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Allelopathic effects of seven common species on the growth of alien invasive plant *Phytolacca americana*

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ABSTRACT

We hypothesized that some dominant plant species can regulate the community invasibility via allelopathy. We studied the allelopathic effects of seven common plant species, 4-Asian species (*Quercus acutissima*, *Pinus thunbergii*, *Pinus densiflora*, and *Rhus chinensis*) and 3-American species (*Phytolacca americana*, *Robinia pseudoacacia* and *Amorpha fruticosa*) on the performance of invasive species *Phytolacca americana* in Lab. bioassay and pot culture experiments. We found that the allelopathy of 7-common species significantly differed and exerted variable effects on the soil properties (soil pH, available nutrients, and nitrogen cycle) and had variable allelopathic effects on the growth of *P. americana*. The changes in soil properties due to allelopathy were more important, as they affected the aboveground and belowground biomass accumulation of recipient invasive species by change in the biomass allocation strategies. The results suggested that the influence of dominant plants on the soil environment via allelopathy partly determines the community invasibility.

Keywords: Alien plant, allelopathy, *Amorpha fruticosa,* bioassay, biomass, community invasibility, *Phytolacca americana*, *Pinus densiflora*, *Pinus thunbergii*, pot culture, *Quercus acutissima*, *Rhus chinensis, Robinia pseudoacacia*, soil properties.

INTRODUCTION

Alien plant invasion is becoming a global problem as they cause serious damage, hence, have received great attention (37,40). It is necessary to determine, which factors regulats the community invasibility (9) and the successful plant invasions are related to which characteristics of invaded communities (4,6,14,17). Some studies have shown that biotic factors (biodiversity, functional groups and species traits), play crucial role in resisting the invasions of alien plants (16,19,36,52,53). While other studies have suggested that environmental factors (resource heterogeneity, climate, and disturbance), are also important in invasions of alien plants (13,17,43). However, plants and environments interact, i.e., environmental factors determine the composition and dynamics of plant communities, while the plants activities change the environment (18). Therefore, both biotic and abiotic factors should be considered together in studying community invasibility (5,11).

Allelopathy is an important chemical means by which plants compete for limited resources (7,8). The novel weapons hypothesis suggests that because of the lack of a co-evolutionary history, allelochemicals produced by alien invasive plants are novel to native plants, and native species may be more strongly impacted by these allelochemicals (7,22,39,47). Several studies have found that in invaded communities, the allelochemicals

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of native plants, particularly those of community-dominant species, can also affect the invasion by exotic plants (12,21,33). However, the allelopathic effects of native plants on the performance of alien invasive plants have not been well studied.

Plants release allelochemicals into the surrounding environment via rain leaching, litter decomposition, root exudation, etc., and these allelochemicals directly affect the growth and competitive ability of neighbouring plants (7,8,51). In addition, the indirect effects of allelopathy may also be important in natural conditions (23,49). Most of the allelochemicals released by plants eventually enter the soil, and a series of interactions occur with soil abiotic and biotic factors (soil nutrients, microbes, moisture, etc.), indirectly affecting the plant performance (20,23,24). Among the various effects of allelochemicals, their effects on soil nutrients forms and availability via complexation, adsorption, acid solubilization etc. (10,20,27). Allelochemicals also affects the nutrients availability by affecting the soil microbial activity. For example, the reduced NO_3^- in invaded communities is due to the inhibition of nitrifying bacteria by the secondary metabolites produced by invasive plants (46). Overall, both direct and indirect allelopathic effects can affect the performance of neighbouring plants.

Photograph 1. Invasive *Phytolacca americana* weed

In this study, we selected 7-common plants: 4- Asian origin plants (*Quercus acutissima* Carruth., *Pinus thunbergii* Parl., *Pinus densiflora* Sieb. et Zucc., and *Rhus chinensis* Mill.) and 3- American origin plants (*Phytolacca americana* L., *Robinia pseudoacacia* L., and *Amorpha fruticosa* L.) They are widely distributed at the study site and studied their direct and indirect allelopathic effects on the growth performance of serious invasive plant *P. americana*, from America. We tested: (i) the allelopathic effects of 7-common plants on the seeds germination of *P. americana* and the soil properties; (2) the direct and indirect allelopathic effects of 7-common plants effects on biomass accumulation of *P. americana*.

