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The nitrogen-sulfur ratio of acid rain modulates the leaf- and root-mediated co-allelopathy of *Solidago canadensis*

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Abstract
The majority of allelopathic studies on invasive plants have focused primarily on their leaf-mediated allelopathy, with relatively little attention paid to their root-mediated allelopathy, especially co-allelopathy mediated by both leaves and roots. It is conceivable that the diversified composition of acid rain may influence the allelopathy of invasive plants. This study aimed to evaluate the leaf and root-mediated co-allelopathy of the invasive plant *Solidago canadensis* L. under acid rain with different nitrogen-sulfur ratios (N/S) on *Lactuca sativa* L. via a hydroponic incubation. The root-mediated allelopathy of *S. canadensis* was found to be more pronounced than the leaf-mediated allelopathy of *S. canadensis* with nitric acid at pH 4.5, but the leaf-mediated allelopathy of *S. canadensis* was observed to be more pronounced than the root-mediated allelopathy of *S. canadensis* with sulfuric-rich acid at pH 4.5. The leaf and root-mediated co-allelopathy of *S. canadensis* was more pronounced than that of either part alone with sulfuric acid at pH 5.6 and nitric acid at pH 4.5, but not with nitric-rich acid at pH 4.5 and sulfuric-rich acid at pH 4.5. Sulfuric acid and sulfuric-rich acid with stronger acidity intensified the leaf-mediated allelopathy of *S. canadensis*. Nitric acid and nitric-rich acid attenuated the leaf-mediated allelopathy of *S. canadensis*, and most types of acid rain (especially nitric acid and nitric-rich acid) also attenuated the root-mediated allelopathy of *S. canadensis* and the leaf and root-mediated co-allelopathy of *S. canadensis*. Sulfuric acid and sulfuric-rich acid produced a more pronounced effect than nitric acid and nitric-rich acid. Hence, the N/S ratio of acid rain influenced the allelopathy of *S. canadensis* under acid rain with multiple N/S ratios.

Keywords Allelopathic chemicals · Hydroponic incubation · *Lactuca sativa* L. · Leaf aqueous extracts · Root aqueous extracts

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Introduction

Invasive plants have the potential to significantly alter the community composition of native ecosystems (Wang et al. 2019; Nsikani et al. 2021; Sampaio et al. 2021; Dimitrakopoulos et al. 2022). Elucidating the mechanisms that facilitate the successful establishment of invasive species is a significant and compelling task for ecologists (Glisson et al. 2022; Keet and Richardson 2022; Xu et al. 2023; Yu et al. 2023a).

A multitude of invasive plants have been observed to gain a competitive advantage by releasing the allelopathic chemicals that interfere with or even inhibit the establishment and growth of their competitors (Girotto et al. 2021; Sucur et al. 2021; Xu et al. 2023; Yu et al. 2023b). The allelopathic chemicals released by invasive plants can cause significant allelopathy on the seed germination and seedling growth (abbreviated as Sge-sgr) of their competitors, especially native plants (Cheng et al. 2021a; Mozdzen et al.

2021; Xu et al. 2023; Yu et al. 2023b). The allelopathic chemicals of invasive plants are primarily released from their leaves (including leaf debris) and roots (through root secretions) (Chon and Nelson 2011; Ferreira et al. 2020; Sun et al. 2021; Yu et al. 2022; Wang et al. 2024). Nevertheless, research on the allelopathy of invasive plants has predominantly focused on the leaf-mediated allelopathy, with relatively little attention paid to the root-mediated allelopathy, especially co-allelopathy mediated by both leaves and roots (Yu et al. 2022).

China is among the top three regions in the world most affected by acid rain (Liu et al. 2017; Wang et al. 2017b; Du et al. 2020; Zhong et al. 2022). China is currently undergoing a transformation in the composition of acid rain, shifting from sulfuric-rich acid rain to mixed sulfuric and nitric acid rain with an increased ratio of nitrogen to sulfur (N/S) in rainfall in China. This change has been attributed to the alterations in the adjustment of energy policy, particularly the strict control of coal use (Liu et al. 2017; Du et al. 2020; Zhong et al. 2022; Zhong et al. 2023). However, the alterations in the type of acid rain may alter the competitive advantage of invasive plants by changing their allelopathy (Wang et al. 2012a; Wang et al. 2012b; Wang et al. 2016; Cheng et al. 2021a; Zhong et al. 2023). Consequently, it is of great importance to elucidate the allelopathy of invasive plants with a particular focus on the leaf and root-mediated co-allelopathy of invasive plants, under the influence of multiple types of acid rain. This will facilitate an understanding of the mechanisms that drive the successful invasion of invasive plants under different acid rain regimes. However, there has been minimal advancement in this field.

This study aimed to evaluate the leaf (using the leaf aqueous extracts, abbreviated as SCL) and root (using the root aqueous extracts, abbreviated as SCR)-mediated co-allelopathy of the invasive plant *Solidago canadensis* L. under acid rain with multiple N/S ratios on Sge-sgr of *Lactuca sativa* L. via a hydroponic incubation. As an Asteraceae perennial herb, *S. canadensis* originated in North America and was introduced as an ornamental plant in China during the 1930s. The successful spread of this plant is mainly attributed to its allelopathy (Zandi et al. 2020; Cheng et al. 2021a; Yu et al. 2022; Zhou et al. 2022). *Lactuca sativa* is a commonly encountered horticultural plant in the environments (e.g., agricultural land and wasteland), where *S. canadensis* also thrives. Due to the high sensitivity of Sge-sgr to the allelopathic chemicals, *L. sativa* has been extensively studied in the field of allelopathic research (Kyaw and Kato-Noguchi 2020; Rob et al. 2020; da Cruz-Silva et al. 2021; Medic et al. 2021). The regions of China where *S. canadensis* is present have been subjected to severe acid rain with multiple N/S ratios (Wang et al. 2016; Liu et al. 2018; Liu et al. 2020; Cheng et al. 2021a).

This study investigated three questions: (i) Which of the two parts, leaf or root, is the primary source of the allelopathy of *S. canadensis*? (ii) Does the leaf and root-mediated co-allelopathy of *S. canadensis* result in synergistic effects on *L. sativa* that are greater than those observed when either part is considered separately? (iii) Does acid rain, and if so, which type, intensify the leaf and root-mediated co-allelopathy of *S. canadensis*?

