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RESEARCH ARTICLE

# The allelopathy of horseweed with different invasion degrees in three provinces along the Yangtze River in China

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**Abstract** The effect of allelopathy from invasive alien plants (IAPs) on native species is one of the main factors for their adaptation and diffusion. IAPs can have different degrees of invasion under natural succession and are distributed in numerous regions. Seed germination and seedling growth (SGe-SGr) play a crucial role in population recruitment. Thus, it is critical to illustrate the differences in the allelopathy caused by an IAP with different degrees of invasion in numerous regions on SGe-SGr of native species to describe the primary force behind their adaptation and diffusion. This study assessed the allelopathy of the notorious IAP horseweed (*Conyza canadensis* (L.) Cronq.) on SGe-SGr of the native lettuce species (*Lactuca sativa* L.) under different degrees of invasion (light degree of invasion and heavy degree of invasion) in three provinces (Jiangsu, Anhui, and Hubei) along the Yangtze River in China. The allelopathy of horseweed leaf extract on lettuce SGe-SGr remarkably increased with the increased degree of invasion, which may be due to the buildup of allelochemicals generated by horseweed with a heavy degree of invasion compared with a light degree of invasion. A high concentration of horseweed leaf extract resulted in noticeably stronger allelopathy on lettuce SGe-SGr compared to the extract with a low concentration. There are noticeable differences in the allelopathy of the extract of horseweed leaves from different provinces on lettuce SGe-SGr with the following order i.e. Jiangsu > Hubei > Anhui. This may be due to the high latitudes for the three sampling sites in Jiangsu compared with the latitudes for the collection sites in Hubei and Anhui. There are certain differences in the environments among the three provinces. Thus, the allelopathy of horseweed on SGe-SGr of lettuce may have a greater negative impact in Jiangsu compared to the other two provinces.

**Keywords** Allelochemicals · Alien invasive plants · *Conyza canadensis* (L.) Cronq. · Seed germination · Seedling growth

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## Introduction

Invasive alien plants (IAPs) have greatly affected the structure and function of native environments in which IAPs flourishes (Wang et al. 2018a, 2019a, b, 2020a, 2021a, b; Wu et al. 2019). Thus, the main factors of the adaptation and diffusion of IAPs have become key themes in the research area of invasion ecology lately. Several hypotheses have described the factors for the adaptation and diffusion of IAPs. Specifically, the Novel Weapons Hypothesis (Callaway and Ridenour 2004) proposes that numerous IAPs can release a variety of biochemical compounds (named allelochemicals) that are toxic to native species and subsequently facilitate their adaptation and diffusion in a new habitat (Thorpe et al. 2009; Djurdjević et al. 2011, 2012; Carvalhoa et al. 2019). The allelochemicals generated by IAPs can produce multiple effects on native species including reduced seed germination and seedling growth (SGe-SGr) (Wang et al. 2016a, 2017a, b, 2018b, 2019c, 2020b; Carvalhoa et al. 2019; Wei et al. 2020a, b). As the first step in the life cycle, SGe-SGr plays a major role in population recruitment (Hu and Zhang 2013; Carvalhoa et al. 2019; Lu et al. 2020). Thus, the powerful allelopathy created by IAPs can result in a significant decrease in the growth performance of native species (Wang et al. 2016a, 2017a, b, 2018b, 2019c, 2020b; Carvalhoa et al. 2019; Wei et al. 2020a, b).

IAPs have different degrees of invasion under natural succession in environments when IAPs gradually occupy new environments after moving from their natural range (Wang et al. 2017a, 2018a, 2021a, b; Wu et al. 2019). Further, the diversified ecosystems in China make the country sensitive to colonization by IAPs (Weber et al. 2008; Li et al. 2009; Yan et al. 2014). Accordingly, numerous IAPs, such as horseweed (*Conyza canadensis* (L.) Cronq.), are distributed in numerous regions across China at present (Yan et al. 2014; Wang et al. 2016b, 2017a, b, 2018a, 2021b). Progressive variations in the degree of invasion of IAPs in numerous regions have the potential to modify their allelopathy on the SGe-SGr of native species and could have a significant effect on their further diffusion. Thus, understanding the differences in the allelopathy resulting from IAPs with different degrees of invasion in numerous regions on SGe-SGr of native species is important for a better understanding of the factors for IAP diffusion. However, limited research has been conducted on the differences in the allelopathy of IAPs with different degrees of invasion in numerous regions on SGe-SGr of native species.