METHODS AND MATERIALS

I. Study Site

Zhenshan Mountain (Latitude and longitude: N 37°30'-37°32', E 121°19'-121°21') is located on the Yellow Sea coast of Shandong Peninsula, China. It has continental monsoon climate with mean daily temperature of 12°C and mean annual rainfall of 740.3 mm. Its average altitude is 230-250 metres. Due to frequent human activity, the original vegetation has been destroyed, and the existing vegetation is mainly of secondary type. *P. americana* (perennial herbaceous plant originating from North America), is a serious alien invasive species in the shelterbelts in the hilly coastal area of Shandong Province. In 2009, the State Forestry Administration (No. 5 of 2009) classified *P. americana* as an invasive plant. Now it is is widely distributed on Zhenshan Mountain, and has different invasion potential into various communities. In field investigations, we found less *P. americana* invasions in *Q. acutissima* forests than in *R. pseudoacacia* forests.

II. Bioassays

In laboratory bioassays the allelopathic effects of 7-plant species on seed germination of *P. americana* were determined. Fresh leaves from 3-American species (*P. americana*, *R. pseudoacacia*, and *A. fruticosa*) and from the 4-Asian species (*Q. acutissima*, *P. thunbergii*, *P. densiflora,* and *R. chinensis*) were collected from Zhenshan Mountain in July 2016. These were dried in drying oven at 60 °C for 72 h. Five hundred g dry material was immersed in 5 L distilled water for 24 h. The leachate was filtered with double gauze and considered as the stock solution (0.1 g/mL). This stock solution was diluted with distilled water to 3 concentrations (0.1 g/mL, 0.05 g/mL and 0.025 g/mL) of aqueous leachate. All solutions were stored in refrigerator at 4°C until use.

Seeds of *P. americana* were collected from Zhenshan Mountain and their dormancy was broken before sowing, by soaking the seeds in 15% H_2O_2 for 7 h. For each replication, 20-seeds of *P. americana* were placed in a Petri dish (9 cms in dia) lined with filter paper. Five mL of the aqueous leachates (7-plant species, 3-concentrations of each species) was added as per treatment. Distilled water was used as control. There were 6 replications. All Petri dishes were placed in light incubator 28°C/light (12 h) and 26°C/dark (12 h). The number of germinated seeds was recorded daily and seeds with roots measuring > 1 mm in length were considered as germinated. This experiment was conducted for 14 days.

III. Soil properties conditioning and analysis

To study the effects of 7-plant species on soil properties by allelopathy, a soil conditioning experiment was done in greenhouse. The soil's chemical properties were pH 5.94, total C: 14.15 g/kg, total N: 2.15 g/kg, ammonium N: 3.17 mg/kg, nitrate N: 33.29 mg/kg, available P: 14.63 mg/kg and available K: 144.66 mg/kg. Pots (13 cm dia and 13.5 cm deep) were filled with 1 kg mixed soil collected from a non-forested land on Zhenshan Mountain. Plants were not sown in these pots, but were watered monthly with 300 mL leachate/pot. All pots were watered during the experiment to keep the soil moist. Distilled water was used as control. There were 6 replications. Soil samples were collected from each pot 80 days after aqueous leachate treatment and divided into two parts.

(i). The first part was kept in plastic bags and stored in refrigerator at 4°C. The initial soil NO_3^- and NH_4^+ were extracted by KCl solution and measured by spectrophotometer and their concentrations in the soil were expressed on dry weight basis. Soil net N mineralization and nitrification were assessed using laboratory incubation method. Fresh 10-g soil subsamples were placed in tubes and sealed with Parafilm perforated for ventilation and then incubated in incubator at 28°C for 28 days. During incubation, the soil moisture was maintained by weighing the soil and adjusting the water content daily by adding distilled water. After the incubation period, the concentrations of NO_3^- and NH_4^+ were determined. Net mineralization was calculated as the net NO_3^- and NH_4^+ production, and net nitrification was calculated as the net NO_3^- produced during the 28-day incubation.