Materials and methods

Preparation of SCL and SCR

The leaf and root samples of *S. canadensis* were collected from Zhenjiang (32.20–32.22°N, 119.51–119.53°E), China in late September 2021. The collected leaf and root samples of *S. canadensis* were meticulously cleaned and air-dried at 25 °C until the weight remained constant. The air-dried leaf and root samples of *S. canadensis* were leached in sterile distilled water at a concentration of 10 g L^{-1} (Lu et al. 2020; Yu et al. 2023b; Zhong et al. 2023; Li et al. 2024) for ≈48 h at 25 °C to obtain the SCL and SCR of *S. canadensis*. The SCL and SCR of *S. canadensis* were applied to *L. sativa* seeds, either alone (representing the condition with the leaf-mediated allelopathy or the root-mediated allelopathy of *S. canadensis*) or combined SCL and SCR (abbreviated as SCRL) at a 1:1 *v/v* mixture (representing the condition with the leaf and root-mediated co-allelopathy of *S. canadensis*), in comparison to distilled water as the control (0 g L^{-1}; representing the condition without the allelopathy of *S. canadensis*). The SCL and SCR were stored at 4 °C for a maximum of 7 d to prevent contamination by bacteria and the production of algae.

Preparation of acid rain solution

Acid rain solution was prepared to simulate acid rain by mixing 0.5 M HNO_3 and 0.5 M H_2SO_4 with two acidity levels (i.e., pH 5.6 and pH 4.5; representing the condition with acid rain). In general, the pH of normal rainfall without acid rain and the pH of natural rainfall in Zhenjiang are ≈5.6 and ≈4.5, respectively; and NO_3^- and SO_4^{2-} were the main acidic components of natural rainfall in Zhenjiang (Wang et al. 2016; Liu et al. 2017; Liu et al. 2018; Zhong et al. 2022). The modeled acid rain comprised four types with different N/S ratios: (1) nitric acid (N/S ratio = 1:0); (2) sulfuric acid (N/S ratio = 0:1); (3) nitric-rich acid (N/S ratio = 3:1); and (4) sulfuric-rich acid (N/S ratio = 1:3) (Wang et al. 2017b; Zhong et al. 2023). Distilled water (pH 7.0; representing the absence of acid rain) was used as the control.

Experimental design of hydroponic incubation

The seeds of *L. sativa* (cultivar name: cv. Chunfeng) were surface-sterilized by inimmersion in 1% NaClO for ≈15 min and subsequently washed with deionized water for ≈30 min. A total of 30 seeds of *L. sativa* with uniform in size were placed in a Petri dish (9 cm) with two layers of filter paper per treatment. The Petri dishes were maintained at a temperature of ≈25 °C with a 12-hour light cycle from April 1^{st} to April 8^{th}, 2022. The light intensity was ≈27.5 µmol m^{-2} s^{-1}. During the incubation period, 1 mL of deionized water, the SCL and SCR, or acid rain solution was added to each Petri dish daily. The SCL and SCR, and acid rain solution in the combined treatments were mixed in an equivalent ratio. The number of seeds that had undergone normal germination was confirmed daily basis throughout the course of the hydroponic incubation. Germination was defined as the emergence of the radicle.

The hydroponic incubation of *L. sativa* involves three factors (i.e., the source of aqueous extracts, the acidity of acid rain, and the type of acid rain). Each factor is categorized into two, three, or four levels, respectively. The source of aqueous extracts is categorized into three levels (i.e., SCL, SCR, and SCRL). The acidity of acid rain is categorized into two levels (i.e., pH 4.5 and pH 5.6). The type of acid rain is categorized into four levels (i.e., nitric acid, sulfuric acid, nitric-rich acid, and sulfuric-rich acid). A total of three Petri dishes were utilized for each treatment, with each dish containing 90 seeds of *L. sativa* per treatment.

Determination of Sge-sgr variables

Following a seven-day period of hydroponic incubation, ten seedlings of *L. sativa* were collected from each Petri dish, thus a total 30 seedlings of *L. sativa* per treatment, which were used for the determination of Sge-sgr variables. This was done in order to evaluate the growth status of *L. sativa*.

The stress intensity of the treatments on Sge-sgr variables was calculated using the stress intensity index.

The methodology employed for the measurement of Sge-sgr variables and the stress intensity index is detailed in Supplementary Table S1.

Statistical analysis

The deviations from normality and homogeneity of the variances were estimated by employing the Shapiro–Wilks's test and Bartlett's test, respectively. A multiple comparison with the Tukey's test was employed to assess differences in the values of *L. sativa* variables and the stress intensity index among the various treatments. A three-way ANOVA was employed to assess the effects of the source of aqueous extracts, the acidity of acid rain, and the type of acid rain on the values of *L. sativa* variables and the stress intensity index. The Partial Eta Squared (η^2) values were also evaluated to estimate the effect size of each factor for use in two-way ANOVA. Statistically significant differences were indicated by a threshold of $p \leq 0.05$. Statistical analyses were conducted using IBM SPSS Statistics (26.0).

Results

Effects of aqueous extracts of *S. canadensis* on *L. sativa* seed germination variables under acid rain with multiple N/S ratios

The sources of aqueous extracts did not significantly affect all seed germination variables compared to the control (Fig. 1a–e; $p > 0.05$). The acidity and type of acid rain also did not significantly affect the germination percentage or the germination potential (Fig. 1a, b; $p > 0.05$).