Therefore, this study aimed to assess the allelopathy of horseweed (using leaf extract) with different degrees of invasion (i.e., light degree of invasion and heavy degree of invasion) in three provinces (i.e., Jiangsu, Anhui, and Hubei) along the Yangtze River, China (YRC) on the SGe-SGr of the native lettuce species (*Lactuca sativa* L.). As an annual herbaceous species, horseweed originated in North America (Djurdjević et al. 2011, 2012; Hao et al. 2011; Shah et al. 2014). Currently, horseweed is one of the most devastating IAPs in China due to its wide distribution and the remarkable effects on native ecosystems (Weber et al. 2008; Hao et al. 2011; Wang et al. 2018a, 2021b). The strong allelopathic effect of horseweed on native species is thought to be the key to its adaptation and diffusion (Djurdjević et al. 2011, 2012; Hu and Zhang 2013; Wang et al. 2017a; Lu et al. 2020). The SGe-SGr of lettuce, a commonly grown crop in the area colonized by horseweed, reacts quickly to allelochemicals; therefore, lettuce SGe-SGr is widely used in the studies to elucidate the allelopathy of IAPs (Li and Wang 2014; Wang et al. 2016a, 2017a, 2018b, 2019c, 2020b; Carvalhoa et al. 2019; Lu et al. 2020; Wei et al. 2020a, b). Both horseweed and lettuce are *Compositae* species, a family that presently includes numerous IAP species (92 species) in China (Yan et al. 2014; Wang et al. 2016b). Moreover, horseweed and lettuce frequently coexist within an ecosystem (such as farmland).

Herein, we tested the following hypotheses: (I) the allelopathy of horseweed on lettuce SGe-SGr may increase with the degree of invasion; (II) the allelopathy of horseweed on lettuce SGe-SGr may increase with the increased concentration of leaf extract; and (III) the allelopathy of horseweed on lettuce SGe-SGr may be similar among the three provinces.

## Materials and methods

### Experimental design

Horseweed samples were randomly harvested from nine cities in three provinces (three cities per province) along the Yangtze river in China (YRC) in July 2018. Table 1 gives the geographic location, climate type, and climate summaries of the nine cities in three provinces along the YRC. Horseweed was in the "vegetative propagation/booting (main shoot)" growth stage based on the BBCH-scale for weeds (Hess et al. 1997). The degree of invasion of horseweed was divided into light degree of invasion (< 50%) and heavy degree of invasion (≥ 50%) based on its relative abundance in the colonized communities (Wang et al. 2017a, 2018a, 2021b). This was measured in each city included in this study. The relative abundance of horseweed was assessed as the ratio of the number of horseweed individuals to all plant species in the invaded communities (Wang et al. 2018a, 2019a, b, 2021a, b). The light degree of invasion simulated the colonization stage, whereas the heavy degree of invasion represented an expansion into the outbreak stage (Wang et al. 2017a, 2018a, 2021a, b; Wu et al. 2019). A total of 12 quadrats (size: 2 m × 2 m) were selected per degree of invasion in each city; therefore, there were a total of 24 quadrats sampled per city, resulting in a total of 216 quadrats sampled in the nine cities in three provinces along the YRC. Three horseweed individuals were randomly collected per quadrat (2 m × 2 m) and mature, complete leaves were collected from the horseweed individuals, with the leaves homogenized into one sample from the quadrats with the same degree of invasion.

The horseweed leaf samples were adequately washed and completely air-dried for approximately 72 h at room temperature. The air-dried horseweed leaves were soaked with the sterile distilled water in flasks at approximately 25 °C for 48 h to prepare leaf extract (i.e., water-soluble leaf surface chemicals). Insoluble material was filtered out