(ii). The second part of soil samples was naturally air dried, sieved through 2-mm mesh and stored in plastic bags at room temperature. Soil pH was measured using an electrode pH meter in a 1:2.5 (w/v) soil-water suspension. The soil total C and N were determined using dry combustion with an elemental analyzer. For the determination of soil available P, 5.0 g soil samples were extracted with 25 mL 0.05 mol·L^{-1} HCl-0.025 mol·L^{-1} (1/2 H_2SO_4), and the P concentration of the extract was determined by spectrophotometer. To determine the soil available K, 5.0 g soil samples were extracted with 50 mL 1 mol·L^{-1} NH_4OAc, and the K concentration of the extract was determined by flame photometry detector. All chemical analyses were based on the methods described by Bao (2).

IV. Pot culture experiments

To study the allelopathic effects of 7-plant species on *P. americana* growth, a pot culture experiment was done in greenhouse. Pots (6 cm dia and 8 cm depth) were filled with the same soil used in the soil conditioning experiment. *P. americana* seeds (after broken dormancy) were sown in seedling bed to obtain similar-sized seedlings. When the seedlings of *P. americana* were about 3 cm tall (10 days after sowing), uniform seedlings were selected and transplanted one seedling per pot. Five mL leachates from different species were added to the pots each week as per the treatment. Distilled water was used as control. There were 6 replications for each treatment in completely randomized design. All pots were watered with 5 mL distilled water once a week to keep the soil moist. The *P. americana* plants were harvested after 30 days. The shoots were clipped at ground level. The roots were rinsed gently with water to clear the adhering soil. The biomass of *P. americana* was dried for 72 h at 60 °C and then weighed. The root-shoot ratio (R:S) was based on the ratio of root biomass to shoot biomass.

V. Statistical analysis of Data

We calculated a response index (RI) to evaluate the effects of allelopathy on plant seed germination, biomass accumulation and allocation (28,29,50). The RI was calculated as follows: ($variable_{leachate}$ - $variable_{water}$) / $variable_{water}$, where $variable_{water}$ was the average value of six replicates with water addition when evaluating the allelopathy of the leachate. RI >0 : Positive effect, RI <0 : Inhibitory effect, and RI=0 : No effect. The absolute value of RI indicates the effect of intensity.

We calculated an indicator of the principal component composite score to assess the effect of allelopathy on all the soil variables together. The principal component scores were calculated as per Shi (40). The principal component composite score was calculated as under:

$$y=(a_1x_1+a_2x_2+\ldots\ldots+a_nx_n) / (a_1+a_2+\ldots\ldots+a_n)$$

Where, "y" : Principal component composite score, "a" : Proportion of variance, and "x" : Principal component score. Finally, the RI of the composite score was calculated as under:

$$\text{RI of the composite score} = y_{\text{leachate}} - y_{\text{water}}$$

The statistical analysis was done using IBM SPSS statistics 24 (IBM Inc., USA). Two-way ANOVA was conducted to test the effects of both species and concentration on seed germination, soil properties, biomass accumulation and allocation in *P. americana*. One-way ANOVA was conducted to test the difference of the seven species in each concentration and three leachate concentrations in each species on seed germination, soil properties, biomass accumulation and allocation in *P. americana*. A Student-Newman- Keul multiple range test was used to identify statistically significant differences at $P<0.05$. All plots were drawn using SigmaPlot 10.0 (Systat Software Inc., Poland).

RESULTS AND DISCUSSION

I. Seed germination in bioassays

Both plant species and aqueous leachate concentration had significant effects on the seed germination and there was significant interaction between the plant species and aqueous leachate concentrations ($P<0.05$, Table 1). The leachates from all 7-common plants inhibited the seeds germination of *P. americana* seeds ($P<0.05$, Figure 1). The inhibitory effects were enhanced with increase in concentration i.e. was concentration dependent. There were significant differences among the leachates concentrations of *P. americana*, *R. pseudoacacia, A. fruticosa* and *Q. acutissima* but not among the leachates concentrations of *P. thunbergii*, *P. densiflora* and *R. chinensis* ($P < 0.05$, Figure 1). The RI of germination rate differed significantly among the species in leachates of high (0.1 g/mL) and middle (0.05 g/mL) concentrations, but not in low concentration (0.025 g/mL).