SCL treated with sulfuric acid and sulfuric-rich acid at pH 4.5 significantly reduced the germination index compared to SCL (Fig. 1c; $p < 0.05$). SCR treated with sulfuric acid at pH 4.5 significantly reduced the germination index compared to SCR (Fig. 1c; $p < 0.05$). SCRL treated with nitric acid at pH 4.5 significantly reduced the germination index compared to SCRL (Fig. 1c; $p < 0.05$). SCL treated with sulfuric acid, nitric-rich acid, and sulfuric-rich acid at pH 4.5 significantly reduced the germination index compared to SCL treated with those types of acid rain at pH 5.6 (Fig. 1c; $p < 0.05$). SCR treated with sulfuric acid at pH 4.5 significantly reduced the germination index compared to SCR treated with sulfuric acid at pH 5.6 (Fig. 1c; $p < 0.05$). SCRL treated with nitric acid at pH 4.5 significantly reduced the germination index compared to SCRL treated with nitric acid at pH 5.6 (Fig. 1c; $p < 0.05$). The germination index under SCL treated with nitric acid and nitric-rich acid was significantly higher than that under SCL treated with sulfuric acid and sulfuric-rich acid regardless of the acidity (Fig. 1c; $p < 0.05$). The germination index under SCR treated with nitric acid at pH 5.6 was significantly higher than that under SCR treated with sulfuric acid, nitric-rich acid, and sulfuric-rich acid at pH 5.6 (Fig. 1c; $p < 0.05$). The germination index under SCR treated with nitric acid at pH 4.5 was significantly higher than that under SCR treated with sulfuric acid at pH 4.5 (Fig. 1c; $p < 0.05$). The germination index under SCRL treated with nitric-rich acid at pH 4.5 was significantly higher than that under SCRL treated with nitric acid at pH 4.5 (Fig. 1c; $p < 0.05$).

SCL treated with sulfuric acid and sulfuric-rich acid at pH 4.5 significantly reduced the germination rate index

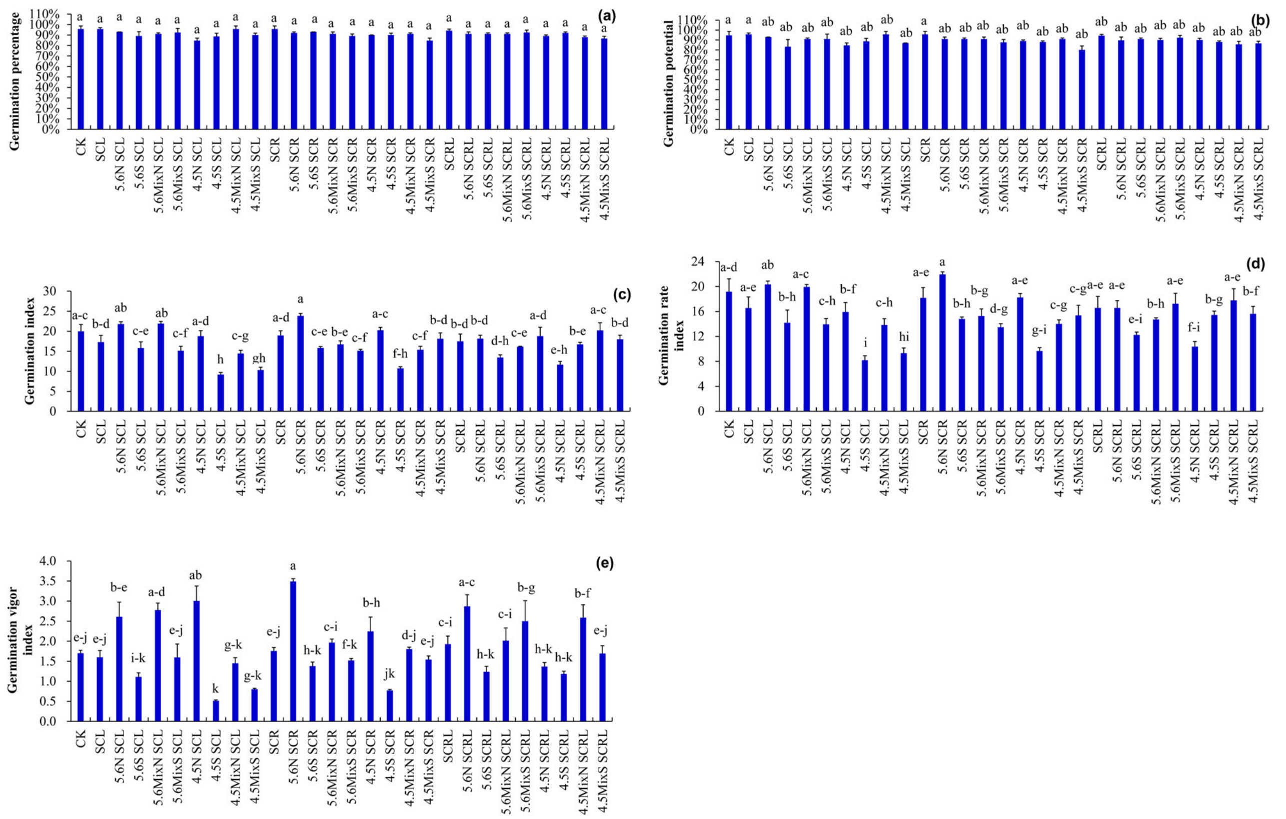

Fig. 1 The values (means and SE; $n = 30$) of seed germination variables of *L. sativa* (**a**, germination percentage; **b**, germination potential; **c**, germination index; **d**, germination rate index; **e**, germination vigor index). Bars with different letters indicate statistically significant differences ($p < 0.05$). CK control, SCL leaf aqueous extracts of *S. canadensis*, SCR root aqueous extracts of *S. canadensis*, SCRL combined leaf and root aqueous extracts, N nitric acid, S sulfuric acid, MixN nitric-rich acid, MixS sulfuric-rich acid, 5.6 acid rain at pH 5.6, 4.5 acid rain at pH 4.5

compared to SCL (Fig. 1d; $p < 0.05$). Both SCR and SCRL treated with sulfuric acid at pH 4.5 significantly reduced the germination rate index compared to SCR and SCRL, respectively (Fig. 1d; $p < 0.05$). SCL treated with sulfuric acid at pH 4.5 significantly reduced the germination rate index compared to SCL treated with sulfuric acid at pH 5.6 (Fig. 1d; $p < 0.05$). SCRL treated with nitric acid at pH 4.5 significantly reduced the germination rate index compared to SCRL treated with nitric acid at pH 5.6 (Fig. 1d; $p < 0.05$). The germination rate index under SCL treated with nitric acid was significantly higher than that under SCL treated with sulfuric-rich acid regardless of the acidity (Fig. 1d; $p < 0.05$). The germination rate index under SCL treated with nitric acid and nitric-rich acid at pH 4.5 was also significantly higher than that under SCL treated with sulfuric acid at pH 4.5 (Fig. 1d; $p < 0.05$). The germination rate index under SCR treated with nitric acid at pH 5.6 was significantly higher than that under SCR treated with sulfuric acid, nitric-rich acid, and sulfuric-rich acid at pH 5.6 (Fig. 1d; $p < 0.05$). The germination rate index under SCR treated with nitric acid at pH 4.5 was significantly higher than that under SCR treated with sulfuric acid at pH 4.5 (Fig. 1d; $p < 0.05$). The germination rate index under SCRL treated with nitric-rich acid at pH 4.5 was significantly higher than that under SCRL treated with nitric acid at pH 4.5 (Fig. 1d; $p < 0.05$).

