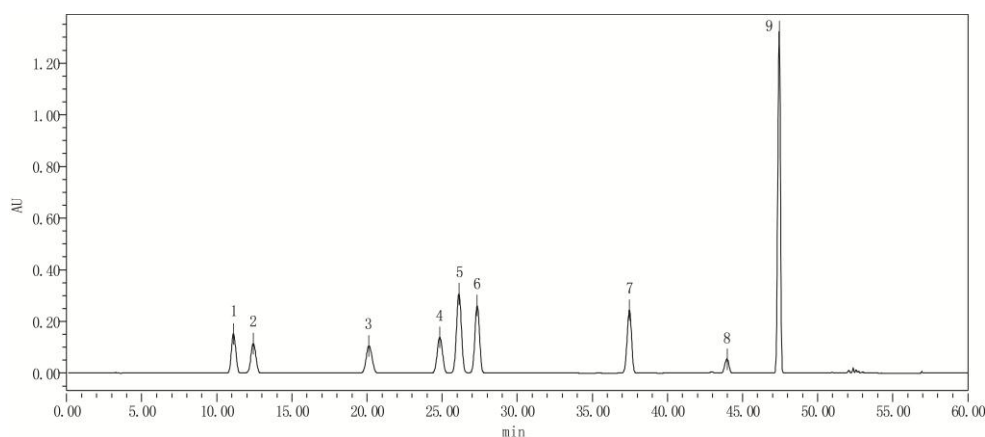


Figure 1. Chromatogram of nine phenolic acids standard at 280 nm
1. *p*-Coumaric acid; 2. Protocatechuic acid; 3. *p*-Hydroxybenzoic acid; 4. Vanillic acid; 5. Caffeic acid; 6. Syringic acid; 7. Ferulic acid; 8. Salicylic acid; 9. Cinnamic acid

HPLC separations were conducted using the following mobile phase solutions: mobile phase of aqueous formic acid solution (0.1%, v/v) and acetonitrile, a column temperature of 30°C, 20 µL of injection volume, a flow rate of 1.0 mL·min⁻¹ and gradients of 6–10% acetonitrile (0–16 min), 10–22% (16–36 min), 22–50% (36–46 min), 50–100% (46–48 min) and held for 5 min. The column was equilibrated for 10 min between injections.

V. Statistical analysis

A one-way ANOVA was done to test the allelopathic effects of each treatment on the seed germination rate, germination speed index and root length of *L. sativa* and *R. typhina*. In addition, a one-way ANOVA was done to test the effects of different soil origins on each phenolic acid concentration. An LSD test was used to identify the statistically significant differences at $P < 0.05$ using the SPSS 16.0 statistical software package. The figures were processed using Microsoft Excel.

RESULTS AND DISCUSSION

I. Seed germination and seedling growth

(i). ***L. sativa***: The *Q. acutissima* litter leachates significantly inhibited the seed germination and seedling growth of *L. sativa* compared with distilled water control (Figure 2). The *Q. acutissima* litter leachates decreased the seed germination rate of *L. sativa* by 72.22 % (0.05 g·mL⁻¹) and 66.67 % (0.01 g·mL⁻¹) (Figure 2A); the germination speed index of *L. sativa* decreased by 92.67 % (0.05 g·mL⁻¹) and 89.03 % (0.01 g·mL⁻¹) (Figure 2B); and the root length of *L. sativa* decreased by 74.79 % (0.05 g·mL⁻¹) and 60.74 % (0.01 g·mL⁻¹), respectively (Figure 2C). There was no significant difference in the *R. pseudoacacia* treatment compared to the control. Besides, the response index data also showed that the allelopathic inhibitory effects of *Q. acutissima* were stronger on the seed germination and seedling growth of *L. sativa* than *R. pseudoacacia* in laboratory bioassay (Figure 3).

(ii). ***R. typhina*** : The *Q. acutissima* litter leachates significantly inhibited the seeds germination rate of *R. typhina* (55.88 %) at high concentration (0.05 g·mL⁻¹) compared with distilled water control. There were no significant difference between other treatments and control (Figure 4A).