**Table 1** The geographic location, climate type, and climate summaries of the nine cities in three provinces along YRC

| Site | | Geographic location | | Climate type | Index | Values | | Data sources |
|---|---|---|---|---|---|---|---|---|
| Province | City | Latitude (N) | Longitude (E) | | | Maximum | Minimum | |
| Jiangsu | Nantong | 31°57’ | 120°53’ | North subtropical oceanic climate | AMT | 16.6 | | Li (2017) |
| | | | | | MMT | 29.0 (Aug.) | 3.2 (Jan.) | |
| | | | | | AMP | 1921.4 | | |
| | | | | | MMP | 470.2 (Jun.) | 22.9 (Feb.) | |
| | | | | | AMS | 1782.0 | | |
| | | | | | MMS | 301.1 (Aug.) | 42.5 (Oct.) | |
| Jiangsu | Zhenjiang | 32°9’ | 119°31’ | North subtropical monsoon climate | AMT | 15.9 | | Hang and Wu (2019) |
| | | | | | MMT | 28.2 (Jul.) | 3.1 (Jan.) | |
| | | | | | AMP | 1101.4 | | |
| | | | | | MMP | 213.8 (Jul.) | 35.1 (Dec.) | |
| | | | | | AMS | 1996.8 | | |
| | | | | | MMS | 195.5 (May.) | 129.4 (Feb.) | |
| Jiangsu | Nanjing | 32°6’ -32°8’ | 118°54’ -118°57’ | North subtropical monsoon climate | AMT | 16.5 | | Zhang (2016) |
| | | | | | MMT | 27.3 (Aug.) | 5.1 (Jan.) | |
| | | | | | AMP | 1765.6 | | |
| | | | | | MMP | 661.5 (Jun.) | 12.3 (Dec.) | |
| | | | | | AMS | 1848.2 | | |
| | | | | | MMS | 217.6 (Aug.) | 84.6 (Nov.) | |
| Anhui | Wuhu | 31°12’ -31°22’ | 118°23’ -118°25’ | North subtropical monsoon climate | AMT | 17 | | Wang (2017) |
| | | | | | MMT | 30 (Aug.) | 3.8 (Jan.) | |
| | | | | | AMP | 1983.2 | | |
| | | | | | MMP | 486.4 (Jul.) | 33.4 (Feb.) | |
| | | | | | AMS | Approximately 1900–2000 | | |
| | | | | | MMS | No data | No data | |
| Anhui | Tongling | 30°59’ | 117°51’ | North subtropical monsoon climate | AMT | 17.4 | | Xiao (2017) |
| | | | | | MMT | 29.8 (Aug.) | 4.1 (Jan.) | |
| | | | | | AMP | 2392.2 | | |
| | | | | | MMP | 495.9 (Jul.) | 43.4 (Feb.) | |
| | | | | | AMS | 1,895.7 | | |
| | | | | | MMS | No data | No data | |
| Anhui | Chizhou | 30°37’ | 117°32’ | North subtropical monsoon climate | AMT | 16.6 | | Wu (2016) |
| | | | | | MMT | 26.9 (Aug.) | 4.7 (Dec.) | |
| | | | | | AMP | 1908.9 | | |
| | | | | | MMP | 398.3 (Jun.) | 10.4 (Dec.) | |
| | | | | | AMS | 1650.3 | | |
| | | | | | MMS | 210.8 (Aug.) | 55.1 (Nov.) | |

**Table 1** continued

| Site | | Geographic location | | Climate type | Index | Values | | Data sources |
|---|---|---|---|---|---|---|---|---|
| Province | City | Latitude (N) | Longitude (E) | | | Maximum | Minimum | |
| Hubei | Qichun | 30°6’ | 115°21’ | North subtropical monsoon climate | AMT | 18.3 | | Wen (2017) |
| | | | | | MMT | No data | No data | |
| | | | | | AMP | 2096.7 | | |
| | | | | | MMP | No data | No data | |
| | | | | | AMS | 1577.0 | | |
| | | | | | MMS | No data | No data | |
| Hubei | Ezhou | 30°21’ | 114°54’ | North subtropical monsoon climate | AMT | 17.2 | | Huang and Su (2014) |
| | | | | | MMT | 29.1 (Jul.) | 4.6 (Jan.) | |
| | | | | | AMP | 1346.20 | | |
| | | | | | MMP | 227.6 (Jun.) | 32.2 (Dec.) | |
| | | | | | AMS | 1943.7 | | |
| | | | | | MMS | 245 (Aug.) | 101.9 (Feb.) | |
| Hubei | Wuhan | 30°22’ | 114°21’ | North subtropical monsoon climate | AMT | 17.3 | | Meng and Chen (2017) |
| | | | | | MMT | 29.2 (Aug.) | 3.6 (Jan.) | |
| | | | | | AMP | 1810.00 | | |
| | | | | | MMP | 676.1 (Jul.) | 7.5 (Sept.) | |
| | | | | | AMS | 1614.6 | | |
| | | | | | MMS | 214.6 (Aug.) | 44.3 (Jan.) | |

*AMT* annual mean temperature (°C), *MMT* monthly mean temperature (°C), *AMP* annual mean precipitation (mm), *MMP* monthly mean precipitation (mm), *AMS* annual mean sunshine hours (h), *MMS* monthly mean sunshine hours (h)

from horseweed leaf extract solutions using cheesecloth and two layers of filter paper. Horseweed leaf extract was diluted with distilled water to generate a concentration gradient (per gram of dry horseweed leaves), specifically, the CK (control with the distilled water, 0 g $L^{-1}$), L (low concentration horseweed leaf extract: 20 g $L^{-1}$) and H (high concentration horseweed leaf extract: 40 g $L^{-1}$). Subsequently, the prepared horseweed leaf extracts were stored at 4 °C for no more than 7 d.