SCL treated with nitric-rich acid at pH 5.6 significantly increased the germination vigor index compared to SCL (Fig. 1e; $p < 0.05$). SCL treated with nitric acid at pH 4.5 significantly increased the germination vigor index but SCL treated with sulfuric acid at pH 4.5 significantly reduced the germination vigor index compared to SCL (Fig. 1e; $p < 0.05$). SCR treated with nitric acid at pH 5.6 significantly increased the germination vigor index compared to SCR (Fig. 1e; $p < 0.05$). SCL treated with nitric-rich acid at pH 4.5 significantly reduced the germination vigor index compared to SCL treated with nitric-rich acid at pH 5.6 (Fig. 1e; $p < 0.05$). Both SCR and SCRL treated with nitric acid at 4.5 significantly reduced the germination vigor index compared to SCR and SCRL treated with nitric acid at pH 5.6, respectively (Fig. 1e; $p < 0.05$). The germination vigor index under both SCL and SCRL treated with nitric acid at pH 5.6 was significantly higher than that under SCL and SCRL treated with sulfuric acid at pH 5.6, respectively (Fig. 1e; $p < 0.05$). The germination vigor index under SCL treated with nitric-rich acid at pH 5.6 was also significantly higher than that under SCL treated with sulfuric acid and sulfuric-rich acid at pH 5.6 (Fig. 1e; $p < 0.05$). The germination vigor index under SCL treated with nitric acid at pH 4.5 was significantly higher than that under SCL treated with sulfuric acid, nitric-rich acid, and sulfuric-rich acid at pH 4.5 (Fig. 1e; $p < 0.05$). The germination vigor index under SCR treated with nitric acid at pH 5.6 was significantly higher than that under SCR treated with sulfuric acid, nitric-rich acid, and sulfuric-rich acid at pH 5.6 (Fig. 1e; $p < 0.05$). The germination vigor index under SCR treated with nitric acid at pH 4.5 was significantly higher than that under SCR treated with sulfuric acid at pH 4.5 (Fig. 1e; $p < 0.05$).

Effects of aqueous extracts of *S. canadensis* on *L. sativa* seedling growth variables under acid rain with multiple N/S ratios

All sources of aqueous extracts did not significantly affect seedling height compared to the control (Fig. 2a; $p > 0.05$). All sources of aqueous extracts treated with all types of acid rain at pH 5.6 significantly increased seedling height compared to only aqueous extracts (Fig. 2a; $p < 0.05$). SCL treated with sulfuric acid and sulfuric-rich acid at pH 4.5 significantly reduced and increased seedling height compared to SCL, respectively (Fig. 2a; $p < 0.05$). SCR treated with sulfuric acid at pH 4.5 significantly increased seedling height compared to SCR (Fig. 2a; $p < 0.05$). SCRL treated with nitric acid and sulfuric acid at 4.5 significantly reduced seedling height compared to SCRL (Fig. 2a; $p < 0.05$). Seedling height under all sources of aqueous extracts treated with all types of acid rain at pH 5.6 was significantly higher than that under all sources of aqueous extracts treated with all types of acid rain at pH 4.5 (except under SCL treated with sulfuric-rich acid) (Fig. 2a; $p < 0.05$). Seedling height under SCL treated with nitric acid and nitric-rich acid was significantly higher than that under SCL treated with sulfuric acid and sulfuric-rich acid regardless of the acidity (Fig. 2a; $p < 0.05$). Seedling height under SCR treated with nitric acid at pH 5.6 was significantly higher than that under SCR treated with sulfuric acid at pH 5.6 (Fig. 2a; $p < 0.05$). Seedling height under SCR treated with nitric acid and nitric-rich acid at pH 4.5 was significantly higher than that under SCR treated with sulfuric acid at pH 4.5 (Fig. 2a; $p < 0.05$). Seedling height under SCRL treated with sulfuric acid at pH 5.6 was