Allelopathy is an important chemical means of plant interactions (7,8). The results of bioassay showed that allelopathic potential all 7-common plants inhibited the seeds germination of *P. americana*. The inhibitory effects of non-native American origin plants (*P. americana*, *R. pseudoacacia* and *A. fruticose*) were significantly stronger than 4-Asian plants (Figure 1). The allelopathic effects of American and Asian plants differ in terms of their effects on performance of *P. americana*, may be due to their lack of coevolutionary history (28,29,50). However, Medina-Villar *et al*. (31) found that the allelopathic effects of alien plants were not stronger than native plants. The plant allelopathic interactions between the donor and target species may be species-specific (31,53). Many legumes have strong allelopathic effects (12,45), the *R. pseudoacacia* and *A. fruticosa* are both legumes, hence, show strong allelopathy. Therefore, care should to be taken when discussing the issue of plant allelopathy along with origin. The bioassay experiments without soil usually overestimate the plant allelopathy (31).

Table 1. Significance level (*F* value) of the effects of species, concentration, and the interaction between species and concentration on the variables measured in the experiment based on two-way ANOVA. Statistically significant values (P< 0.01) are denoted by bold font.

Variables	Species		Concentrations		Species × Concentrations	
	F	***P***	***F***	***P***	***F***	***P***
RI of germination rate	**39.535**	<**0.001**	**118.565**	<**0.001**	**9.474**	<**0.001**
RI of composite scores	**17.960**	<**0.001**	**25.980**	**<0.001**	1.860	0.060
RI of total biomass	**56.124**	<**0.001**	**11.032**	<**0.001**	**4.546**	<**0.001**
RI of R:S	**12.438**	<**0.001**	1.518	0.224	2.160	0.019

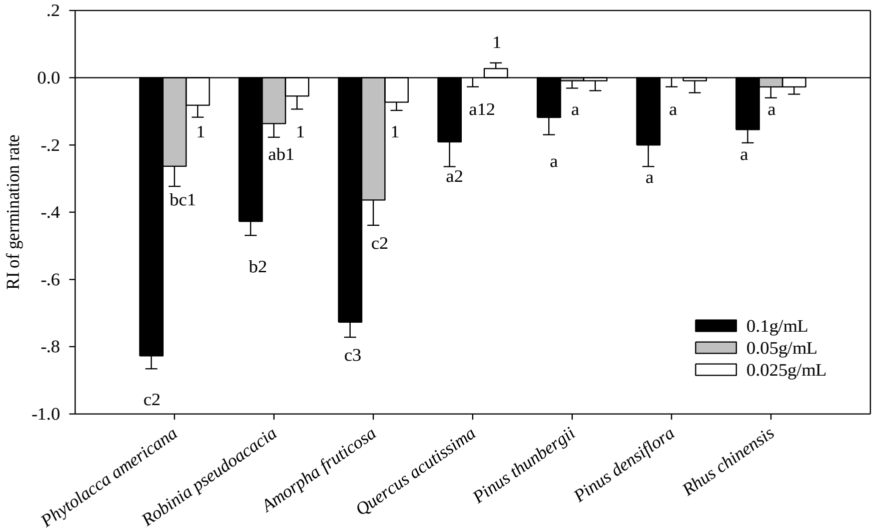

Figure 1. RI of the germination rate of *Phytolacca americana* seeds affected by aqueous leachates of 7-donor plants. 3-American species (*P. americana*, *R. pseudoacacia*, and *A. fruticose*) and 4-Asian species (*Q. acutissima*, *P. thunbergii*, *P. densiflora,* and *R. chinensis*). Statistically significant differences among species of each concentration are denoted by different letters; statistically significant differences among three concentrations of each species are denoted by different number, statistically non-significant differences were not marked (P <0.05).

