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The allelopathic effects of invasive plant *Solidago canadensis* on seed germination and growth of *Lactuca sativa* enhanced by different types of acid deposition

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Abstract Invasive species can exhibit allelopathic effects on native species. Meanwhile, the types of acid deposition are gradually changing. Thus, the allelopathic effects of invasive species on seed germination and growth of native species may be altered or even enhanced under conditions with diversified acid deposition. This study aims to assess the allelopathic effects (using leaves extracts) of invasive plant *Solidago canadensis* on seed germination and growth of native species *Lactuca sativa* treated with five types of acid deposition with different SO_4^{2-} to NO_3^- ratios (1:0, sulfuric acid; 5:1, sulfuric-rich acid; 1:1, mixed acid; 1:5, nitric-rich acid; 0:1, nitric acid). *Solidago canadensis* leaf extracts exhibited significantly allelopathic effects on germination index, vigor index, and germination rate index of *L. sativa*. High concentration of *S. canadensis* leaf extracts also similarly exhibited significantly allelopathic effects on root length of *L. sativa*. This may be due to that *S. canadensis* could release allelochemicals and then trigger allelopathic effects on seed germination and growth of *L. sativa*. Acid deposition exhibited significantly negative effects on seedling biomass, root length, seedling height, germination index, vigor index, and germination rate index of *L. sativa*. This may be ascribed to the decreased soil pH values mediated by acid deposition which could produce toxic effects on seedling growth. Sulfuric acid deposition triggered more toxic effects on seedling biomass and vigor index of *L. sativa* than nitric acid deposition. This may be attributing to the difference in exchange capacity with hydroxyl groups (OH^-) between SO_4^{2-} and NO_3^- as well as the fertilizing effects mediated by nitric deposition. All types of acid deposition significantly enhanced the allelopathic effects of *S. canadensis* on root length, germination index, vigor index, and germination rate index of *L. sativa*. This may be due to the negatively synergistic effects of acid deposition and *S. canadensis* on seed germination and growth of *L. sativa*. The ratio of SO_4^{2-} to NO_3^- in acid deposition was an important factor that profoundly affected the allelopathic effects of *S. canadensis* on the seed germination and growth of *L. sativa* possibly because the difference in exchange capacity with hydroxyl groups (OH^-) between SO_4^{2-} and NO_3^- as well as the fertilizing effects triggered by nitric deposition. Thus, the allelopathic effects of invasive species on seed germination and growth of native plants might be enhanced under increased and diversified acid deposition.

Keywords Acid deposition · Allelopathic effects · Seed germination · Invasive plant · *Solidago canadensis*

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Introduction

With the continuing increase in human activities in recent decades, numerous regions have been seriously affected by environmental pollution, such as acid deposition; this phenomenon is especially serious in the three largest acid rain areas in the world (i.e., United States, Europe, and China) (Zhang et al. 2007; Wang and Xu 2009; Zhang and Chang 2012). Acid deposition is a global problem that triggers changes in ecosystem functions, such as the decrease of soil pH (Wang et al. 2010, 2011, 2012a; Lv et al. 2014), reduction in microbial function (Wang et al. 2010, 2011; Lv et al. 2014), alteration of forest species composition (Schaberg et al. 2001), and plant litter decomposition (Wang et al. 2010, 2011, 2012a; Lv et al. 2014). The major sources of acid deposition are sulfur dioxide (SO_2) and nitrogen oxides (NO_x), which react with water molecules in the atmosphere to produce acids (Zhang et al. 2007). Since the late 1990s, the proportion of sulfate ion (SO_4^{2-}) in precipitation has shown a decreasing tendency along with emerging policies on controlling and mitigating SO_2 emissions and energy structure changes in China (Tu et al. 2005; Liu and Chen 2007; Lv et al. 2014). Meanwhile, the emission of NO_x increased because of the enormous increase in the number of motor vehicles and the amount of fertilizer application. The relative contribution of nitrate ion (NO_3^-) to acidification has subsequently increased in China (Tu et al. 2005; Liu and Chen 2007; Lv et al. 2014). Thus, the ratio of SO_4^{2-} to NO_3^- in precipitation in China has decreased, and the type of acid deposition is changing from acid rain dominated by sulfuric acid rain to acid rain with a mixture of sulfuric and nitric acids (mixed acid rain, MAR), and then to acid rain dominated by nitric acid (NAR) in China (Xu and Ji 2001; Tu et al. 2005; Liu and Chen 2007; Lv et al. 2014). The change in acid deposition types further complicates the ongoing challenge of ecosystem functions (Xu and Ji 2001; Lv et al. 2014). Thus, a single type of acid deposition experiment cannot provide a precise image of its ecological effects.