The treatment combinations (three regions * four treatments per region * five replicates; the distilled water as the negative control) in this study were as follows: (I) CK, control with distilled water; (II) JSLIL, the extract of horseweed leaves from Jiangsu (JS) under a light degree of invasion (LI) with a low concentration; (III) JSLIH, the extract of horseweed leaves from JS under LI with a high concentration; (IV) JSHIL, the extract of horseweed leaves from JS under a heavy degree of invasion (HI) with a low concentration; (V) JSHIH, the extract of horseweed leaves from JS under HI with a high concentration; (VI) AHLIL, the extract of horseweed leaves from Anhui (AH) under LI with a low concentration; (VII) AHLIH, the extract of horseweed leaves from AH under LI with a high concentration; (VIII) AHHIL, the extract of horseweed leaves from AH under HI with a low concentration; (IX) AHHIH, the extract of horseweed leaves from AH under HI with a high concentration; (X) HBLIL, the extract of horseweed leaves from Hubei (HB) under LI with a low concentration; (XI) HBLIH, the extract of horseweed leaves from HB under LI with a high concentration; (XII) HBHIL, the extract of horseweed leaves from HB under HI with a low concentration; (XIII) HBHIH, the extract of horseweed leaves from HB under HI with a high concentration. Each treatment group was performed in five replicates.

## Determination of lettuce SGe-SGr parameters

The lettuce (*L. sativa* cultivar Jiuzhouhong) SGe-SGr experiment was completed via the hydroponic incubation method in Petri dishes with thirty seeds per Petri dish in late October 2018. A detailed incubation method for the lettuce SGe-SGr experiment followed previously explained methods (Wang et al. 2016a, 2017a, b, 2018b, 2019c). The number of germinated lettuce seeds was recorded per day beginning the day after sowing. Specifically, the germination of lettuce seeds was determined via radicle protrusion.

After 11 d incubation, ten lettuce seedlings (i.e., 50 lettuce seedlings per treatment group) per Petri dish were randomly selected for the estimation of the following lettuce SGe-SGr parameters: germination percentage (represents the germination ability; Wang et al. 2017a, b, 2018b, 2019c), germination potential (represents the germination capacity and uniformity; Wang et al. 2016a, 2017a, b, 2018b, 2019c), germination index (represents the germination speed and vitality; Hou et al. 2014; Ding et al. 2018), germination rate index (represents the germination speed and vitality; Steinmaus et al. 2000; Mollard et al. 2014), germination vigor index (represents the germination speed and vitality; Li and Wang 2014; Ding et al. 2018), promptness index (represents the robust responsiveness of seed germination; Asci 2011; Toscano et al. 2017), seedling height (represents the competitive ability of seedlings to acquire sunlight acquisition; Wang et al. 2016a, 2017a, b, 2018b, 2019a, c, 2020c), root length (represents the competitive ability of seedlings to acquire water and inorganic salt acquisition; Wang et al. 2016a, 2017a, b, 2018b, 2019c, 2020c), leaf size (including leaf length and width; represents the competitive ability of seedlings to acquire sunlight acquisition; Wang et al. 2018b, 2019a, c, 2020c), green leaf area (represents leaf photosynthetic area of seedlings; Xia et al. 2016; Huang et al. 2018), seedling biomass (including seedling fresh and dry weights; represents seedling growing ability; Wang et al. 2016a, 2017a, b, 2018b, 2019c, 2020c), and plant moisture content (represents seedling water content; Wang et al. 2018b, 2019c, 2020c). The stress intensity of different treatments on lettuce SGe-SGr parameters was adjudged by using the stress intensity index (*SII*). *SII* was defined as $SII = 1 - X_s/X_{ns}$), where $X_s$ and $X_{ns}$ represent the mean value of all lettuce SGe-SGr parameters with horseweed leaf extract and without horseweed leaf extract, respectively (Zangi 2005; Ballesta et al. 2020).

### Statistical analyses

Deviations from normality and the homogeneity of the variances were evaluated by using Shapiro–Wilk's test and Bartlett's test, respectively. The results of normality test and homogeneity of variance test are shown in Table S1 and Table S2, respectively. Differences in the values of lettuce SGe-SGr parameters among all treatment groups were measured using an analysis of variance (ANOVA) with Tukey's test. A three-way ANOVA was implemented to determine the effects of the degree of invasion of horseweed, the concentration of horseweed leaf extract, and the geographic location of horseweed on the values of lettuce SGe-SGr parameters. Partial eta squared ($\eta^2$) values were also calculated to assess the effect size of each factor for use in the three-way ANOVA. Statistical analyses were performed using IBM SPSS Statistics 25.0.

## Results

### Effects of horseweed leaf extract on lettuce SGe-SGr parameters compared to the control

All measured SGe-SGr parameters of lettuce were significantly reduced when subjected to JSLIH ($P < 0.05$; Figs. 1 and 2). Root length was significantly reduced when subjected to all present treatment groups that included horseweed leaf extract ($P < 0.05$; Fig. 2). The germination percentage and germination rate index of lettuce were significantly decreased when subjected to JSHIL ($P < 0.05$; Figs. 1 and 2). The germination rate index, germination vigor index, seedling height, leaf length, seedling biomass (fresh weight), and plant moisture content of lettuce were significantly decreased when subjected to JSHIH ($P < 0.05$; Figs. 1 and 2). The germination potential, germination index, germination rate index, and germination vigor index of lettuce were significantly decreased when subjected to AHLIH ($P < 0.05$; Fig. 1). The germination percentage and germination rate index of lettuce were significantly reduced but leaf length, leaf width, and seedling biomass (fresh weight) of lettuce were significantly increased when subjected to AHHIL ($P < 0.05$; Figs. 1 and 2). The leaf width and seedling biomass (dry weight) of lettuce significantly increased when subjected to HBHIL ($P < 0.05$; Figs. 1 and 2). The germination percentage, germination rate index, germination vigor index, seedling height, leaf length, green leaf area, seedling biomass (fresh weight), and plant moisture content of lettuce were significantly decreased when subjected to HBHIH ($P < 0.05$; Figs. 1 and 2).