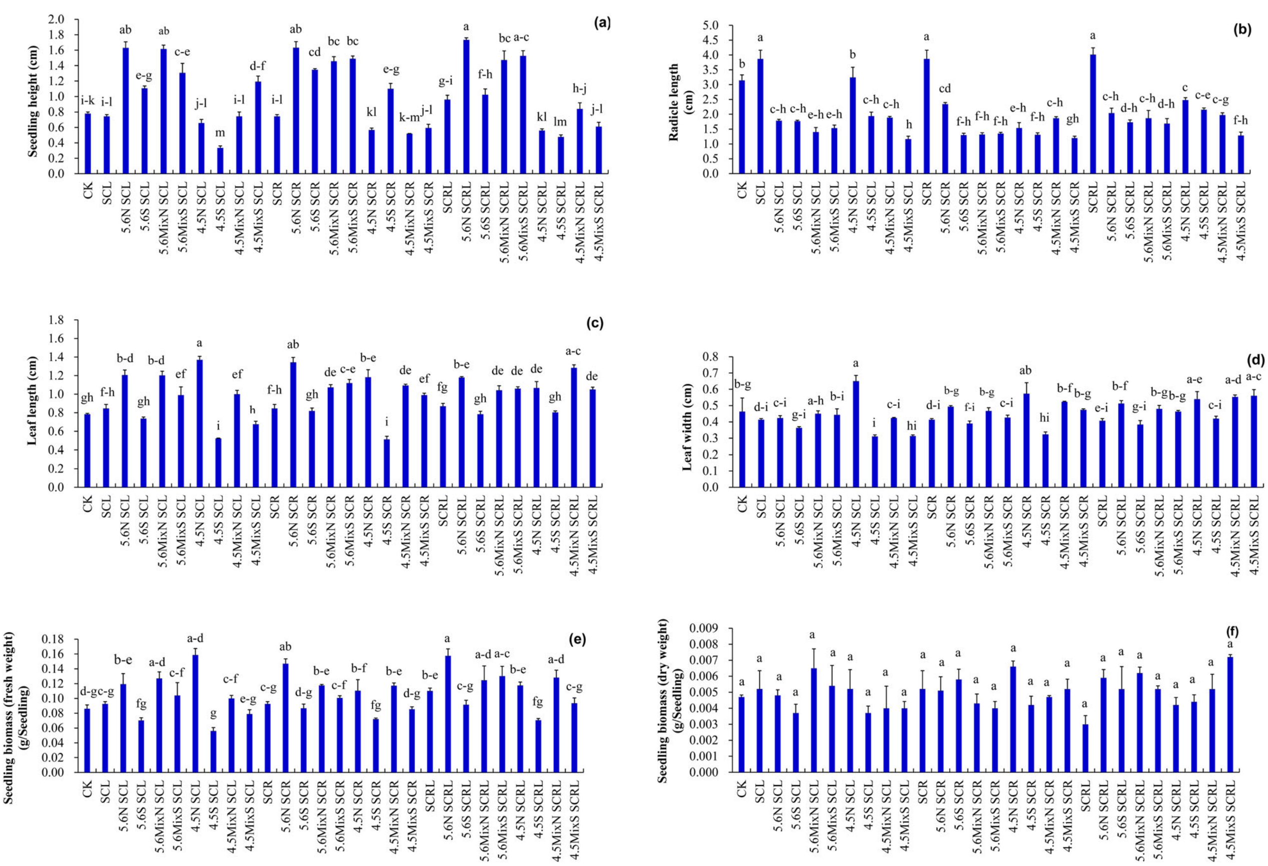

Fig. 2 The values (means and SE; $n = 30$) of seedling growth variables of *L. sativa* (**a**, seedling height; **b**, radicle length; **c**, leaf length; **d**, leaf width; **e**, fresh weight; **f**, dry weight). Bars with different letters indicate statistically significant differences ($p < 0.05$). Abbreviations have the same meanings as defined in Fig. 1

significantly lower than that under SCRL treated with nitric acid, nitric-rich acid, and sulfuric-rich acid at pH 4.5 (Fig. 2a; $p < 0.05$). Seedling height under SCRL treated with nitric-rich acid at pH 4.5 was significantly higher than that under SCR treated with nitric acid and sulfuric acid at pH 4.5 (Fig. 2a; $p < 0.05$).

All sources of aqueous extracts significantly increased radicle length compared to the control (Fig. 2b; $p < 0.05$). All sources of aqueous extracts treated with all types of acid rain regardless of the acidity significantly increased radicle length compared to only aqueous extracts (Fig. 2b; $p < 0.05$). Radicle length under SCL treated with nitric acid at pH 5.6 was significantly higher than that under SCL treated with nitric acid at pH 4.5, but it's the opposite for SCR (Fig. 2b; $p < 0.05$). Radicle length under SCL treated with nitric acid at pH 4.5 was significantly higher than that under SCL treated with sulfuric acid, nitric-rich acid and sulfuric-rich acid at pH 4.5 (Fig. 2b; $p < 0.05$). Radicle length under SCR treated with nitric acid at pH 5.6 was significantly higher than that under SCR treated with sulfuric acid, nitric-rich acid and sulfuric-rich acid at pH 5.6 (Fig. 2b; $p < 0.05$). Radicle length under SCRL treated with nitric acid and sulfuric acid at pH 4.5 was significantly higher than that under SCRL treated with sulfuric-rich acid at pH 4.5 (Fig. 2b; $p < 0.05$).

All sources of aqueous extracts did not significantly affect leaf length compared to the control (Fig. 2c; $p > 0.05$). SCL treated with nitric acid and nitric-rich acid at pH 5.6 significantly increased leaf length compared to SCL (Fig. 2c; $p < 0.05$). SCL treated with nitric acid and sulfuric acid at pH 4.5 significantly increased and decreased leaf length compared to SCL, respectively (Fig. 2c; $p < 0.05$). SCR treated with nitric acid, nitric-rich acid, and sulfuric-rich acid at pH 5.6 significantly increased leaf length compared to SCR (Fig. 2c; $p < 0.05$). SCR treated with nitric acid and nitric-rich acid at pH 4.5 significantly increased leaf length, but SCR treated with sulfuric acid at pH 4.5 significantly decreased leaf length, compared to SCR (Fig. 2c; $p < 0.05$). SCRL treated with nitric acid, nitric-rich acid, and sulfuric-rich acid regardless of the acidity significantly increased leaf length compared to SCRL (Fig. 2c; $p < 0.05$). Leaf length under SCL treated with nitric acid at pH 5.6 was significantly higher than that under SCL treated with nitric acid at pH 4.5, but it's the opposite for sulfuric acid, nitric-rich acid, and sulfuric-rich acid (Fig. 2c; $p < 0.05$). Leaf length under SCR treated with sulfuric acid at pH 5.6 was significantly higher than that under SCR treated with sulfuric acid at pH 4.5 (Fig. 2c; $p < 0.05$). Leaf length under SCRL treated with nitric-rich acid at pH 5.6 was significantly lower than that under SCRL treated with nitric-rich acid at pH 4.5 (Fig. 2c; $p < 0.05$). Leaf length under all sources of aqueous extracts treated with different types of acid rain regardless of the acidity generally exhibited a decreasing order as follows: nitric acid > nitric-rich acid > sulfuric-rich acid > sulfuric acid (Fig. 2c; $p < 0.05$).

All sources of aqueous extracts did not significantly affect leaf width compared to the control (Fig. 2d; $p > 0.05$). SCL and SCR treated with nitric acid regardless of the acidity significantly increased leaf width compared to SCL and SCR, respectively (Fig. 2d; $p < 0.05$). Leaf width under SCL treated with nitric acid at pH 5.6 was significantly higher than that under SCL treated with nitric acid at pH 4.5 (Fig. 2d; $p < 0.05$). Leaf width under SCL treated with nitric acid at pH 4.5 was significantly higher than that under SCL treated with sulfuric acid, nitric-rich acid, and sulfuric-rich acid at pH 4.5 (Fig. 2d; $p < 0.05$). Leaf width under SCR treated with sulfuric acid at pH 4.5 was significantly lower than that under SCR treated with nitric acid, nitric-rich acid, and sulfuric-rich acid at pH 4.5 (Fig. 2d; $p < 0.05$). Leaf width under SCRL treated with nitric acid at pH 5.6 was significantly higher than that under SCRL treated with sulfuric acid at pH 5.6 (Fig. 2d; $p < 0.05$).

