

# Increased nitrogen deposition alleviated the competitive effects of the introduced invasive plant *Robinia pseudoacacia* on the native tree *Quercus acutissima*

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## Abstract

**Background and aims** Increasing atmospheric nitrogen (N) deposition and biological invasion have become major concerns with global environmental change. This study aimed to determine the effects of an exotic species on a native one under increasing N deposition. **Methods** We conducted a greenhouse experiment in which the exotic species *Robinia pseudoacacia* and the native species *Quercus acutissima* were grown in mixture and monocultures under four levels of simulated N deposition (0, 3, 6, 12 g m<sup>-2</sup> year<sup>-1</sup>). After 12 weeks of treatment, plant growth, leaf physiological traits and soil chemical properties were determined.

**Results** With its strong capability for nutrient absorption and carbon assimilation, *R. pseudoacacia* dominated in competition. *R. pseudoacacia* reduced the growth of *Q. acutissima*, but the relative competition index decreased with increasing N deposition. At the end of the

experiment, the soil available phosphorus (P) in mixture was significantly lower than that in the monoculture of *Q. acutissima*, while the soil available N in the two cultivations did not show obvious differences.

**Conclusions** Increased N deposition alleviated the competitive effects of *R. pseudoacacia* on *Q. acutissima*. In the future, besides N, increased P availability should also be considered in the interaction between the two species.

**Keywords** Nitrogen deposition · Plant invasion · Competition · Functional traits · Soil available nitrogen · Soil available phosphorus

## Introduction

Because of its huge ecological impacts, increasing atmospheric nitrogen (N) deposition has aroused widespread

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concern (Reay et al. 2008; Stevens et al. 2011; Liu et al. 2013b). Owing to frequent anthropogenic activities, such as fossil fuel burning and fertilizer use, atmospheric N deposition has risen sharply since the Industrial Revolution (Reay et al. 2008; Maskell et al. 2010). Elevated N deposition can enhance the content of soil available N and has been proven to promote plant production (Bai et al. 2010; Zhang et al. 2013). On the other hand, excess N may cause a series of problems such as N and base cation leaching and soil acidification (Fang et al. 2009; Lu et al. 2009), and thus limit plant growth, reduce biological diversity and affect ecosystem functioning (Reich 2009; Bobbink et al. 2010; Zhang et al. 2013). In addition, the level of N deposition is also considered to relate to the invasibility of ecosystems (Davis et al. 2000). Positive correlations have been found between N deposition and the abundance of invasive species at different scales (Scherer-Lorenzen et al. 2007).

As an important component of human-caused global climate change, biological invasion is considered one of the most severe environmental problems (Sala et al. 2000; Jiang et al. 2009). Generally, invasive plants grow fast and are capable of allocating more resources to photosynthesis and using resources more efficiently. With these strategies, they may out-compete the co-occurring native species (Jiang et al. 2009). Additionally, invasive species may alter the soil nutrient conditions, modify the soil biota and release allelochemicals (Callaway and Ridenour 2004; Jordan et al. 2008; Perkins and Nowak 2013), all of which may decrease the fitness of native species. At a larger scale, biological invasion may threaten the species richness and diversity of native communities, change ecosystem carbon and nitrogen cycles and affect ecosystem structure and functioning (Ehrenfeld 2010; Vilà et al. 2011; Pyšek et al. 2012).

In the context of increasing atmospheric N deposition, the magnitude and pattern of the influence of invasive species on natives may be changed (Dukes and Mooney 1999; Bradford et al. 2007). As pointed out by Dukes and Mooney (1999), increased N deposition may benefit fast-growing invasive species and therefore threaten slow-growing native species adapted to low resource levels. Several studies have demonstrated that elevated N availability increases the competitive ability of invasive species over natives (Vasquez et al. 2008; He et al. 2012). However, other research has not confirmed such a conclusion (e.g. Thomsen et al. 2006;

Bradford et al. 2007). If the growth of exotic and native species is restricted by different resources, elevated N availability may not exacerbate the competitive effects of exotics (Bradford et al. 2007). On the whole, experimental evidence is still insufficient and the impact of increasing atmospheric N deposition on the competitive effects of invasive species remains to be confirmed.

To examine how the impacts of invasive species on natives respond to increasing N deposition, a greenhouse experiment was conducted with an exotic tree species (*Robinia pseudoacacia*) and a native tree species (*Quercus acutissima*). *R. pseudoacacia* is a deciduous member of the Fabaceae family. Native to North America, it is now widespread across Europe and Asia (Von Holle et al. 2006; Cierjacks et al. 2013) and is accounted one of the most invasive species in the world (Boring and Swank 1984). Kawaletz et al. (2013a, b) reported that strong competitiveness enabled *R. pseudoacacia* to suppress the growth of native species. However, because of its N<sub>2</sub>-fixation ability, *R. pseudoacacia* is also considered to facilitate the growth of neighboring plants (Von Holle et al. 2006; Ding et al. 2012). Therefore, the relationships between *R. pseudoacacia* and native species still remain an open question. *Q. acutissima*, a deciduous member of the Fagaceae family, is one of the most important constructive species (dominant species in the tree layer of a community) of forests in North China (Wang and Zhou 2000). Both species are widely used in reforestation, therefore mixed forests of *R. pseudoacacia* and *Q. acutissima* are very common (Wang and Zhou 2000). It was reported that a strong capacity for root lateral extension and clonal growth enabled *R. pseudoacacia* to intrude into nearby *Q. acutissima* forest and suppress the growth of young oaks (Wang and Wang 1996; Zhang et al. 2008). A similar phenomenon was also found in South Korea (Lee et al. 2004).