### Effects of horseweed leaf extract with different degrees of invasion on lettuce SGe-SGr parameters

The germination index and germination rate index of lettuce were significantly lower when subjected to JSLIH compared with those treated with JSHIH ($P < 0.05$; Fig. 1). The germination vigor index, root length, leaf length, leaf width, green leaf area, seedling biomass (fresh weight), and plant moisture content of lettuce were significantly higher when subjected to HBLIH compared with those in the HBHIH ($P < 0.05$; Figs. 1 and 2).

The value of stress intensity index of JSLIH was greater than that of JSHIH ($P < 0.05$; Fig. 3).

### Effects of horseweed leaf extract with different concentrations on lettuce SGe-SGr parameters

When subjected to JSLIL, all present SGe-SGr parameters of lettuce, except seedling biomass (dry weight), were

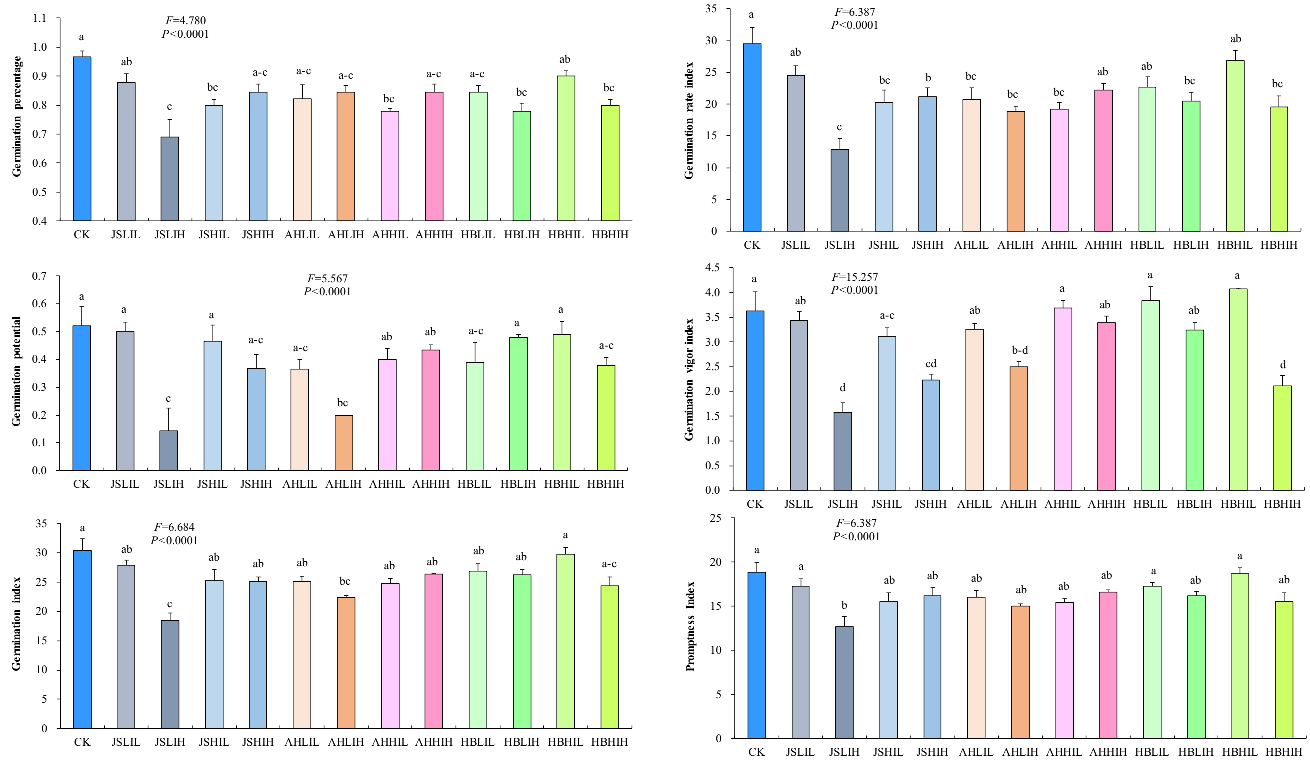


**Fig. 1** The values of germination parameters of lettuce. Bars (means and SE; $n$ = 50) with different letters characterize a significant difference ($P < 0.05$)