II. Effects of allelopathy on soil properties

The donor plant species and leachate concentrations significantly affected the soil properties. The top four principal components (based on cumulative variance > 80%) included 89.52 % of the information from the original variables, and the first principal component was an important one (the variance was 45.83%), mainly including information regarding the pH, total N, NO_3^-, net mineralization and nitrification rate, available P and available K (Table 2).

Table 2. Principal component eigenvectors (*top*) and proportion of variance (*bottom*) for the tested soil.

Variables	1st principal component	2nd principal component	3rd principal component	4th principal component
pH	**0.42**	-0.06	-0.16	-0.06
Total C	0.16	**0.32**	**0.30**	-0.02
Total N	0.34	0.21	0.18	-0.16
NH_4^+	0.26	-0.01	0.05	**0.40**
NO_3^-	0.33	-0.10	-0.25	-0.12
Net mineralization rate	0.35	-0.28	0.20	0.01
Net nitrification rate	0.31	-0.30	0.21	-0.06
Available P	0.39	0.17	-0.13	0.15
Available K	0.37	0.18	-0.14	-0.07
Variance (%)	45.83	17.83	15.19	10.66
Variance cumulative (%)	45.83	63.66	78.86	89.52

Both the test plant species and leachate concentration significantly affected the composite scores of the soil ($P< 0.05$, Table 1). All plants increased the composite scores, but the magnitude of increase in score differed greatly; the strongest was of *P. americana* and the weakest was of *P. thunbergii* ($P< 0.05$, Figure 2). The composite scores differed significantly among species in leachates of high (0.1 g/mL) and middle (0.05 g/mL) concentrations, but not in low concentration (0.025 g/mL). The composite scores significantly different among the three concentrations of *P. americana* and *R. pseudoacacia* and ($P< 0.05$, Figure 2).

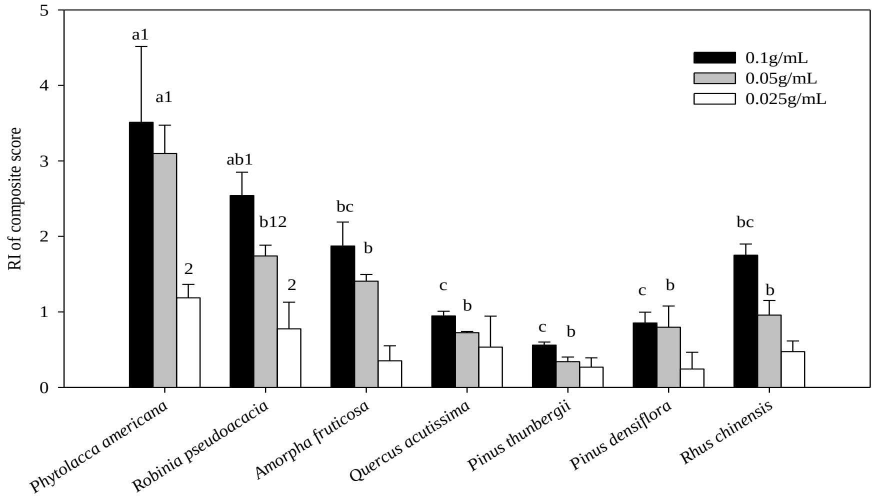

Figure 2. Effects of aqueous leachates of 7-donor plants on RI of composite scores of soil. Three American origin species: *P. americana*, *R. pseudoacacia*, and *A. fruticosa*, and 4-Asian species: *Q. acutissima*, *P. thunbergii*, *P. densiflora,* and *R. chinensis*. Statistically significant differences among species of each concentration are denoted by different letters; statistically significant differences among three concentrations of each species are denoted by different number, statistically no-significant differences were not marked ($P< 0.05$).