As one of the major global environmental problems, biological invasion has incurred serious threats to native ecosystems; in particular, changing the structure and/or functions of the ecosystems in which these invasions occur (Powell et al. 2013; Si et al. 2013; Yuan et al. 2013). Numerous studies have suggested that certain plants successfully invade certain environments because such species could release toxic chemicals that have remarkably allelopathic effects on the seed germination and growth of native species (Yang et al. 2007; Abhilasha et al. 2008; Sun and He 2010; Yuan et al. 2013). As one of the most destructive and widespread invasive species, *Solidago canadensis* is now widely distributed throughout most provinces in China, particularly in Southern China (Abhilasha et al. 2008; Yang et al. 2008; Zhao et al. 2015). Meanwhile, increasing amounts of anthropogenic acid precipitation are also deposited into ecosystems in China (Wang et al. 2007; Zhang et al. 2007; Wang and Xu 2009; Zhang and Chang 2012). As natural atmospheric acid deposition involves various components and the types of acid deposits may change in the future (Xu and Ji 2001; Tu et al. 2005; Liu and Chen 2007; Lv et al. 2014), diversification in the type of anthropogenic acid deposition may complicate the invasion mechanisms of invasive plants. Thus, the increasing degree of plant invasion poses a question of the potential allelopathic effects of the notorious invader *S. canadensis* on seed germination and growth of native species, especially under different types of acid deposition. Most studies on the effects of acid deposition on the allelopathic effects of invasive plants have focused on the effects of a single acid rain type with different acidity gradients (Wang et al. 2012a, b). However, knowledge on the effects of different types of acid deposition (especially MAR) on the allelopathic effects of invasive plants on the seed germination and growth of native species is limited.

S. canadensis is a herbaceous perennial plant of the Asteracea family. This plant is native to North America. *S. canadensis* was introduced to Shanghai, China, as a horticultural plant in the early 1930s. At present, the species has become naturalized in most of China and is one of the most destructive and widespread invasive species in the country. *S. canadensis* poses a serious threat to the diversity and/or abundance of native plants and agricultural productivity in the country (Abhilasha et al. 2008; Yang et al. 2008; Zhao et al. 2015). To date, the species has been established in Europe, large parts of Asia, Australia, and New Zealand (Weber 2001; Lu et al. 2007) and grows mainly in meadows and pastures, along roads, ditches, upland forests, savannas, and limestone glades (Abhilasha et al. 2008). *S. canadensis* is a highly aggressive plant. Once established, the plant can reduce species diversity or locally out-compete all native plants (Abhilasha et al. 2008). The severe allelopathic effects of *S. canadensis* on native species is cited as a main reason for its successful invasion (Yang et al. 2007; Abhilasha et al. 2008; Sun and He 2010; Yuan et al. 2013). Meanwhile, *Lactuca sativa* (Asteracea) seeds are sensitive to allelochemicals (Jefferson et al. 2003; Hao et al. 2007). This study addressed the following hypotheses: (1) *S. canadensis* exhibit allelopathic effects on seed germination and growth of *L. sativa* (Yang et al. 2007; Abhilasha et al. 2008; Sun and He 2010; Yuan et al. 2013); (2) acid deposition has negative effects on seed germination and growth of *L. sativa* (Fan and Wang 2000), and such effects vary with acid deposition types; and (3) the allelopathic effects of *S. canadensis* on seed germination and growth of *L. sativa* may be enhanced under acid deposition (Wang et al. 2012a, b), and such effects vary with acid deposition types.