significantly higher compared with those in JSLIH ($P < 0.05$; Figs. 1 and 2). The root length, leaf length, green leaf area, and seedling biomass (fresh weight) of lettuce were significantly higher in JSHIL than JSHIH ($P < 0.05$; Fig. 2). The root length, leaf length, and green leaf area of lettuce were significantly higher in AHLIL compared to AHLIH ($P < 0.05$; Fig. 2). The leaf length of lettuce was significantly higher in AHHIL than AHHIH ($P < 0.05$; Fig. 2). The root length of lettuce was significantly higher in HBLIL than HBLIH ($P < 0.05$; Fig. 2). The germination vigor index, seedling height, root length, leaf length, leaf width, green leaf area, seedling biomass (fresh weight), and plant moisture content of lettuce were significantly higher in HBHIL compared to HBHIH ($P < 0.05$; Figs. 1 and 2).

The value of the stress intensity index of JSLIH was greater compared to that under JSLIL ($P < 0.05$; Fig. 3). Similarly, the value of the stress intensity index of HBHIH was greater than that of HBHIL ($P < 0.05$; Fig. 3).

## Effects of horseweed leaf extract with different geographic location on lettuce SGe-SGr parameters

The root length of lettuce was significantly lower in JSLIL compared to HBLIL ($P < 0.05$; Fig. 2). The germination potential, seedling biomass (fresh weight), and plant moisture content of lettuce were significantly lower in JSLIH compared with AHLIH and HBLIH ($P < 0.05$; Figs. 1 and 2). The germination index, germination vigor index, root length, leaf length, leaf width, and green leaf area of lettuce were significantly lower in JSLIH than HBLIH ($P < 0.05$; Figs. 1 and 2). The seedling height of lettuce was significantly lower in JSHIL than HBHIL ($P < 0.05$; Fig. 2). The seedling biomass (fresh weight) of lettuce was significantly lower in JSHIL than AHHIL ($P < 0.05$; Fig. 2). The germination vigor index, root length, and leaf length of lettuce were significantly lower in JSHIH than AHHIH ($P < 0.05$; Figs. 1 and 2). The leaf width, green leaf area and seedling biomass (fresh weight) of lettuce were significantly lower in HBHIH than AHHIH ($P < 0.05$; Fig. 2). The plant moisture content of lettuce was significantly lower in JSHIH and HBHIH compared to AHHIH ($P < 0.05$; Fig. 2).

The value of stress intensity index was greater in JSLIH compared to HBLIH ($P < 0.05$; Fig. 3). The mean value of stress intensity index of horseweed extract from the three provinces on lettuce SGe-SGr decreased in the following order: Jiangsu (0.2545) > Hubei (0.2259) > Anhui (0.1638) (Fig. 3).