The soil allelopathy has important effects on plants growth (20,23,49). We found that allelopathy caused by different donor plants significantly affected the soil properties (Figure 2). These effects are reflected in soil pH, available nutrients (nitrogen, phosphorus, potassium), and nitrogen cycle (mineralization and nitrification rates) (Table 2). Some studies have indicated that allelochemicals (tannins, phenolics and volatile terpenoids) changed the soil pH and soil nutrients cycling (10,30,46). The changes in soil properties may lead to other potential effects. For example, the pH strongly influences the characteristics of microbial communities (2,3,15), which affects the nutrients availability (38,46). In addition, the alien invasive weed *P. americana* had great effects on soil properties (soil pH, available nutrients and nitrogen cycle) than other plant species (Figure 2). Studies have shown that the secondary metabolites of invasive plants can directly or indirectly alter the soil environment and affects the nutrients cycling, which differs from the effects of native plants (10,20,49), these effects may be positive or negative depending on the plant species (32,42,44). The results indicated that the allelopathy caused by the dominant plants affects the soil conditions of their communities, which may affect the species composition and community invasibility.

III. Plants growth in pot experiments

The donor plant species and leachate concentration, significantly affected the total biomass and the interaction between the plant species and leachate concentration was statistically significant. The R:S was significantly affected by donor plant species ($P< 0.05$, Table 1). The total biomass of *P. americana* was increased by leachates of *P. americana*, *R. pseudoacacia* and *A. fruticosa*, but was reduced by leachates of *Q. acutissima* (Figure 3a). The high concentration leachates of *P. thunbergii, P. densiflora* and *R. chinensis* reduced the total biomass of *P. americana,* but increased at low concentration (Figure 3a). The R:S of *P. americana* was increased by *Q. acutissima* leachates but reduced by itself. The effects of *P. americana* leachates on the R:S of other species, depended on the concentration (Figure 3b).

The 7-donor plants had significant effects on the growth of alien invasive plant *P. americana* (Figure 2). The change in soil nutrients caused by plant allelopathy, affected the biomass accumulation by changing the biomass allocation strategies between the aboveground and underground biomass (Figures 3). The leachates of *P. americana*, *R. pseudoacacia* and *A. fruticosa* promoted the growth of *P. americana*. While the other four species (*Q. acutissima*, *P. thunbergii*, *P. densiflora,* and *R. chinensis*) inhibited the growth of *P. americana* and this inhibition was partly due to nutrients limitation caused by allelopathy. The scarcity of soil nutrients is strong form of abiotic resistance to invasions (14,17). Some but not in all cases, plant allelopathy in invaded communities resists the invasion from native plants (12,33,48). Our results demonstrated that the effect was achieved through changes in soil conditions driven by allelopathy. In fact, we speculate that the direct and indirect effects of allelopathy on the soil jointly affect the plant growth. For example, the allelopathy caused by *P. americana* greatly improved the soil conditions (Figure 2), which stimulated its own growth, but the stimulatory effects at high concentrations were weaker than that of *R. pseudoacacia* (Figure 2a). Therefore, we conclude that the allelopathic effects on plant growth are not solely dependent on the intensity of direct or indirect effects but the relative intensity of direct and indirect effects. That is why the weaker allelopathy caused by several plants inhibited the growth of *P. americana*.