In our greenhouse experiment, seedlings of *R. pseudoacacia* and *Q. acutissima* were grown both in monocultures and mixture. Four levels of N were applied to simulate increasing atmospheric N deposition. The following questions were addressed:

1. Is there a competition between *R. pseudoacacia* and *Q. acutissima* in mixture? If so, what plant traits contribute to the competitiveness of *R. pseudoacacia*?
2. Is the competitive pressure of *R. pseudoacacia* on *Q. acutissima* exacerbated with increasing N levels?

## Materials and methods

### Study site

The experiment was carried out at the Fanggan Research Station of Shandong University, Shandong Province, China (36°26'N, 117°27'E). The station is located in the Central Mountainous Region of Shandong Province. This area has a typical temperate monsoon climate with a mean annual temperature of  $13 \pm 1$  °C and a mean annual precipitation of  $700 \pm 100$  mm. The soil type is a yellow cinnamon soil with limestone as the parent material (Wang and Zhou 2000). The whole experiment was carried out in a greenhouse at the station to ensure a controlled and homogenous environment. Made up of steel pipes, the framework of the greenhouse was covered by plastic film. By rolling up the plastic film at the sides, the greenhouse was kept well ventilated. Using a portable temperature and humidity data logger (MicroLog EC650, Fourtec, USA), the microclimate in the greenhouse was monitored. During the growth period of the plants, the average temperature in the greenhouse ranged from 20.3 to 36.2 °C during the day and 10.0 to 26.7 °C during the night. The average day length relative humidity varied from 30.9 to 88.0 %.

### Plant materials

Seeds of *R. pseudoacacia* and acorns of *Q. acutissima* were collected from hills near the research station in October, 2012 and stored at 0–4 °C during the winter. In mid-April 2013, they were soaked in distilled water for 24 h and stimulated to germinate in a growth chamber. When the radicles were about 2 cm long, healthy and uniform seedlings were selected and transplanted into plastic pots (25 cm × 24 cm, height × diameter). Each pot was filled with 6.3 kg loam and 2.1 kg sand, which were carefully sieved to remove debris and stones. The substrates were mixed thoroughly and their chemical properties were determined as pH 6.51, available N  $50.20 \text{ mg kg}^{-1}$  and available P  $31.14 \text{ mg kg}^{-1}$ . During the experiment, all of the pots received enough water. Weeds and insects were controlled manually.

### Experimental design

The seedlings were arranged into three cultivation types: monocultures with two seedlings of the same species

(*R. pseudoacacia* or *Q. acutissima*) and a mixture with one seedling of each species. Each cultivation type received four N treatments: 0, 3, 6 and  $12 \text{ g m}^{-2} \text{ year}^{-1}$  (designated N0, N1, N2 and N3). N0 was set as the control; N1 and N2 corresponded to levels of N deposition already recorded in some areas of northern and southern China (Lü and Tian 2007; Zhang et al. 2011); N3 represented a high deposition level that may be reached in the future. There were 12 treatment combinations in total and each combination contained six pots as replicates. All of the pots were arranged randomly and rearranged regularly during the experiment.

Beginning on June 16, the N treatments were applied biweekly seven times in total, ending on September 8. According to the report that the ratio of  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  in atmospheric N deposition in China was about two in recent years (Liu et al. 2013b), we simulated the N deposition by adding mixed solutions of  $(\text{NH}_4)_2\text{SO}_4$  and  $\text{KNO}_3$  (1:1, M/M).  $\text{K}_2\text{SO}_4$  and KCl solutions of different concentrations were also added to different N treatments to ensure that all treatments received the same amount of K as well as S. Since about 70 % of the annual precipitation falls during June to August in North China (Wang and Zhou 2000), solutions corresponding to 10 % of the annual N deposition were added each time. The compositions and concentrations of the solutions applied to the four N treatments during the experiment are shown in Table 1.

**Table 1** Compositions and concentrations of the solutions applied to the four N treatments during the experiment

Nitrogen treatment ( $\text{g m}^{-2} \text{ year}^{-1}$ )	Solution composition	Concentration ( $\text{mol L}^{-1}$ )
0	$\text{K}_2\text{SO}_4$	0.0052
3	$(\text{NH}_4)_2\text{SO}_4$	0.0013
	$\text{KNO}_3$	0.0013
	$\text{K}_2\text{SO}_4$	0.0039
	KCl	0.0013
	$(\text{NH}_4)_2\text{SO}_4$	0.0026
6	$\text{KNO}_3$	0.0026
	$\text{K}_2\text{SO}_4$	0.0026
	KCl	0.0026
	$(\text{NH}_4)_2\text{SO}_4$	0.0052
12	$\text{KNO}_3$	0.0052
	KCl	0.0052
	$(\text{NH}_4)_2\text{SO}_4$	0.0052

## Measurements

Seedling height (H) was measured at the beginning and end of the N treatment. The relative growth rate of height (RGR<sub>H</sub>) during the N treatment was calculated with the formula:  $RGR_H = (\ln H_2 - \ln H_1) / t$ , in which  $H_2$  and  $H_1$  stood for the seedling height at the end and the beginning of the N treatment, and  $t$  stood for the time duration (88 days).