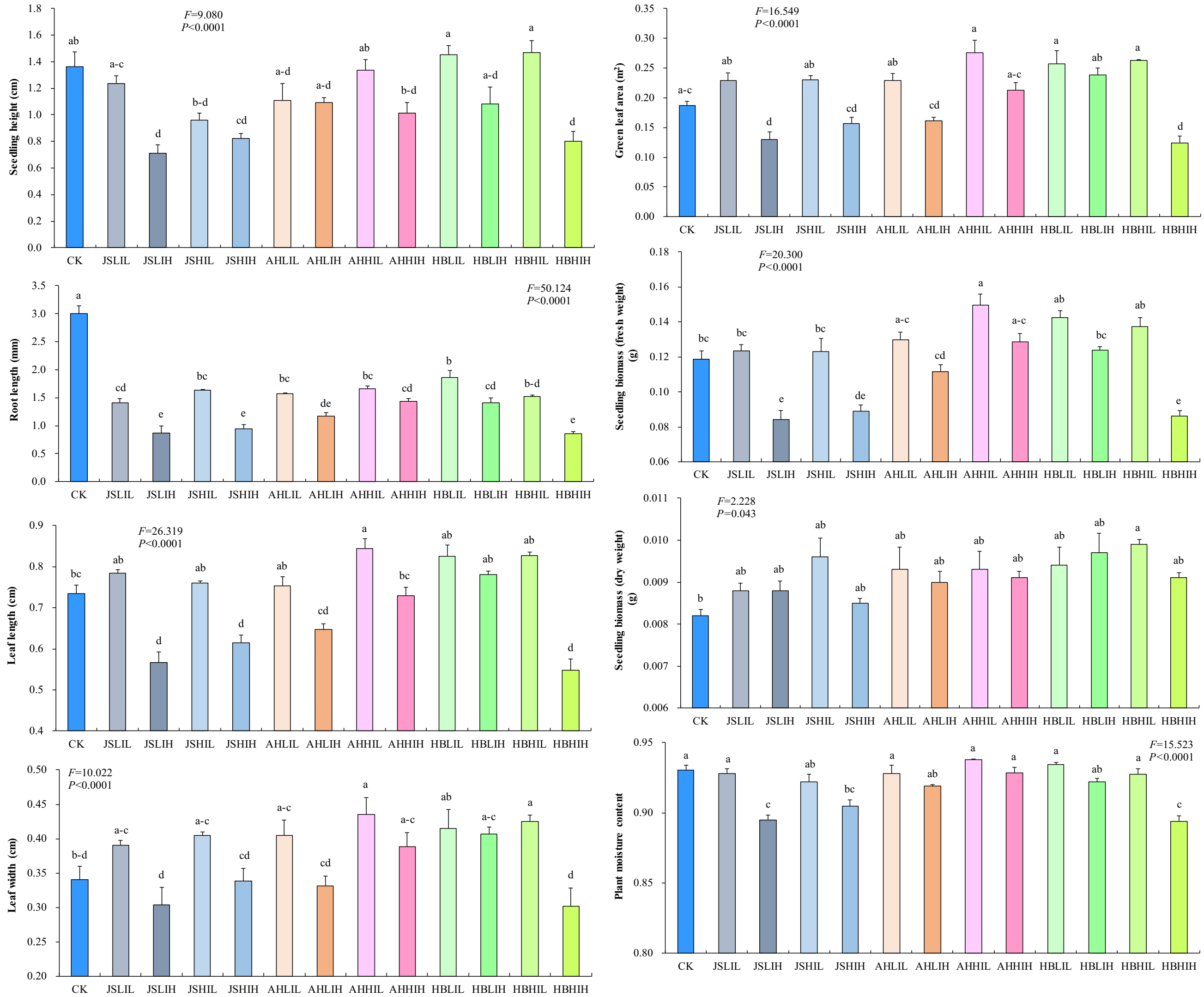


**Fig. 2** The values of seedling growth parameters of lettuce. Bars (means and SE; $n$ = 50) with different letters characterize a significant difference ($P < 0.05$)

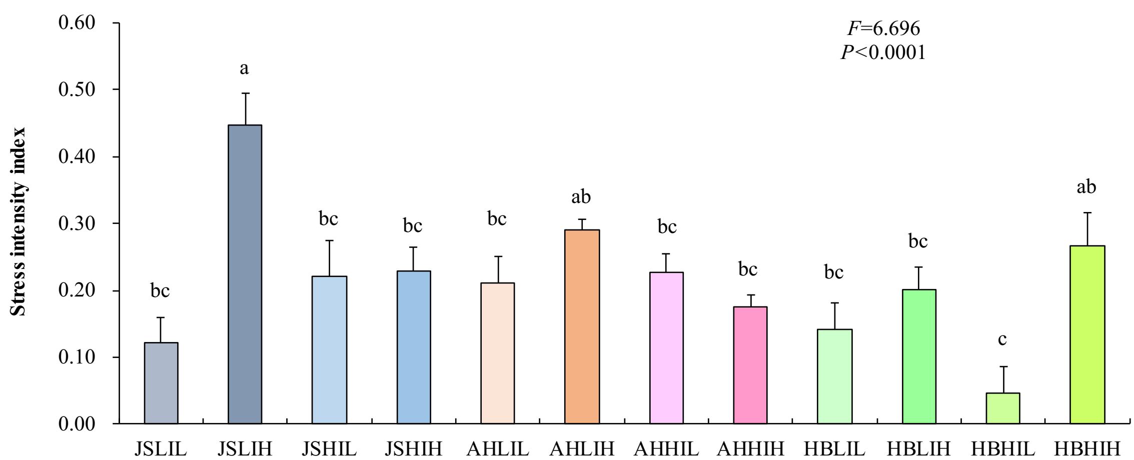


**Fig. 3** The values of the stress intensity index of different treatments on lettuce. Bars (means and SE; $n$ = 50) with different letters characterize a significant difference ($P < 0.05$)

### Three-way ANOVA on the effects of the degree of invasion of horseweed, the concentration of horseweed leaf extract, and the geographic location of horseweed on the values of lettuce SGe-SGr parameters

The results of the ANOVA analysis indicated that the degree of invasion of horseweed significantly affected the germination potential and germination index of lettuce ($P < 0.05$; Table 2). The concentration of horseweed leaf extract significantly affected all measured SGe-SGr parameters of lettuce, except seedling biomass (dry weight) ($P < 0.05$; Table 2). The geographic location of horseweed significantly affected all measured SGe-SGr parameters of lettuce, except germination percentage, germination potential, and germination rate index ($P < 0.05$; Table 2). The interaction of the degree of invasion of horseweed, the concentration of horseweed leaf extract, and the geographic location of horseweed significantly affected all measured lettuce SGe-SGr parameters, except root length and seedling biomass (dry weight) ($P < 0.05$; Table 2).