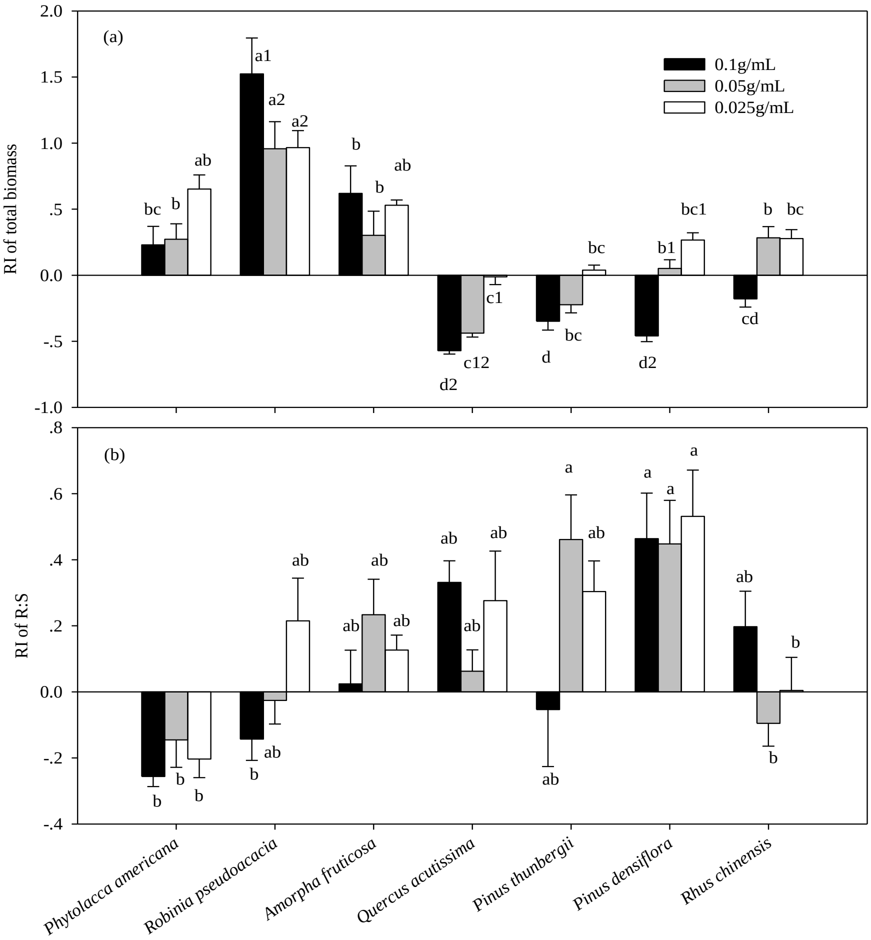

Figure 3. The effects of aqueous leachates of 7-donor plants on the (a) RI of total biomass and (b) RI of R:S of *Phytolacca americana* seedlings. Three American origin species: *P. americana*, *R. pseudoacacia*, and *A. fruticosa*, and 4-Asian: *Q. acutissima*, *P. thunbergii*, *P. densiflora,* and *R. chinensis*. Statistically significant differences among species of each concentration are denoted by different letters; statistically significant differences among three concentrations of each species are denoted by different number, statistically no-significant differences were not marked ($P < 0.05$).

P. americana promoted its own growth. Some studies have shown that alien plants invading the new communities can promote nutrients cycling and are more conducive to their own growth (20,25). *R. pseudoacacia* and *A. fruticosa* also promoted the growth of *P.*

americana. Key features of community (target invader legacy effects and shifting environmental conditions), promotes the secondary invasions (25,34,35). Lazzaro *et al*. (26) reported that the nitrogen-fixing tree *R. pseudoacacia* is major invasive specie worldwide, as it is widely used in forestry production and promotes the soil nutrients cycling, which may further promote the secondary invasion by *P. americana*. Therefore, caution should be taken, when using *R. pseudoacacia* for afforestation. Unfortunately, *R. pseudoacacia* is widely distributed in our study area through plantations and natural expansion, which increases the risk of invasion by *P. americana*. In general, the influence of dominant plants on the soil conditions via allelopathy partly determines the community invasibility, and the ability of dominant plants to conserve nutrients via allelopathy may reduce community invasibility.

Overall, 3-American species and 4-Asian species had variable effects on the plant performance of *P. americana* and soil chemical properties. *P. americana* germination was most adversely affected but grew better with 3-American species. In addition, we might overestimate the plant allelopathy because the leachates concentrations used might be much higher than the naturally-released chemicals from plants. More field experiments are needed in future studies. In addition, we only tested the allelopathic potential of dominant native plants on community invasibility, but the species composition is complex in natural communities, and the non-dominant native plant species might also play a role in affecting the invasive plant via allelopathy.

CONCLUSIONS

The allelopathic potential of 7-plants significantly differed and exerted variable effects on the soil properties (soil pH, available nutrients, and nitrogen cycle). The 3-American and 4-Asian species had differed in allelopathic effects on the growth of *P. americana*. The changes in soil properties due to allelopathy were more important, as they affected the biomass accumulation of invasive species *P. americana* by changing the aboveground and belowground biomass allocation strategies. The results suggested that the effects of dominant plants on soil properties via allelopathy partly determine the invasibility of community.

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