After 64 days of N treatment, the maximum net photosynthetic rate ( $A_{max}$ ) was measured between 8:30 and 12:00 from 19 to 21 August, 2013. All 3 days were sunny. Using a portable leaf gas exchange system (GFS-3000, Walz GmbH, Effeltrich, Germany), a PPFD of  $1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$  was provided by a red-blue light-emitting diode to ensure that all seedlings were light-saturated (derived from a pre-experiment, data not shown). Three to four fully expanded leaves from the upper shoots were selected in each treatment (one leaf per pot for monocultures and one leaf per species per pot for mixture) and the measurements were conducted alternately among different treatments. The mean air temperature, relative humidity and  $\text{CO}_2$  concentration

values in the leaf cuvette were  $27.51^\circ\text{C}$ ,  $51.0\%$  and  $399.5 \mu\text{mol mol}^{-1}$ .

Leaf morphology was measured at the beginning of September. Five to six fully expanded leaves from the upper shoots in each treatment (one leaf per pot for monocultures and one leaf per species per pot for mixture) were scanned and images were obtained. Then, the leaf area was calculated with the WinFOLIA Pro 2009a software (Regent Instruments, Inc., Quebec, Canada). After scanning, these leaves were oven-dried at  $80^\circ\text{C}$  for 48 h and weighed. Specific leaf area (SLA) was calculated as leaf area/leaf dry mass.

At the end of the experiment, all seedlings were harvested and the roots were washed carefully with tap water. Each whole seedling was divided into four parts: leaf, stem, main root and lateral root. The main root was determined to be the one that grew directly from the seed, while the lateral roots were those that branched laterally from the main root (Guo et al. 2013). All seedling parts were oven-dried at  $80^\circ\text{C}$  for 48 h and weighed. Total biomass and biomass allocation were calculated as follows:

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total biomass(TB) = leaf biomass + stem biomass + main root biomass + lateral root biomass;  
 root to shoot ratio (RSR) = root biomass / (leaf biomass + stem biomass);  
 main root to lateral root ratio (MLR) = main root biomass / lateral root biomass.

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The total biomass in monocultures was averaged from the two individuals in the same pot.

The effect of interaction between the two species was assessed by the relative competition index (RCI). The RCI was calculated with the following equation (Werner et al. 2010):

$$RCI = (TB_{ii} - TB_{ij}) / TB_{ij}$$

where  $TB_{ii}$  stands for the average total biomass of one species in monoculture, and  $TB_{ij}$  for the total biomass of the same species in mixture.

After the measurement of biomass, 4 to 6 leaf samples in each treatment were kept for the determination of leaf nitrogen (LN) and leaf phosphorus (LP) concentrations with the Kjeldahl method and the Molybdenum antimony-D-isoascorbic-acid colorimetry method (Yuan et al. 2013). Then the photosynthetic nitrogen use efficiency (PNUE) and photosynthetic phosphorus use efficiency (PPUE)

(Hidaka and Kitayama 2009) were calculated as follows:

$$PNUE = A_{max} / (LN \times LMA \times 1/14)$$

$$PPUE = A_{max} / (LP \times LMA \times 1/31)$$

where LMA means leaf mass per area, the reciprocal of SLA; 14 and 31 are the relative atomic masses of N and P.

Soil samples were collected from all pots after the experiment for chemical analyses. Soil available N was analyzed with the alkaline hydrolysis diffusion method (Zhang et al. 2013) and soil available P was analyzed colorimetrically after extraction by sodium bicarbonate (Olsen et al. 1954). The chemical analyses of soil were performed at Shandong Agricultural University.

## Statistical analysis

Two-way analysis of variance (ANOVA) was performed to test the effects of cultivation and N treatment and their

interactions. One-way ANOVA and Duncan’s multiple range tests (DMRT) at  $p \leq 0.05$  were conducted to find the differences among treatments. Before ANOVA, the data were checked for normality and homogeneity of variance. When necessary, log transformation or square root transformation was applied. All statistical analyses were performed with the SPSS 17.0 software (SPSS Inc., Chicago, IL, USA). All figures were drawn with the Origin 8.0 software (Originlab Co., Northampton, MA, USA).

**Results**

**Plant growth**

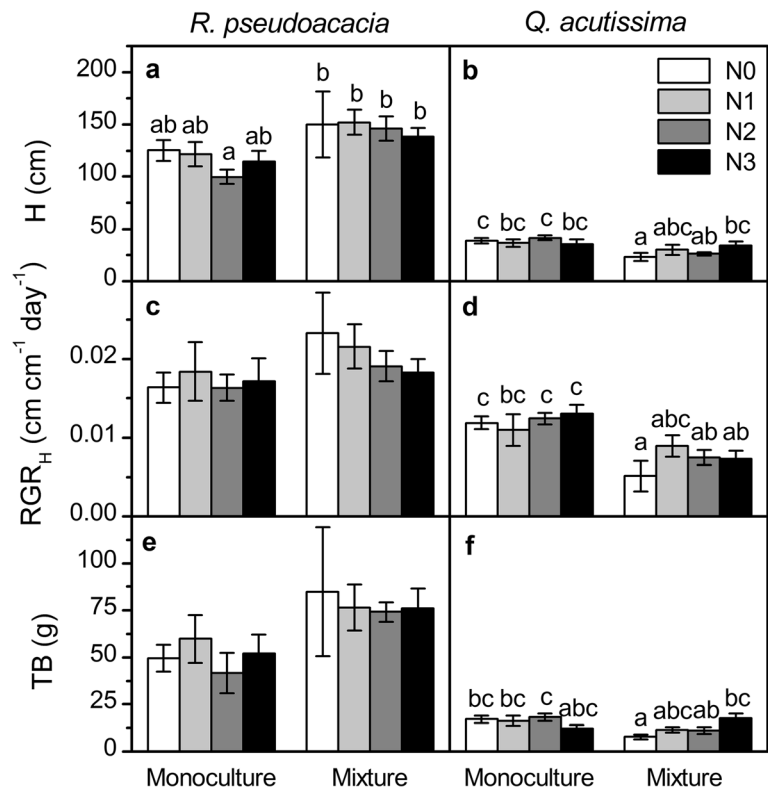
The seedling height (H), relative growth rate of height ( $RGR_H$ ) and total biomass (TB) of *R. pseudoacacia* were much higher than those of *Q. acutissima* (Fig. 1). For *R. pseudoacacia*, mixed cultivation significantly increased H (Table 2, Fig. 1). In mixture, H of *R. pseudoacacia* tended to be higher compared with monoculture, but the differences were mostly not statistically significant (Fig. 1a). No significant interaction was confirmed between cultivation and N addition (Table 2).