The *Q. acutissima* litter leachates significantly reduced the germination speed index of *R. typhina* (62.64 %) at high concentration (0.05 g·mL⁻¹) compared with distilled water control. The germination speed index of *R. typhina* was reduced by 30.15 % (0.05 g·mL⁻¹) and 37.54 % (0.01 g·mL⁻¹) when treated by the *R. pseudoacacia* litter leachates (Figure 4B).

The *Q. acutissima* litter leachate significantly inhibited (64.98 %) the root length of *R. typhina* seedlings only at high concentration (0.05 g·mL⁻¹) than distilled water control. There was no significant difference between other treatments and control (Figure 4C).

Like the *L. sativa*, the response index data to *R. typhina* also indicated that the allelopathic inhibitory effects of *Q. acutissima* were stronger on the seed germination and seedling growth of exotic plant *R. typhina* than *R. pseudoacacia* in laboratory bioassay (Figure 5).

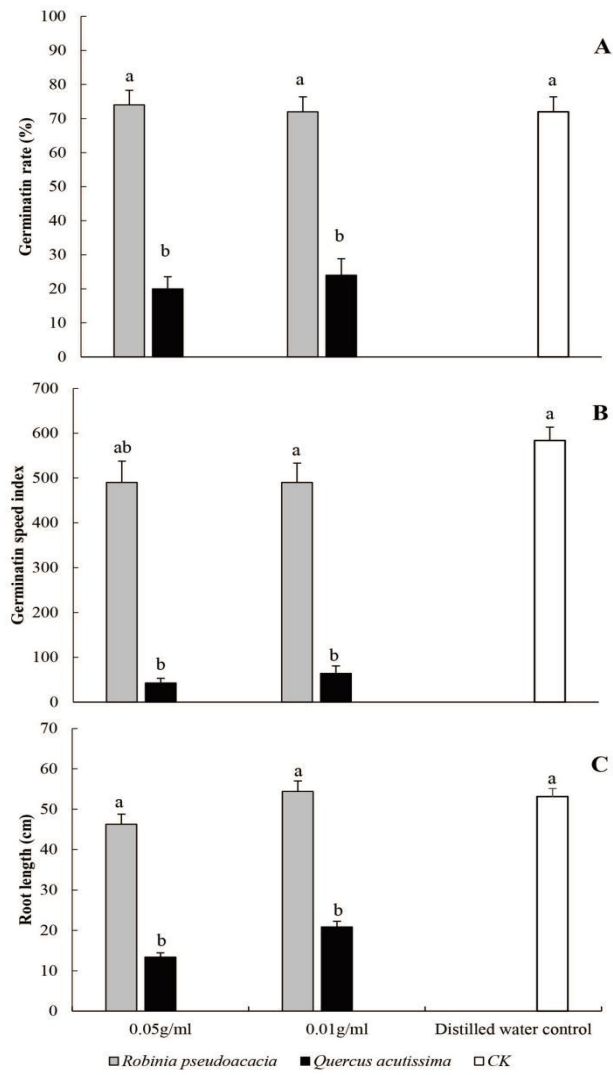


Figure 2. Allelopathic effects of litter leachates from *Robinia pseudoacacia* and *Quercus acutissima* on the seed germination and seedling growth of *Lactuca sativa*