Materials and methods

Materials

In this study, *S. canadensis* was selected as the invasive species. Leaves of *S. canadensis* were collected from Zhenjiang (32.20°N, 119.51°E), China. The leaf samples were washed, air dried for 48 h and then stored at 4 °C for further study. *L. sativa* seeds, which were selected as the native seeds, were bought from a local vegetable market.

Leaf extract preparation

Air-dried leaves of *S. canadensis* (80 g) were placed in flasks containing 800 mL distilled water and were soaked for 48 h at room temperature. Extracts were strained through cheese cloth and two layers of filter paper to remove solid material. The stock solution (100 g L^{-1}) was stored at 4 °C for further study. Dilutions were made with distilled water prior to use to create a series with gradient contents, namely, CK (control, 0 g L^{-1}), LE1 (25 g L^{-1}), and LE2 (50 g L^{-1}).

Experimental design

Experiments were performed by incubation in Petri dishes. *L. sativa* seeds were surface-sterilized (1 % NaClO for approximately 15 min) and then thoroughly washed thrice with deionized water. Thirty whole seeds of *L. sativa* were placed in a 9 cm Petri dish and covered with two layers of filter paper. The seeds were treated with 10 mL of *S. canadensis* leaf extracts or sterile deionized water (CK). In this experiment, we used a full-factorial experimental design with three contents of *S. canadensis* leaf extracts × five types of simulated acid deposition. Five types of simulated acid deposition were prepared by mixing 0.5 M L^{-1} H_2SO_4 and 0.5 M L^{-1} HNO_3 at ratios of 1:0 (sulfuric acid, SA), 5:1 (sulfuric-rich acid, SRA), 1:1 (mixed acid, MAR), 1:5 (nitric-rich acid, NRA), and 0:1 (nitric acid, NA). For MAR, the pH value of basic solution was finally buffered to 5.6 by adding the stock solutions of H_2SO_4 and HNO_3 at a ratio of 1:1. For the four other types of simulated acid deposition, the pH values of basic solution were finally buffered to 5.0 by adding the five stock solutions. In this study, pH 5.6 and the ratio of 5:1 for SO_4^{2-} and NO_3^- were the natural values of unpolluted rainfall, and pH 5.0 was the approximate annual average pH value of rainfall in the study site (Wang et al. 2007). The samples were incubated in a climate-controlled incubator at 25 °C with diurnal lighting (light intensity was set at 2200 Lux on a 12:12 h light–dark cycle) for 7 days Five replicates were performed per treatment. During the incubation, deionized water, simulated acid rain, and/or *S. canadensis* leaf extracts were supplied daily according to the amount of precipitation in the study site. The number of germinated seeds was counted daily at incubation time, and each seed was considered to have germinated when the radicle emerges.

Data measurements

Ten seedlings per Petri dish were selected at random for measurement on the same day. Seedling biomass (BM, fresh weight), root length (RL), seedling height (H), germination rate (GR), germination potential (GP), germination index (GI), vigor index (VI), and germination rate index (GRI) of *L. sativa* were determined.

BM was determined by using an electronic balance with an accuracy of 0.001 g.

RL and H were measured by using a ruler.

GR was calculated by using the ratio of the final numbers of seed germination to the total numbers of seeds when no new germination occurred after 7 days of incubation.

GP was determined by dividing the numbers of seed germination in the third day by the total numbers of seeds.

GI was calculated by using the following equation: $GI = \sum G_i/I$, where G_i is the number of germination in *I* [the time after cultivation (day)] (Schmer et al. 2012).

VI was determined by using the following equation: $VI = GI \times BM$ (Lin et al. 2000).

Germination rate index (GRI) was calculated using the following equation: $GRI = GR \times GI$ (Steinmaus et al. 2000).

Statistical analysis

Data were evaluated to determine the deviations from normality and homogeneity of variance prior to data analysis. Differences among various dependent variables were assessed by using analysis of variance between groups, followed by multiple comparisons by using SPSS (version 17.0). Statistically significant differences were set at *P* values equal to or lower than 0.05.