For *Q. acutissima*, H,  $RGR_H$  and TB were all significantly decreased by mixed cultivation, but N addition did not show significant effects (Table 2, Fig. 1). H was 40.1, 18.0 and 36.7 % lower in mixture than in monoculture under the N0, N1 and N2 treatments and significant differences were observed for the N0 and N2 treatments (Fig. 1b). In mixture,  $RGR_H$  was lower than that in monoculture, and the differences were statistically significant in all N treatments except for N1 (Fig. 1d). TB was 54.5, 29.1 and 39.1 % lower in mixture than in monoculture under the N0, N1 and N2 treatments, and significant differences were observed for the N0 and N2 treatments (Fig. 1f). Specifically, we found a significant interaction between cultivation and N addition on the TB of *Q. acutissima* (Table 2). In monoculture, TB did not exhibit significant changes among N treatments; in mixture, TB showed an obvious rising trend with the addition of N and was significantly higher in N3 than in the N0 treatment (Fig. 1f).

**Biomass allocation**

The root to shoot ratio (RSR) and main root to lateral root ratio (MLR) of *R. pseudoacacia* were both distinctly

**Fig. 1** Seedling height (H), relative growth rate of height ( $RGR_H$ ) during the nitrogen treatment and total biomass (TB) of *R. pseudoacacia* (a, c, e) and *Q. acutissima* (b, d, f) under different cultivations and nitrogen additions. The values are shown as mean  $\pm$  SE ( $n=4-6$ ). Different letters denote significant differences ( $p \leq 0.05$ ) with Duncan’s test



lower than those of *Q. acutissima* in all N treatments (Fig. 2). For *Q. acutissima*, RSR was significantly increased by mixed cultivation (Table 2, Fig. 2). In mixture, it was significantly higher than in monoculture except for the N1 treatment (Fig. 2b).

#### Leaf traits

Nitrogen addition did not significantly affect the leaf traits of the two species, and cultivation only significantly influenced the PPUE and SLA of *Q. acutissima* (Table 2). The  $A_{max}$ , PNUE, PPUE and SLA of *R. pseudoacacia* were all much higher than those of *Q. acutissima* (Fig. 3).

In addition, the leaf N:P ratios of the two species in mixture were significantly affected by N addition. The leaf N:P ratio of *R. pseudoacacia* under the N3 treatment was significantly lower than that under N1 (Fig. 4a), while for *Q. acutissima*, it was significantly lower with N addition than in the control group (Fig. 4b).

#### Competitive effects of *R. pseudoacacia* on *Q. acutissima*

The relative competition index (RCI, derived from the total biomass of *Q. acutissima*) was significantly

affected by N addition. With increasing N deposition, it showed an obvious declining trend and a significant difference was found between the N0 and N3 treatments. With the highest N addition level, the RCI was negative, while in the other three N treatments it was positive (Fig. 5).

#### Soil available N and P

After the experiment, the soil available N was not significantly different among the three cultivation types. However, the soil available P in the monoculture of *Q. acutissima* was significantly higher than that in mixture and the monoculture of *R. pseudoacacia* among most N treatments (Table 3).

## Discussion

#### Plant growth

In our experiment, the seedling height (H), relative growth rate of height (RGR<sub>H</sub>) and total biomass (TB) of *Q. acutissima* all tended to be lower in mixture than in monoculture under the same N treatment. Significant differences were observed for H and TB under the 0

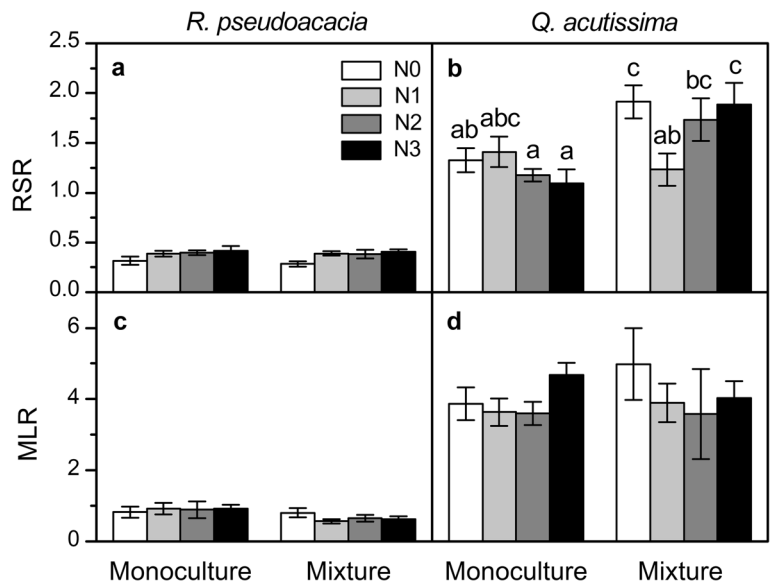
**Table 2** Two-way ANOVA of the effects of cultivation (C) and nitrogen addition (N) on plant growth, biomass allocation and leaf traits of *R. pseudoacacia* and *Q. acutissima*