All sources of aqueous extracts did not significantly affect fresh weight compared to the control (Fig. 2e; $p > 0.05$). SCR and SCRL treated with nitric acid at pH 5.6 significantly increased fresh weight compared to SCR and SCRL, respectively (Fig. 2e; $p < 0.05$). Fresh weight under SCRL treated with nitric acid at pH 5.6 was significantly higher than that under SCRL treated with nitric acid at pH 4.5 (Fig. 2e; $p < 0.05$). Fresh weight under SCL treated with sulfuric acid was significantly lower than that under SCR treated with nitric acid and nitric-rich acid regardless of the acidity (Fig. 2e; $p < 0.05$). Fresh weight under SCR treated with nitric acid at pH 5.6 was significantly higher than that under SCR treated with sulfuric acid and sulfuric-rich acid at pH 5.6 (Fig. 2e; $p < 0.05$). Fresh weight under SCR treated with nitric-rich acid at pH 4.5 was significantly higher than that under SCR treated with sulfuric acid at pH 4.5 (Fig. 2e; $p < 0.05$). Fresh weight under SCRL treated with nitric acid at pH 5.6 was significantly higher than that under SCRL treated with sulfuric acid at pH 5.6 (Fig. 2e; $p < 0.05$). Fresh weight under SCRL treated with nitric acid and nitric-rich acid at pH 4.5 was significantly higher than that under SCRL treated with sulfuric acid at pH 4.5 (Fig. 2e; $p < 0.05$).

No significant differences in dry weight were detected among all treatments (Fig. 2f; $p > 0.05$).

Differences in the value of the stress intensity index under aqueous extracts of *S. canadensis* treated with and without acid rain with multiple N/S ratios on *L. sativa* variables

No significant differences in the value of the stress intensity index were detected among all sources of aqueous extracts (Fig. 3; $p > 0.05$). The value of the stress intensity index under all sources of aqueous extracts treated with nitric acid

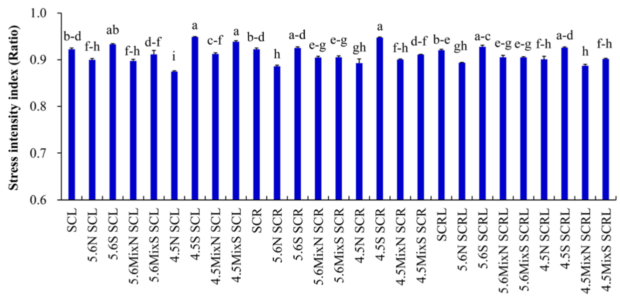

Fig. 3 The values (means and SE; $n = 30$) of the stress intensity index of different treatments on *L. sativa* variables. Bars with different letters indicate statistically significant differences ($p < 0.05$). Abbreviations have the same meanings as defined in Fig. 1

regardless of the acidity was significantly lower than that under only aqueous extracts (Fig. 3; $p < 0.05$). The value of the stress intensity index under SCL and SCR treated with nitric-rich acid at pH 5.6 was significantly lower than that under SCL and SCR, respectively (Fig. 3; $p < 0.05$). The value of the stress intensity index under SCR and SCRL treated with nitric-rich acid at pH 4.5 was significantly lower than that under SCR and SCRL, respectively (Fig. 3; $p < 0.05$). The value of the stress intensity index under SCL and SCR treated with sulfuric acid at pH 4.5 was significantly higher than that under SCL and SCR, respectively (Fig. 3; $p < 0.05$). The value of the stress intensity index under SCL treated with sulfuric-rich acid at pH 4.5 was significantly higher than that under SCL (Fig. 3; $p < 0.05$). The value of the stress intensity index under SCR treated with sulfuric-rich acid at pH 5.6 was significantly lower than that under SCR (Fig. 3; $p < 0.05$). The value of the stress intensity index under SCRL treated with sulfuric-rich acid at pH 4.5 was significantly lower than that under SCRL (Fig. 3; $p < 0.05$). The value of the stress intensity index under all sources of aqueous extracts treated with different types of acid rain regardless of the acidity generally exhibited a decreasing order as follows: sulfuric acid > sulfuric-rich acid > nitric-rich acid > nitric acid (Fig. 3; $p < 0.05$). The value of the stress intensity index under SCL treated with nitric acid at pH 4.5 was significantly lower than that under SCR and SCRL treated with nitric acid at pH 4.5, but it's the opposite for sulfuric-rich acid (Fig. 3; $p < 0.05$). The value of the stress intensity index under SCL treated with nitric-rich acid at pH 4.5 was significantly higherer than that under SCRL treated with nitric-rich acid at pH 4.5 (Fig. 3; $p < 0.05$).

The effects of the source of aqueous extracts, the acidity of acid rain, and the type of acid rain on the values of *L. sativa* variables and the stress intensity index

Based on the results of three-way ANOVA analysis, the source of aqueous extracts significantly affected radicle length, leaf dimensions, fresh weight, and stress intensity index ($p < 0.05$; Supplementary Table S2). The acidity of acid rain significantly affected all Sge-sgr variables (except dry weight) ($p < 0.05$; Supplementary Table S2). The type of acid rain significantly affected the germination index, germination rate index, germination vigor index, seedling height, radicle length, leaf dimensions, fresh weight, and stress intensity index ($p < 0.05$; Supplementary Table S2). The interaction of the source of aqueous extracts and the acidity of acid rain significantly affected the germination index, germination rate index, radicle length, leaf length, and stress intensity index ($p < 0.05$; Supplementary Table S2). The interaction of the source of aqueous extracts and the type of acid rain significantly affected all Sge-sgr variables (except seedling biomass) ($p < 0.05$; Supplementary Table S2). The interaction of the source of the acidity of acid rain the type of acid rain significantly affected the germination index, germination rate index, seedling height, radicle length, leaf length, leaf width, and stress intensity index ($p < 0.05$; Supplementary Table S2). The interaction of the source of aqueous extracts, the acidity of acid rain, and the type of acid rain significantly affected all Sge-sgr variables (except germination percentage, germination potential, and dry weight) ($p < 0.05$; Supplementary Table S2).