Results

GI, VI, and GRI of *L. sativa* decreased significantly with increasing concentrations of *S. canadensis* leaf extracts (Fig. 1, $P < 0.05$). Meanwhile, RL of *L. sativa* was also significantly reduced at LE2 treatment (Fig. 1, $P < 0.05$). While, *S. canadensis* leaf extracts did not significantly affect BM, H, GR, and GP of *L. sativa* (Fig. 1, $P > 0.05$).

All types of acid deposition exhibited significantly negative effects on RL, H, and VI of *L. sativa* (Fig. 1, $P < 0.05$). Meanwhile, all types of acid deposition except NA exhibited significantly negative effects on BM of *L. sativa* (Fig. 1, $P < 0.05$). In addition, all types of acid deposition except SA also exhibited significantly negative effects on GI and GRI of *L. sativa* (Fig. 1, $P < 0.05$). All types of acid deposition did not exert significant effects on GR and GP of *L. sativa* (Fig. 1, $P > 0.05$). BM and VI of *L. sativa* under NA treatment were significantly higher than those under SA treatment (Fig. 1, $P < 0.05$). However, the other germination and seedling growth indices of *L. sativa* were not significantly different between NA treatment and

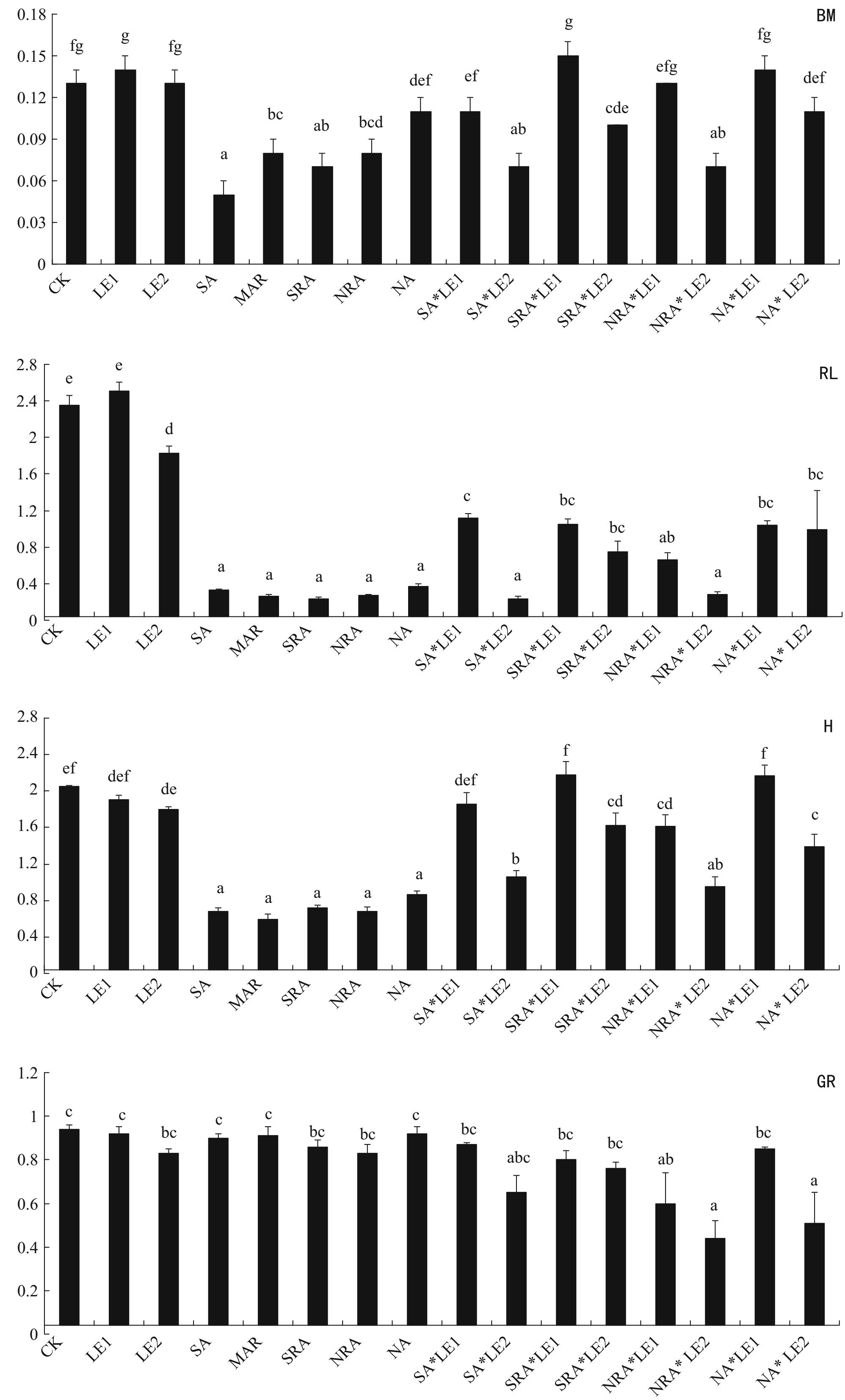

Fig. 1 Indices of *L. sativa* with different treatments. Data with different *letters* indicate a significant difference ($P < 0.05$). *BM* Seedling biomass (fresh weight) (g), *RL* root length (cm), *H* seedling height (cm), *GR* germination rate, *GP* germination potential, *GI* germination index, *VI* vigor index, *GRI* germination rate index