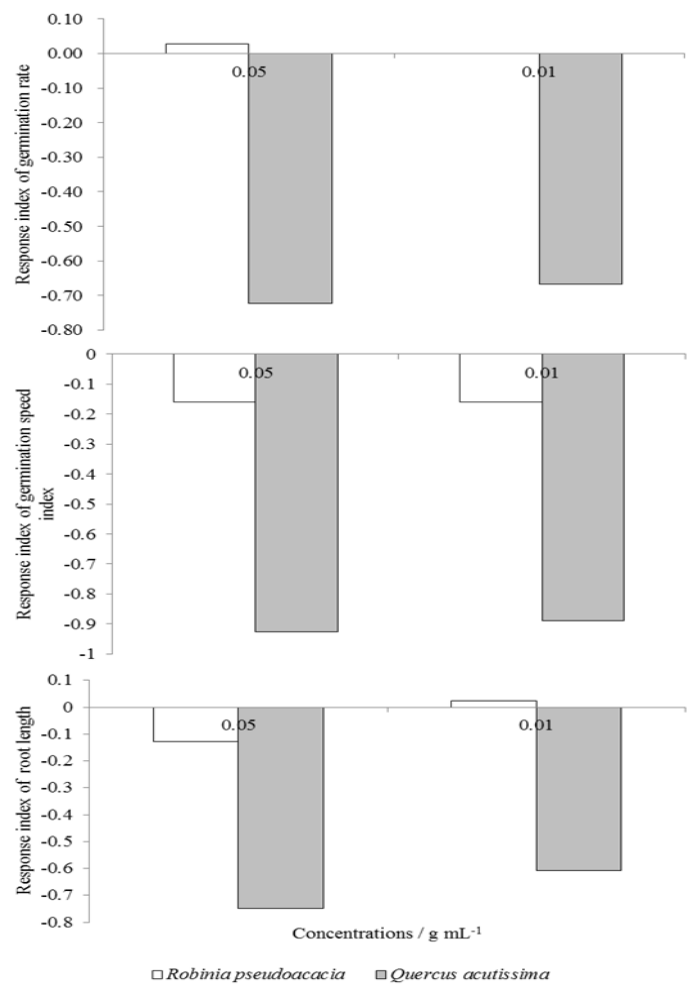


Figure 3. Response index of seed germination and seedling growth of *Lactuca sativa* to the litter leachates from *Robinia pseudoacacia* and *Quercus acutissima*

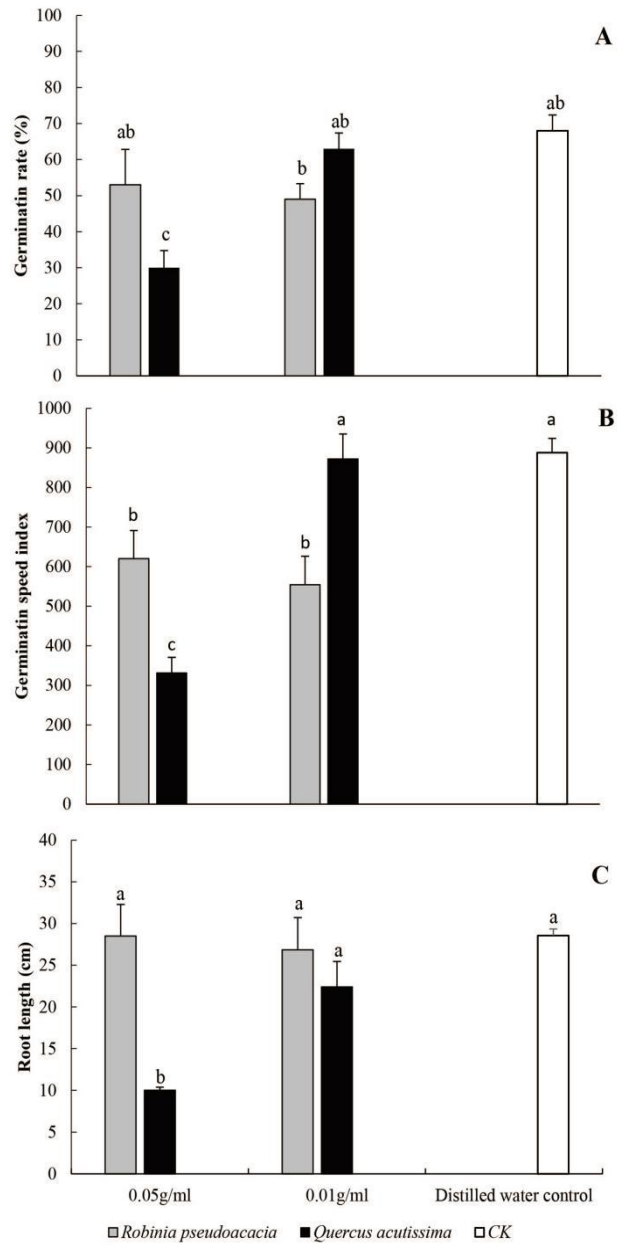


Figure 4. Allelopathic effects of litter leachates from *Robinia pseudoacacia* and *Quercus acutissima* on the seed germination and seedling growth of *Rhus typhina*