Discussion

Allelopathy is a crucial factor in the success of invasive plants (Ferreira et al. 2020; Kalisz et al. 2021; Ullah et al. 2021; Kumar and Garkoti 2022), including *S. canadensis* (Mozdzen et al. 2020; Zandi et al. 2020; Yu et al. 2022; Zhou et al. 2022). The three sources of aqueous extracts of *S. canadensis* did not exhibit any significant allelopathy on *L. sativa*, and only significantly improved the radicle length of *L. sativa* compared to the control (Fig. 2b). This may be attributed to the neutralizing effect of the positive and negative effects of the aqueous extracts of *S. canadensis* on *L. sativa*. The negative effects of the aqueous extracts of invasive plants on their competitors may be mainly due to the allelopathic chemicals that interfere with the physiological processes of the recipient plants. These processes include reduced nutrient uptake, reduced cell division, suppressed cellular functions, and inhibited material synthesis (Amoo et al. 2008; Svensson et al. 2013; Jmii et al. 2020; Zhong et al. 2023). The positive effects of the aqueous extracts of invasive plants on their competitors may be due to the hormonal effects via the reactive oxygen molecules generated (Duke et al. 2006; Agathokleous 2018; Erofeeva 2022; Sebastiano et al. 2022), and/or the facilitated priming effects triggered by the nutrient elements (especially nitrogenous substances) contained in the aqueous extracts of invasive plants (Wang et al. 2020a; Wei et al. 2020a; Wei et al. 2020b).

The allelopathic chemicals of invasive plants originate from both leaf and root (Chon and Nelson 2011; Ferreira et al. 2020; Medina-Villar et al. 2020; Yu et al. 2022). The stress intensity of SCL was found to be lower than that of SCR treated with nitric acid at pH 4.5, whereas the stress intensity of SCL was found to be higher than that of SCR treated with sulfuric-rich acid at pH 4.5 (Fig. 3). Consequently, the allelopathy of SCR was more pronounced than that of SCL treated with nitric acid at pH 4.5, whereas the allelopathy of SCL was more pronounced than that of SCR treated with sulfuric-rich acid at pH 4.5. It can therefore be concluded that the root-mediated allelopathy may be largely attributed to the allelopathy of *S. canadensis* treated with nitric acid at pH 4.5, whereas the leaf-mediated allelopathy may have a stronger contribution to the allelopathy of *S. canadensis* treated with sulfuric-rich acid at pH 4.5. This indicates that the dissimilarities in the allelopathy between the leaf and root of *S. canadensis* may be influenced by the type of acid rain, specifically the N/S ratio of acid rain. One potential explanation for this phenomenon is the varying solubility and metabolic activity of the allelopathic chemicals present in the leaf and root under different types of acid rain (Wang et al. 2016; Zhong et al. 2023). Moreover, it is possible that the quantity and quality of the allelopathic chemicals contained in the leaf and root may diverge due to the morphological and physiological differences between the two organs. Consequently, it can be expected that marked differences in the allelopathy may be observed between leaf and root of invasive plants.

It has been demonstrated that the allelopathic chemicals present in the leaf and root of *S. canadensis* can naturally interact with one another under normal conditions (Yu et al. 2022). Following the mixing of the allelopathic chemicals present in leaf and root of *S. canadensis*, these chemicals can undergo alteration (Yu et al. 2022). The stress intensity of SCRL was found to be higher than that of SCR but it was approximately equal to that of SCL treated with sulfuric acid at pH 5.6, and the stress intensity of SCRL was found to be higher than that of SCL but approximately equal to that of SCR treated with nitric acid at pH 4.5. Conversely, the stress intensity of SCRL was found to be lower than that of SCL whereas it is approximately equal to that of SCR treated with sulfuric-rich acid at pH 4.5, and the stress intensity of SCRL was also found to be lower than that of SCL treated with nitric-rich acid at pH 4.5 (Fig. 3). Thus, SCRL caused stronger co-allelopathy than either part alone treated with sulfuric acid at pH 5.6 and nitric acid at pH 4.5, but conversely with nitric-rich acid at pH 4.5 and sulfuric-rich acid at pH 4.5. Accordingly, the leaf and root of *S. canadensis* exhibited a synergistic co-allelopathy on *L. sativa*, which was more pronounced than that observed when either part was used alone with sulfuric acid at pH 5.6 and nitric acid at pH 4.5, but contrary to that with nitric-rich acid at pH 4.5 and sulfuric-rich acid at pH 4.5. In other words, the leaf and root-mediated co-allelopathy of *S. canadensis* treated with sulfuric acid at pH 5.6 and nitric acid at pH 4.5 can be mainly attributed to its root, but the leaf and root-mediated co-allelopathy of *S. canadensis* treated with nitric-rich acid at pH 4.5 and sulfuric-rich acid at pH 4.5 can be mainly attributed to its leaf. Thus, the leaf and root-mediated co-allelopathy of *S. canadensis* may also be influenced by the type of acid rain, specifically the N/S ratio of acid rain. It can be reasonably assumed that the various types of acid rain may have exerted a significant influence on the synergistic effects of the mixed allelopathic chemicals present in leaf and root (Wang et al. 2016).