Measurements	<i>R. pseudoacacia</i>			<i>Q. acutissima</i>		
	C	N	C × N	C	N	C × N
Plant growth						
H	10.865**	0.604	0.603	14.748***	0.439	1.847
RGR <sub>H</sub>	4.020	0.335	0.194	28.053***	0.630	1.215
TB	8.443**	0.260	0.199	7.400**	0.461	4.808**
Biomass allocation						
RSR	0.331	3.580*	0.084	14.475***	1.069	3.568*
MLR	4.938*	0.040	1.027	0.071	1.557	0.815
Leaf traits						
$A_{max}$	0.001	0.681	0.934	0.039	0.766	1.149
PNUE	0.666	1.932	4.318*	1.072	1.049	0.173
PPUE	0.005	1.903	1.212	4.899*	0.894	1.172
SLA	1.241	0.321	0.045	8.645**	0.168	1.167

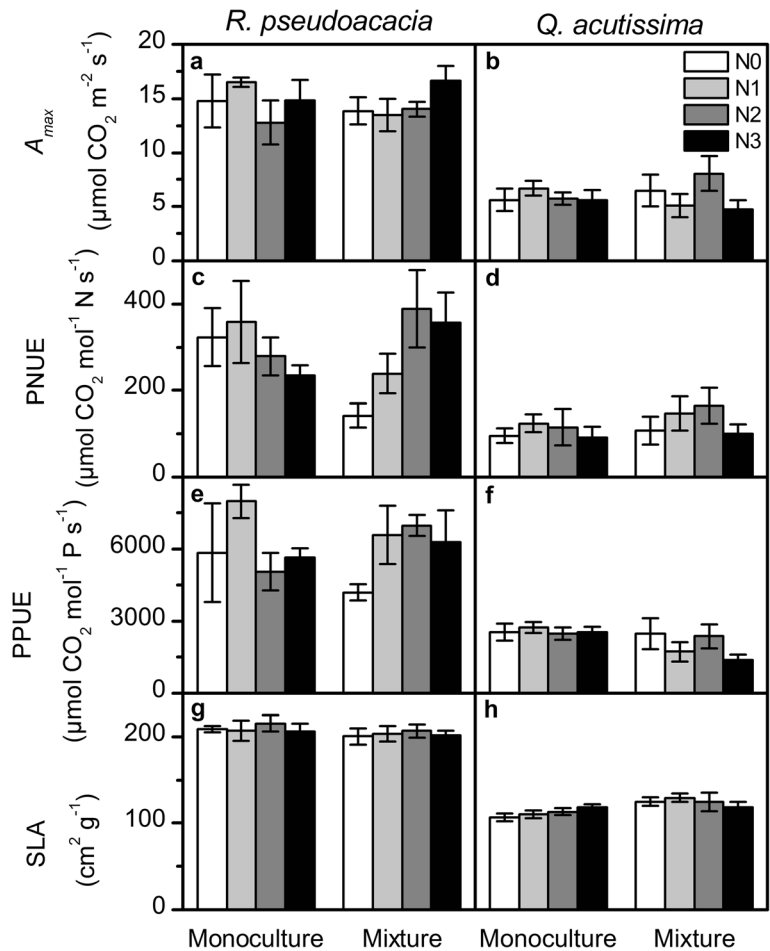
H seedling height, RGR<sub>H</sub> relative growth rate of height, TB total biomass, RSR root to shoot ratio, MLR main root to lateral root ratio,  $A_{max}$  maximum net photosynthetic rate, PNUE photosynthetic nitrogen use efficiency, PPUE photosynthetic phosphorus use efficiency, SLA specific leaf area. H, RGR<sub>H</sub>, TB, RSR, MLR:  $n=4-6$ ,  $A_{max}$ , PNUE, PPUE:  $n=3-4$ , SLA:  $n=5-6$

Numbers in the table represent *F* values; asterisks indicate significant effects: \*\*\*  $p \leq 0.001$ , \*\*  $p \leq 0.01$  and \*  $p \leq 0.05$

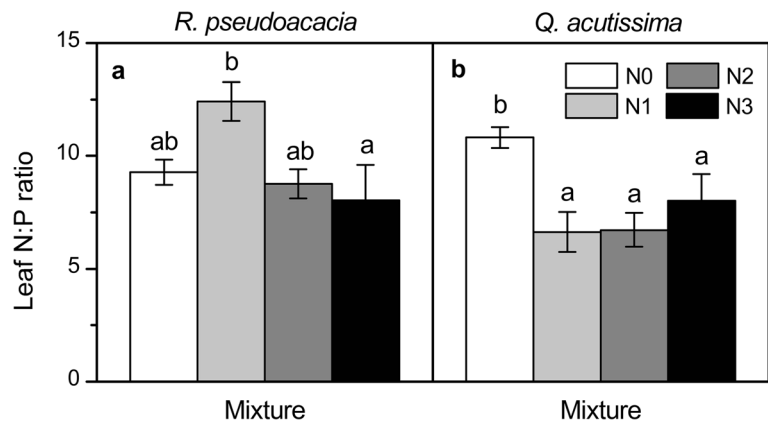
**Fig. 2** Root to shoot ratio (RSR) and main root to lateral root ratio (MLR) of *R. pseudoacacia* (a, c) and *Q. acutissima* (b, d) under different cultivations and nitrogen additions. The values are shown as mean ± SE (n=4–6). Different letters denote significant differences (p≤0.05) with Duncan’s test