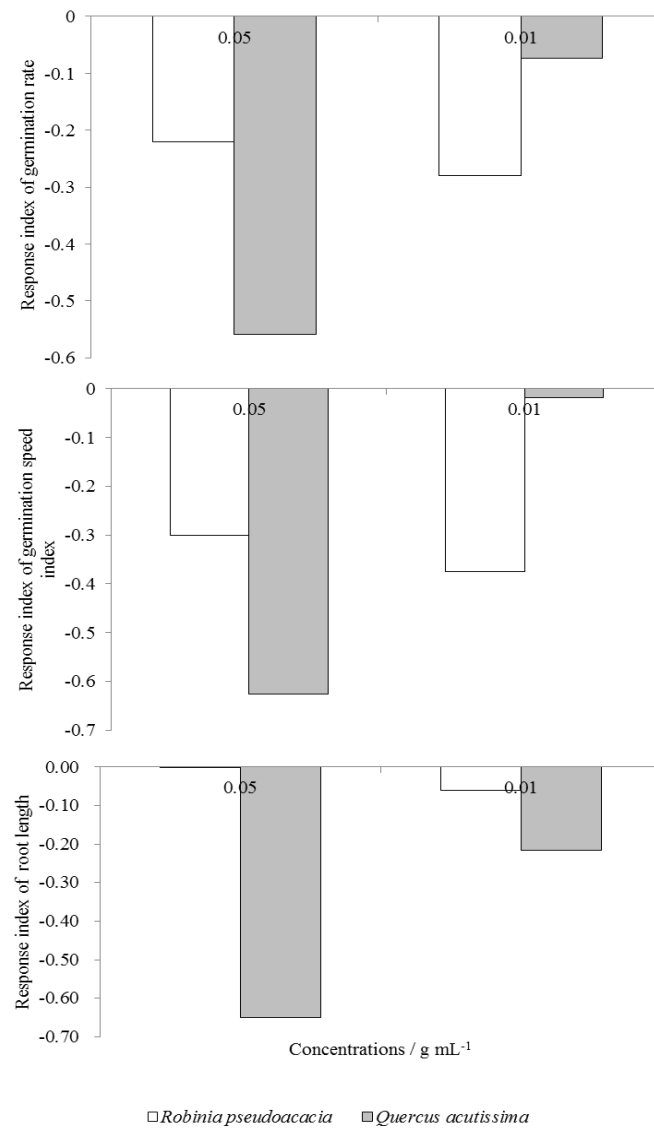


Figure 5. Response index of seed germination and seedling growth of *Rhus typhina* to the litter leachates from *Robinia pseudoacacia* and *Quercus acutissima*

The results in laboratory bioassay showed that at both high and low concentrations, the *Q. acutissima* litter leachates significantly inhibited the seed germination and seedling growth of *L. sativa*. At a high concentration, *Q. acutissima* litter leachates significantly inhibited the seed germination and seedling growth of *R. typhina*. This result is consistent

with our previous research with root leachates of *Q. acutissima*, which also significantly suppressed the seed germination, root and shoot length of *R. typhina* seedlings (31). Compared to the *Q. acutissima* treatments, *R. pseudoacacia* litter leachates had no effects on *L. sativa* and only reduced the germination speed index of *R. typhina*. Callaway and Aschehoug (2) found that North American grasses may not be adapted to allelochemicals release by invasive *Centaurea diffusa* (Eurasian forb). However, Eurasian species from its native land are adapted. Similarly, in this study, we found that *R. typhina* (originated in North American) may not have adapted to allelochemicals released by *Q. acutissima* (originated in Asia). However, *R. typhina* adapted to allelochemical release by *R. pseudoacacia*, which originated from its native land. *R. typhina* as an exotic plant has not been established in the Shandong Peninsula to adapt to the allelochemicals secreted by *Q. acutissima*, which can inhibit the growth of this exotic species to some extent. Alternatively, *R. pseudoacacia* shares the same North American origin with *R. typhina*, and the allelochemicals secreted by *R. pseudoacacia* cannot inhibit the growth of the *R. typhina*.