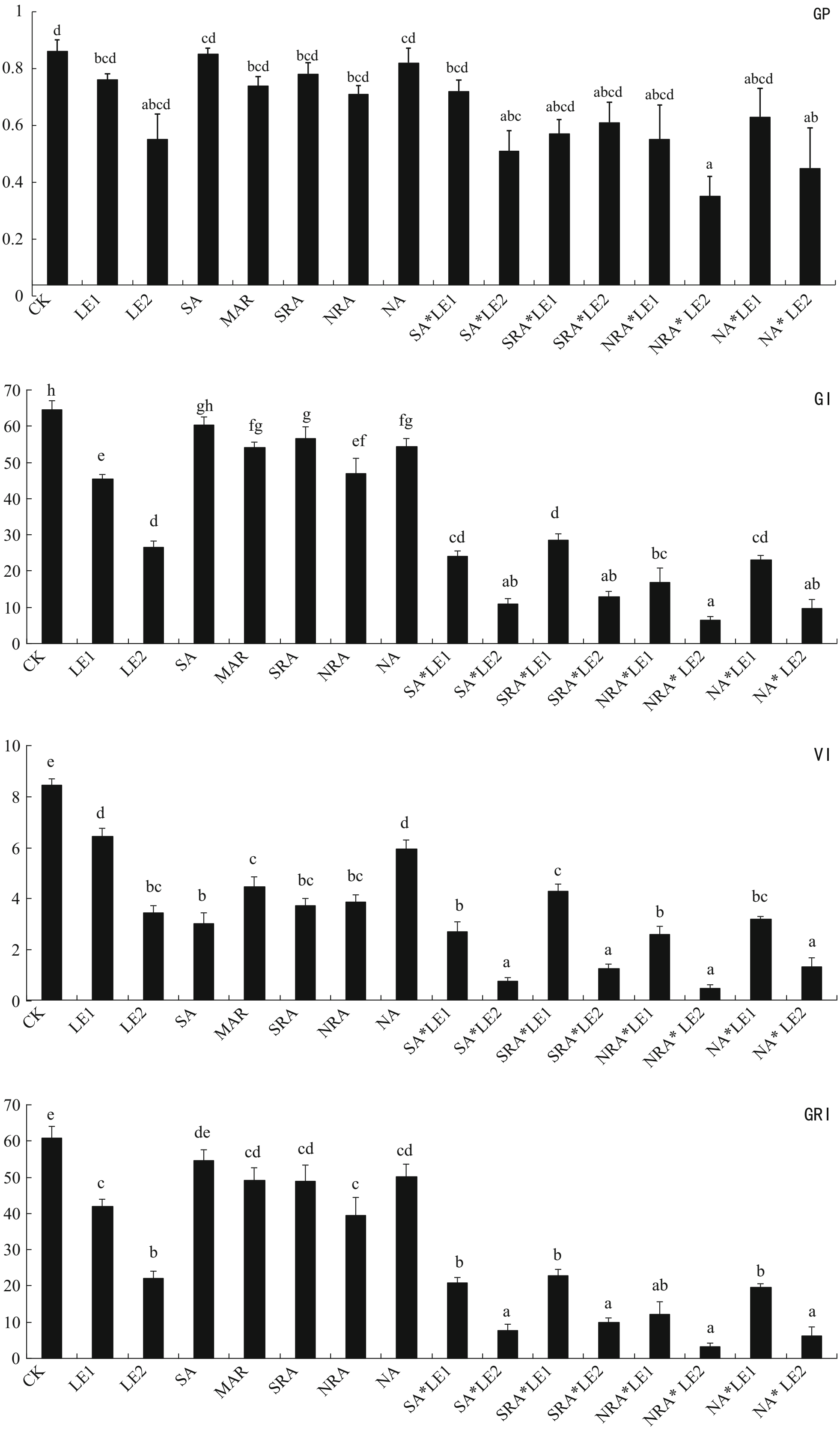

Fig. 1 continued

SA treatment (Fig. 1, $P > 0.05$). GI of *L. sativa* under NRA treatment was significantly lower than that under SRA treatment (Fig. 1, $P < 0.05$). Nevertheless, the difference in the other germination and seedling growth indices of *L. sativa* between NRA treatment and SRA treatment was not significant (Fig. 1, $P > 0.05$).

All types of acid deposition significantly enhanced the allelopathic effects of *S. canadensis* leaf extracts on RL, GI, VI, and GRI of *L. sativa* (Fig. 1, $P < 0.05$). SA, SRA, and NRA treatments significantly enhanced the allelopathic effects of *S. canadensis* leaf extracts on BM of *L. sativa* compared with LE2 treatment (Fig. 1, $P < 0.05$). Similarly, SA treatment significantly enhanced the allelopathic effects of *S. canadensis* leaf extracts on BM of *L. sativa* compared with LE1 treatment (Fig. 1, $P < 0.05$). SA, NRA, and NA treatments significantly enhanced the allelopathic effects of *S. canadensis* leaf extracts on H of *L. sativa* compared with LE2 treatment (Fig. 1, $P < 0.05$). NRA and NA treatments also significantly enhanced the allelopathic effects of *S. canadensis* leaf extracts on GR of *L. sativa* compared with LE2 treatment (Fig. 1, $P < 0.05$). Similarly, NRA treatment significantly enhanced the allelopathic effects of *S. canadensis* leaf extracts on GR of *L. sativa* compared with LE1 treatment (Fig. 1, $P < 0.05$). All types of acid deposition did not significantly affect the allelopathic effects of *S. canadensis* leaf extracts on GP of *L. sativa* (Fig. 1, $P > 0.05$).

Discussion

As one of the most notorious invasive species in China, *S. canadensis* showed strong allelopathic effects on the growth of native species, and this characteristic served a key function in its successful invasion (Yang et al. 2007; Abhilasha et al. 2008; Sun and He 2010; Yuan et al. 2013). The results of this study also showed that *S. canadensis* leaf extracts significantly inhibited seed germination and growth of *L. sativa*. The result was consistent with the first hypothesis and previous studies (Yang et al. 2007; Abhilasha et al. 2008; Sun and He 2010; Yuan et al. 2013). Thus, according to the results, invasive plants could release allelochemicals into the invaded ecosystems and then trigger allelopathic effects on the seed germination and growth of native species to facilitate its further invasion process.