**Fig. 3** Maximum net photosynthetic rate ( $A_{max}$ ) (n=3–4), photosynthetic nitrogen use efficiency (PNUE) (n=3–4), photosynthetic phosphorus use efficiency (PPUE) (n=3–4) and specific leaf area (SLA) (n=5–6) of *R. pseudoacacia* (a, c, e, g) and *Q. acutissima* (b, d, f, h) under different cultivations and nitrogen additions. The values are shown as mean ± SE. Different letters denote significant differences (p≤0.05) with Duncan’s test



**Fig. 4** Leaf N:P ratio of *R. pseudoacacia* (a) and *Q. acutissima* (b) in mixture under different nitrogen additions. The values are shown as mean  $\pm$  SE ( $n=4-6$ ). Different letters denote significant differences ( $p\leq 0.05$ ) with Duncan's test



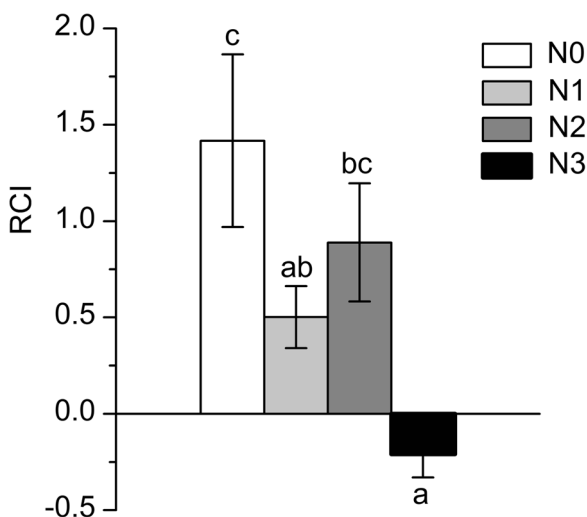
and  $6 \text{ g m}^{-2} \text{ year}^{-1}$  N levels and  $\text{RGR}_H$  under all but the  $3 \text{ g m}^{-2} \text{ year}^{-1}$  N level. These results suggested that the growth of *Q. acutissima* was inhibited by *R. pseudoacacia*. For *R. pseudoacacia*, H,  $\text{RGR}_H$  and TB were mostly not significantly different under the same N treatment between the two cultivation types, indicating that it was largely unaffected by *Q. acutissima*. Therefore, we can conclude that there was an obvious competition between the two species and that *R. pseudoacacia* was the superior competitor. *R. pseudoacacia* was also reported to be strongly competitive with some other native species (Kawaletz et al. 2013a, b). Although it has been confirmed that some exotic species from the Fabaceae family can facilitate the growth of co-occurring native species by sharing the products of

$\text{N}_2$ -fixation (Yang et al. 2009; Hellmann et al. 2011), they may compete with native plants if other limiting resources exist, such as water or soil phosphorus (Kawaletz et al. 2013b).

#### Functional traits under competition

Invasive species are often characterized by a series of functional traits that act synergistically to confer competitive success (Morris et al. 2011). These traits usually include high growth rate, biomass production, photosynthetic rate, and SLA, and efficient use of available resources (Jiang et al. 2009; Lamarque et al. 2011). In our experiment, *R. pseudoacacia* showed a much higher relative growth rate of height ( $\text{RGR}_H$ ) than *Q. acutissima*. From the perspective of community succession, *R. pseudoacacia* is an early successional species that is usually typified by fast growth, especially in the early stage (Boring and Swank 1984; Closset-Kopp et al. 2007; Callaway et al. 2011). This high relative growth rate may lead *R. pseudoacacia* to acquire more resources from the soil, resulting in resource depletion and hindering the growth of neighboring plants (Kawaletz et al. 2013b). Above the ground, the fast-growing *R. pseudoacacia* may overtop *Q. acutissima* rapidly and out-compete it for light since height is the key factor in determining the success of light competition between individuals (Gorchov and Trisiel 2003).

According to Hoffmann and Poorter (2002),  $A_{max}$  and SLA are the most important factors influencing relative growth rate. Generally, SLA is highly negatively correlated with cell wall mass (Onoda et al. 2004), which is linked to leaf toughness, a basic defensive trait (Feng et al. 2009). To grow faster, plants have to distribute more resources to the photosynthetic apparatus, and thus less to



**Fig. 5** Relative competition index (RCI) of *R. pseudoacacia* and *Q. acutissima* in mixture under different nitrogen additions. The values are shown as mean  $\pm$  SE ( $n=4-6$ ). Different letters denote significant differences ( $s\leq 0.05$ ) with Duncan's test



**Table 3** Soil available N and P concentrations after the experiment in mixture and monocultures under four N treatments