II. Phenolic acids content in the *Q. acutissima* and *R. pseudoacacia* soils

The concentrations of protocatechuic acid and cinnamic acid in *Q. acutissima* soil were significantly higher than in non-forest land control (Table 1). There was no significant difference in the concentrations of other phenolic compounds (*p*-coumaric acid, *p*-hydroxybenzoic acid, vanillic acid, caffeic acid, syringic acid, ferulic acid, salicylic acid) among the three soils [*R. pseudoacacia* soil, *Q. acutissima* soil and the non-forested land control of different origins (Table 1)].

Table 1. The 9- phenolic compounds detected in soil samples from the top 10 cms of soils in *Robinia pseudoacacia* forest, *Quercus acutissima* forest and non-forested land (Blank control).

Phenolic compounds	Soil samples ($\mu\text{g g}^{-1}$)		
	Blank control	<i>Robinia pseudoacacia</i>	<i>Quercus acutissima</i>
1. <i>p</i> -Coumaric acid	2.12±0.25a	6.48±0.54a	6.48±2.10a
2. Protocatechuic acid	1.21±0.04b	1.28±0.01ab	1.37±0.06a
3. <i>p</i> -Hydroxybenzoic acid	1.19±0.03a	1.70±0.35a	5.41±2.06a
4. Vanillic acid	1.75±0.20a	2.06±0.40a	4.01±1.11a
5. Caffeic acid	2.38±0.25a	5.17±0.43a	5.66±2.34a
6. Syringic acid	1.34±0.08a	1.42±0.31a	1.98±0.33a
7. Ferulic acid	1.96±0.50a	2.15±0.05a	2.24±0.43a
8. Salicylic acid	1.28±0.02a	11.64±9.13a	4.18±2.71a
9. Cinnamic acid	0.98±0.00b	1.07±0.02ab	1.11±0.05a

Data are means \pm SE, n = 3, different lowercase letters in a row indicate statistically significant differences ($P < 0.05$).

Allelochemicals are plants secondary metabolites released into the environment, which may have direct or indirect beneficial or adverse effects on other plants and

microorganisms (28). Plants usually gain an advantage in the competition for limited resources by releasing the allelochemicals into the environment to inhibit the growth of other adjacent plants (13). Phenolic acid is one of the main chemicals secreted by plants, most phenolic acids are allelopathic and affect the plant development and growth (8,19).

Although there was no significant difference in the phenolic acid concentrations in the soils with growing of *R. pseudoacacia* and *Q. acutissima*, the *Q. acutissima* soil had higher contents of phenolic acids than the *R. pseudoacacia* soil. Therefore, compared with *R. pseudoacacia*, the *Q. acutissima* may secrete more allelochemicals inhibitory to the growth and development of exotic plant *R. typhina*.

Allelochemicals significantly affects the cell division and proliferation (7,14). The growth and elongation of the roots are crucial for the plant development; hence, the inhibition of root growth has negative impact on future resource competition, self-growth and plant community composition (34). After the treatment with vanillic acid, *p*-coumaric acid, caffeic acid and syringic acid, the cells division of bean roots was significantly inhibited (5). The phenolic acids may damage the cell integrity and organelle membranes, sequentially affecting the seed germination and seedling growth.

Field investigation in hilly habitats of Shandong Peninsula shows that exotic plants are rare in the *Q. acutissima* forest, while the *R. pseudoacacia* forest is easily invaded by exotic species (31), such as *R. typhina*, *Phytolacca americana* L., and *Helianthus tuberosus* L. Unlike animals, plants cannot escape or freely change their environment. They can only survive by adapting to the changing environment. In case of lack of resources, plants have limited ability to obtain more resources through physical means, and sometimes they can only increase their competitiveness through chemical means (23). Allelopathy, as an important factor affecting the plant growth and community assembly, could play a crucial role in the resistance of native plant communities against exotic plants invasion.

CONCLUSIONS

We found that native dominant plant *Q. acutissima*, significantly inhibited the growth and development of the exotic species *R. typhina* in the Shandong Peninsula, indicating that the invaders could be adversely affected by the allelochemicals released by some native plants. We found that the allelopathy of some native plants may contribute to the community resistance to exotic species invasion and plant-plant interactions may also play an important role in determining the community composition. In addition, this study provided a scientific basis for invasive plants management.

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