A previous investigator discovered that acid deposition could exert negative effects on seed germination and growth of plants (Fan and Wang 2000). The results of this study also showed that acid deposition depressed seed germination and the growth of *L. sativa* evidently. The inhibited seed germination and growth of *L. sativa* mediated by acid deposition may be ascribed to the decreased soil pH values which could produce toxic effects on plant growth, thereby accelerating the leaching of nutrients from plants (Zhang et al. 2007; Pabian et al. 2012). Meanwhile, the negative effects of acid deposition on seed germination and growth of *L. sativa* varied with the acid deposition types. In particular, sulfuric acid deposition triggered more toxic effects on seedling biomass and vigor index of *L. sativa* than nitric acid deposition. The result may be due to the difference in exchange capacity with hydroxyl groups (OH^-) between SO_4^{2-} and NO_3^- (Christ et al. 1995; Lv et al. 2014). The phenomenon may also be ascribed to nitric deposition possibly exerting a fertilizing effect (Jacobsen et al. 1990). By contrast, sulfuric deposition does not exert a fertilizer effect (Jacobsen et al. 1990). The result was consistent with the second hypothesis, implying that the ratio of SO_4^{2-} to NO_3^- in acid deposition was an important factor that profoundly affected seed germination and growth of *L. sativa*. Previous studies also found that the ratio of SO_4^{2-} to NO_3^- in acid deposition could exert pronounced effects on ecological processes, such as soil microbial biomass (Neuvonen and Suomela 1990) and plant litter decomposition (Lv et al. 2014).

Previous studies showed that acid deposition enhanced the allelopathic potential of invasive species (*Wedelia trilobata*) and then facilitated its invasiveness (Wang et al. 2012a, b). This study achieved the same result. In particular, all types of acid deposition significantly enhanced the allelopathic effects of *S. canadensis* on root length, germination index, vigor index, and germination rate index of *L. sativa*. The phenomenon might be attributed to the following mechanisms. Firstly, in this study, acid deposition and allelopathic compounds all exhibited negative effects on seed germination and growth of *L. sativa*, thereby producing a synergistic effect by their interaction. Secondly, total phenolics (especially polyphenols) constitute some of the primary allelopathic compounds of *S. canadensis* (Zhang et al. 2011; Yuan et al. 2013). Low pH values induced by acid deposition could promote the activity of allelochemicals released by *S. canadensis*, which inhibited seed germination and growth of *L. sativa* presumably because environmental stress factors often enhance allelochemical production and thereby increase potential toxicity (Einhellig 1996; An 2005). Meanwhile, acid rain can also enhance the leaching of acid-soluble materials, such as polyphenols (Lee and Weber 1983). Thirdly, more recalcitrant material often formed after complexation between acid rain and polyphenols (Carreiro et al. 2000). Thus, the results of this study suggested that the allelopathic effects of invasive species on seed germination and growth of native species may be enhanced under acid deposition. Meanwhile, some types of acid deposition significantly enhanced the allelopathic effects of *S. canadensis* on seedling biomass, seedling height, and germination rate of *L. sativa*, respectively. Thus, the enhanced allelopathic effects of *S. canadensis* on the seed germination and growth of *L. sativa* under acid deposition varies with acid deposition types. This trend may be due to the difference in the exchange capacity with hydroxyl groups (OH^-) between SO_4^{2-} and NO_3^- (Christ et al. 1995; Lv et al. 2014), as well as the fertilizing effects of nitric deposition but not sulfuric deposition (Jacobsen et al. 1990). Thus, the ratio of SO_4^{2-} to NO_3^- in acid deposition may perform an important function in the enhanced allelopathic effects of *S. canadensis* on seed germination and growth of *L. sativa*. The result agrees with the third hypothesis.

In general, the allelopathic effects of *S. canadensis* on seed germination and growth of native species may be enhanced under the increased and diversified acid deposition. Meanwhile, the ratio of SO_4^{2-} to NO_3^- in acid deposition is an important factor that profoundly affects the allelopathic effects of *S. canadensis* on seed germination and growth of *L. sativa*. In the future, the ratio of SO_4^{2-} to NO_3^- in acid deposition would change with changes in the natural ecosystem. The influence of the invasion process of invasive species via the variation in allelopathic effects on seed germination and growth of native species would also change.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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