Nitrogen treatment (g m <sup>-2</sup> year <sup>-1</sup> )	Monoculture (mg kg <sup>-1</sup> ) ( <i>Q. acutissima</i> )	Mixture (mg kg <sup>-1</sup> )	Monoculture (mg kg <sup>-1</sup> ) ( <i>R. pseudoacacia</i> )
Soil available N			
0	50.38±2.89 ab	54.26±3.17 abc	62.07±4.03 c
3	54.27±3.64 abc	60.69±3.28 c	57.00±1.48 bc
6	48.18±2.41 a	52.91±2.09 abc	56.12±1.67 abc
12	54.10±2.55 abc	62.80±4.34 c	61.47±1.99 c
Soil available P			
0	29.18±1.73 cd	22.67±3.63 abc	19.56±2.33 ab
3	31.03±1.04 d	22.34±1.03 abc	19.39±3.03 ab
6	25.76±2.51 bcd	21.34±1.53 ab	22.38±3.43 ab
12	32.41±1.92 d	19.48±1.20 ab	18.19±2.32 a

Values in the table are the mean ± SE of 4–6 replicates; different letters represent significant differences ( $p \leq 0.05$ ) with Duncan's multiple range test

structural defense (Feng et al. 2009). Therefore, the much higher SLA of *R. pseudoacacia* may indicate that compared with *Q. acutissima*, it allocated less resources to structural defense and more to photosynthesis, leading to a high  $A_{max}$  and growth rate. In addition, the greater SLA may help *R. pseudoacacia* increase light capture and reduce CO<sub>2</sub> diffusion resistance, and thus to maintain a high  $A_{max}$  and biomass production (Hanba et al. 1999; Hidaka and Kitayama 2009).

The root structure and strategy of biomass allocation might also confer *R. pseudoacacia* a strong competitive ability. The nutrient acquisition of plants is largely affected by root structure, which includes root spatial distribution, surface area and biomass (Lambers et al. 2008). *R. pseudoacacia* is able to both produce deep roots and spread roots horizontally (Stone and Kalisz 1991; Cierjacks et al. 2013), forming an extensive root system. In our experiment, *R. pseudoacacia* produced a much lower main root to lateral root ratio (MLR) than *Q. acutissima*. Therefore, *R. pseudoacacia* occupied most of the rooting space of the pot in mixture with *Q. acutissima*. By intruding into the shared rooting space, *R. pseudoacacia* may obtain additional resources from the soil and hamper the growth of *Q. acutissima* by decreasing its resource supply. Additionally, the large lateral root biomass produced by *R. pseudoacacia* conferred it a large root surface area, which also helps plants absorb nutrients effectively (Yuan et al. 2013). Compared with *Q. acutissima*, *R. pseudoacacia* showed a distinctly lower root to shoot ratio. However, because of its strong photosynthetic capacity and high growth rate, *R. pseudoacacia* in mixture produced 3.4 to 9.8 times more total biomass than *Q. acutissima* under different N levels. Therefore, even with a much lower root to shoot

ratio, it was still able to maintain 1.0 to 2.8 times greater root biomass than *Q. acutissima* and acquire a large amount of nutrients. Moreover, by allocating more biomass aboveground, *R. pseudoacacia* was able to achieve a tall shoot and a large canopy, which enabled it to capture light effectively and suppress the growth of *Q. acutissima* by shading it.

In addition to active nutrient acquisition, *R. pseudoacacia* also showed higher photosynthetic nitrogen and phosphorus use efficiency than *Q. acutissima* in all treatments. Invasive species usually use resources more efficiently than native species (Jiang et al. 2009; Godoy et al. 2011) and this has been predicted to be a crucial feature determining the invasiveness of exotic species (Funk and Vitousek 2007). This strong ability to use resources effectively may also confer *R. pseudoacacia* an advantage to outperform native plants.

Under the strong competition of *R. pseudoacacia*, *Q. acutissima* also changed its strategy for growth and biomass allocation. Compared with monoculture, *Q. acutissima* grown in mixture significantly increased its biomass allocation to roots. This was consistent with the balanced growth hypothesis, which suggests that plants may increase the biomass allocated to organs involved in nutrient acquisition when faced with deficient resource supply (Shipley and Meziane 2002). Because of the high growth rate and strong ability to take up nutrients of *R. pseudoacacia*, *Q. acutissima* may well face a resource deficiency. Therefore, the altered biomass allocation was a response to limited soil resource availability. Although the light available to *Q. acutissima* also decreased because of the shading by *R. pseudoacacia*, alleviating the belowground resource deficiency by

increasing biomass partitioning to roots was more important for *Q. acutissima*. Similar results were also reported by Jose et al. (2003). By contrast, there were no significant changes in the biomass allocation of *R. pseudoacacia* between above- and below-ground organs, suggesting its strong competitiveness or increased resource acquisition efficiency (Kawaletz et al. 2013a). Although *Q. acutissima* adopted this strategy, it still could not offset the strong competition from *R. pseudoacacia*. Its relative growth rate was significantly lower in mixture than in monoculture and its biomass production was also lower in most N treatments.

#### Competitive effects of *R. pseudoacacia* on *Q. acutissima* under increasing N deposition

According to Dukes and Mooney (1999), increased N deposition may create beneficial conditions for fast-growing invasive species, thus disadvantaging slow-growing native species. Many studies have also confirmed that under increased N availability, the rapid response to N enrichment favored invasive species and the competition pressure on less N-responsive native species was intensified (Vasquez et al. 2008; He et al. 2012). However, in our experiment, N addition alleviated the competitive effects of *R. pseudoacacia* on *Q. acutissima*, as indicated by the RCI, which showed a declining trend with increasing N level. At the highest N addition level, RCI was negative and significantly different from that in the control group. Nonetheless, we could not conclude that the growth of *Q. acutissima* was facilitated by *R. pseudoacacia* under the highest N level, since there was no significant increase in the growth of *Q. acutissima* compared with monoculture.