Acid rain can affect the secondary metabolic processes, which in turn can influence the production of secondary metabolites by plants (Shumejko et al. 1996; Debnath et al. 2020; Zhang et al. 2020). It has been observed that acid rain has recently increased and is expected to gradually increase in China in the near future (Liu et al. 2017; Du et al. 2020; Zhong et al. 2022; Zhong et al. 2023). Thus, the allelopathy of invasive plants may undergo a transformation, potentially becoming more pronounced in the context of elevated acid rain. Previous studies have also demonstrated that acid rain, particularly when of a higher acidity, can increase the allelopathy of invasive plants (Wang et al. 2012a; Wang et al. 2012b; Wang et al. 2016; Cheng et al. 2021a; Zhong et al. 2023). Normally, abiotic stresses can increase the allelopathy of plants via the enhanced secondary metabolic processes, as proposed by the Stress Hypothesis of Allelopathy (Reigosa et al. 2002). A number of studies have also corroborated this hypothesis (Selmar and Kleinwächter 2013; Hashoum et al. 2021; Zhou et al. 2022; Zhong et al. 2023). The stress intensity of SCL treated with sulfuric acid at pH 4.5 and sulfuric-rich acid) at pH 4.5 was found to be greater than that of SCL (Fig. 3). This result is consistent with the Stress Hypothesis of Allelopathy (Reigosa et al. 2002), which posits that sulfuric acid and sulfuric-rich acid with higher acidity enhance the leaf-mediated allelopathy of *S. canadensis*. This finding may be attributed to the increased acidity, which has been demonstrated to have toxic effects on plant growth. This is evidenced by the increased energy cost and the suppressed nutrient use efficiency for *L. sativa* performance. Another contributing factor may also be, the accelerated extraction and release processes of acid-soluble substances from SCL (Wang et al. 2012a; Wang et al. 2012b; Cheng et al. 2021a; Zhong et al. 2023), such as phenolics (especially polyphenols), which were identified as one of the main components of the allelopathic chemicals of invasive plants (Djurdjević et al. 2011; Djurdjević et al. 2012; Hussain et al. 2020; Stefanowicz et al. 2021). Consequently, the allelopathy of *S. canadensis* as well as sulfuric acid and sulfuric-rich acid with higher acidity, were found to have an antagonistic influence on the performance of *L. sativa*.

It is noteworthy that the stress intensity of SCL with nitric acid regardless of the acidity and nitric-rich acid at pH 5.6 was found to be lower than that with SCL; the stress intensity of SCR with all types of acid rain (except sulfuric acid regardless of the acidity and sulfuric-rich acid at pH 4.5) was found to be lower than that with SCR but in contrast to sulfuric acid at pH 4.5; the stress intensity of SCRL with nitric acid regardless of the acidity, nitric-rich acid at pH 4.5, and sulfuric-rich acid at pH 4.5 was found to be lower than that with SCRL of *S. canadensis* (Fig. 3). It can be concluded that nitric acid and nitric-rich acid have the effect of reducing the leaf-mediated allelopathy of *S. canadensis*, and most types of acid rain (especially nitric acid and nitric-rich acid) also have the effect of reducing the root-mediated allelopathy and the leaf and root-mediated co-allelopathy of *S. canadensis*. This finding may be attributed to the increased nitrogen availability to *L. sativa*, which has been demonstrated to mitigate the adverse effects mediated by the allelopathy of *S. canadensis* (Shen et al. 2008; Wang et al. 2017a; Wang et al. 2020b). Previous research has also demonstrated that the application of exogenous nitrogen can enhance plant resistance to adverse environments largely due to the most essential role of nitrogen in plant growth (Hassan et al. 2005; Hassan et al. 2008; Cheng et al. 2020; Cheng et al. 2021b). The reduced allelopathy of *S. canadensis* with acid rain, especially nitric acid and nitric-rich acid, may also be attributed to the increased application of exogenous nitrogen, which reduces the concentration of phenolics (especially polyphenols) (Guillén-Román et al. 2018; Min and Shi 2018; Sun et al. 2020), but phenolics (especially polyphenols) are one of the major components of the allelopathic chemicals produced by invasive plants (Djurdjević et al. 2011; Djurdjević et al. 2012; Hussain et al. 2020; Stefanowicz et al. 2021). Thus, the effects of acid rain on the allelopathy of *S. canadensis* may also be contingent upon the specific type of acid rain, specifically the N/S ratio of acid rain.

It is of greater significance that the stress intensity after treatment with the three sources of aqueous extracts of *S. canadensis* treated with sulfuric acid was found to be greater than that with the remaining types of acid rain, and the stress intensity generally decreased in the following order: sulfuric acid > sulfuric-rich acid > nitric-rich acid > nitric acid (Fig. 3). It can be concluded that sulfuric acid and sulfuric-rich acid produced a more pronounced effect on *L. sativa* than nitric acid and nitric-rich acid in general. Hence, the influence of acid rain on *L. sativa* increases with the proportion of sulfur and decreases with the proportion of nitrogen. Consequently, the N/S ratio of acid rain is a key issue that profoundly affects its ecological function. This is primarily attributable to the disparities in ion exchange capacity with hydroxyl between nitrate and sulfate ions (Lindberg et al. 1990; Christ et al. 1995; Chen et al. 2013; Huang et al. 2019). In contrast, nitric acid and nitric-rich acid have been observed to exert nutrient enrichment effects, whereas sulfuric acid and sulfuric-rich acid have not (Hassan et al. 2005; Hassan et al. 2008; Villar-Salvador et al. 2013; van den Elzen et al. 2018).

Conclusions

The root-mediated allelopathy of *S. canadensis* was found to be more pronounced than the leaf-mediated allelopathy of *S. canadensis* treated with nitric acid at pH 4.5, but the leaf-mediated allelopathy of *S. canadensis* was observed to be greater than the root-mediated allelopathy of *S. canadensis* treated with sulfuric-rich acid at pH 4.5. The leaf and root-mediated co-allelopathy of *S. canadensis* was more pronounced than that of either part alone treated with sulfuric acid at pH 5.6 and nitric acid at pH 4.5, but in contrast with nitric-rich acid at pH 4.5 and sulfuric-rich acid at pH 4.5. Sulfuric acid and sulfuric-rich acid with higher acidity resulted in an intensification of the leaf-mediated allelopathy of *S. canadensis*. The application of nitric acid and nitric-rich acid resulted in a reduction in the leaf-mediated allelopathy of *S. canadensis*, and most types of acid rain (especially nitric acid and nitric-rich acid) also exhibited a reduction in the root-mediated allelopathy and the leaf and root-mediated co-allelopathy of *S. canadensis*. Sulfuric acid and sulfuric-rich acid exhibited a more pronounced effect on *L. sativa* than nitric acid and nitric-rich acid. Thus, the allelopathy of *S. canadensis* under acid rain with multiple N/S ratios was found to be influenced by the N/S ratio of acid rain. The findings of this study provide a substantial practical foundation for environmental management of plant species, including the effective early warning prevention and control of invasive plants, especially under different types of acid rain.

Data availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request (e.g., non-commercial academic research).

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Compliance with ethical standards

Conflict of interest The authors declare no competing interests.

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