The negative impacts of *R. pseudoacacia* on *Q. acutissima* were mitigated because in mixture the total biomass of *Q. acutissima* gradually increased while that of *R. pseudoacacia* remained unchanged with increasing N deposition. In monoculture, the total biomass of *Q. acutissima* was not significantly affected by N addition and the soil available N after the experiment was not significantly different from that in mixture, suggesting that the increasing total biomass of *Q. acutissima* in mixture was not promoted by N itself. Combined with the fact that *Q. acutissima* is well adapted to nutrient-poor habitats (Wang and Zhou 2000), we consider that N was not a major limiting factor for the growth of *Q. acutissima*. By contrast, in mixture, the soil available P after the experiment was significantly lower than that in

the monoculture of *Q. acutissima* and showed an obvious decline relative to the soil before the experiment, which indicates that *R. pseudoacacia* may possess a strong competitive capacity for soil P. Other researchers have also concluded that N<sub>2</sub>-fixing species may absorb disproportionately larger amounts of P since the N<sub>2</sub>-fixation process requires a high P level (Killingbeck 1993; Uliassi and Ruess 2002). Additionally, in view of the report that most soils in China are P-limited for plants (Han et al. 2005) and the limited amount of soil used in the pot experiment, *Q. acutissima* in mixture probably experienced P deficiency.

However, there are physiological processes by which plants can enhance their acquisition of P by using N, and as such, higher soil N levels become beneficial in P-limited environments (Treseder and Vitousek 2001; Marklein and Houlton 2012). In mixture, the leaf N:P ratio of *Q. acutissima* with N addition was significantly lower than that in the control group. Nutrients in leaves can be obtained from within the plants and from the soil (Lukac et al. 2010; Liu et al. 2013a), and explicitly mirror the short-term nutrient demands of plants. Therefore, we can conclude that N addition probably mitigated the P deficiency of *Q. acutissima* in mixture caused by the strong competitiveness of *R. pseudoacacia*. Liu et al. (2013a) also found that N addition significantly lowered the leaf N:P ratios of two tree species and suggested that N addition could help the plants to alleviate P limitation. With increased N availability, plants are able to invest excess N to structure extracellular phosphatases (Treseder and Vitousek 2001), which mineralize soil organic P and release phosphate for plants (Pant and Warman 2000). Since they are anchored on the root surface, most of the released phosphate can be obtained by the same plant (Treseder and Vitousek 2001). A meta-analysis by Marklein and Houlton (2012) also suggested that across a wide range of biomes, N fertilization substantially improved the activity of phosphatase on plant roots, thus postponing the negative effects of P deficiency on plant productivity.

As a N<sub>2</sub>-fixing species, *R. pseudoacacia* is able to reduce atmospheric N<sub>2</sub> to available N through symbiotic rhizobia (Cierjacks et al. 2013). The estimated N fixation rates of this species vary from 23 to 300 kg ha<sup>-1</sup> year<sup>-1</sup> (Danso et al. 1995; Noh et al. 2010; Cierjacks et al. 2013), which is comparable with or even much higher than the simulated N deposition rate in our experiment. As a result, short-term addition of N may not promote

the growth of *R. pseudoacacia*. Compared with *Q. acutissima*, the leaf N:P ratio of *R. pseudoacacia* in mixture did not show an obvious trend with increasing N addition. Therefore, we could not infer the nutrient status of *R. pseudoacacia* from the results of our experiment. If the growth of *R. pseudoacacia* was also restricted by soil P availability, increased N addition may not alleviate the P limitation because of the high P requirement for rapid growth and N<sub>2</sub>-fixation (Uliassi and Rues 2002; Vitousek et al. 2010). As a result, the growth of *R. pseudoacacia* could not be promoted either. Nevertheless, the reason why increased N addition did not stimulate the growth of *R. pseudoacacia* was unclear and the underlying mechanisms remain to be explored.

In short, because of its widely recognized invasiveness and extensive use in reforestation, the relationships between *R. pseudoacacia* and native plants remain a matter of concern in the context of future global change. In this study, seedlings were only treated with N deposition for 3 months; therefore, the results may not reflect the responses of mature trees to long-term N deposition accurately. Since greenhouse studies cannot simulate the complicated biotic and abiotic environmental factors in natural conditions, our results should not be extrapolated to the field arbitrarily.

## Conclusion

In summary, *R. pseudoacacia* adopted an active strategy for resource absorption and utilization. In competition with *Q. acutissima*, *R. pseudoacacia* achieved success in resource acquisition through a high growth rate in the early stage as well as a high root biomass. In return, it was able to invest more resources into photosynthesis and growth, and thus obtain a higher biomass and greater competitive advantage. However, the competitive effects of *R. pseudoacacia* on *Q. acutissima* were alleviated with increasing N deposition. Like N, P is also an important nutrient element for plant growth and is often limited in the soil. Since P deficiency may limit or alter the responses of plants to increased N availability, in the future, pot experiments with both elevated N and P availability should be conducted for *R. pseudoacacia* and native plants. In addition, to reflect the effects of *R. pseudoacacia* on native forests accurately, field experiments are also necessary.

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