The effect size of the degree of invasion of horseweed on the germination potential ($F = 7.5887$; $P = 0.0106$) and germination index ($F = 4.4213$; $P = 0.0453$) of lettuce were higher compared to the other SGe-SGr parameters of lettuce (Table 2). The effect size of the concentration of horseweed leaf extract on the germination vigor index ($F = 90.6955$; $P < 0.0001$), seedling height ($F = 50.2901$; $P < 0.0001$), root length ($F = 119.3995$; $P < 0.0001$), leaf length ($F = 183.9342$; $P < 0.0001$), leaf width ($F = 63.6336$; $P < 0.0001$), green leaf area ($F = 115.2610$; $P < 0.0001$), seedling biomass (fresh weight) ($F = 126.3511$; $P < 0.0001$), and plant moisture content ($F = 83.6527$; $P < 0.0001$) were clearly greater compared with the other SGe-SGr parameters of lettuce (Table 2). The geographic location of horseweed on the germination vigor index ($F = 16.6980$; $P < 0.0001$), seedling height ($F = 11.5835$; $P < 0.0001$), root length ($F = 11.2584$; $P < 0.0001$), leaf length ($F = 13.9920$; $P < 0.0001$), green leaf area ($F = 9.7524$; $P = 0.0007$), seedling biomass (fresh weight) ($F = 29.9139$; $P < 0.0001$), and plant moisture content ($F = 19.5951$; $P < 0.0001$) were distinctly larger than the other SGe-SGr parameters of lettuce (Table 2).

## Discussion

Generally, the allelopathy of IAPs on the SGe-SGr of native species plays a decisive role in their spread throughout a non-native location (Wang et al. 2016a, 2017a, b, 2018b, 2019c, 2020b; Carvalhoa et al. 2019; Wei et al. 2020a, b). In this study, we have observed that horseweed leaf extract has a negative effect on lettuce SGe-SGr in this study. All present treatment groups with horseweed leaf extract included in this study distinctively reduced the root length of lettuce. Thus, the competitive ability of lettuce seedlings to acquire water and inorganic salt acquisition will be dramatically suppressed by horseweed leaf extract. Accordingly, the attenuated performance of SGe-SGr of native species when subjected to the horseweed allelopathy may facilitate its spread throughout its non-native range. However, the competitive ability of seedlings to acquire sunlight acquisition and seedling growing ability of lettuce markedly enhanced in AHHIL and HBHIL. Thus, in a few cases, the allelopathy mediated by IAPs also promotes the SGe-SGr performance of native species, possibly due to the lower accumulation of allelochemicals, resulting in the occurrence of reactive oxygen species in plant cell, which in turn can stimulate SGe-SGr of plant species (Duke et al. 2006; Takao et al. 2011; Lu et al. 2020; Wei et al. 2020a, b). This process may be due to the persuaded hormesis effects (low-dose stimulation), which are frequently considered to be a vital plant response to changes in ecological factors (Forbes 2000; Duke et al. 2006; Takao et al. 2011). Hence, IAP does not always result in a distinctly negative effect on SGe-SGr performance of native species.

Our observations also suggest that a high concentration of horseweed leaf extract triggers stronger allelopathy on lettuce SGe-SGr compared to the low concentration, especially for JSLIH and JSLIL. Further, the stress intensity of JSLIH on lettuce SGe-SGr is markedly greater than that of JSLIL in this study. Our observations support earlier results (Wang et al. 2016a, 2017a, 2018b, 2019c) and the second hypothesis. This may be due to the higher concentration of horseweed allelochemicals in the high concentration of horseweed leaf extract compared to the low concentration.

Intraspecific competition among IAP individuals increase with an increasing degree of invasion (Wang et al. 2019a, b, 2021a, b; Wu et al. 2019). Therefore, IAPs possess a higher growth competitiveness and fitness advantage via obtaining resources required for growth. Hence, IAPs with HI will allocate more biomass to leaf structures per unit area to increase its competitiveness and fitness. Previous studies have also found that the biomass allocation per unit of leaf area increased dramatically with the increase of population density (Liu et al. 2009; Tobin et al. 2011). Thus, it is expected that IAPs with HI may invest more biomass in leaf structure to obtain a higher growth competitiveness and fitness advantage. Consequently, the leaves of IAPs with HI may contain more secondary metabolites compared to those with LI. The greater intraspecific competition can also increase the allelopathic potential of plants (Lawrence et al. 1991;

**Table 2** Three-way ANOVA on the effects of the degree of invasion of horseweed (ID), the concentration of horseweed leaf extract (EC), and the geographic location of horseweed (GL) on the values of lettuce SGe-SGr parameters

| | Dependent variable | df | *F* | *P* | $\eta^2$ |
|---|---|---|---|---|---|
| ID | Germination percentage | 1 | 1.0942 | 0.3052 | 0.0404 |
| | Germination potential | 1 | 7.5887 | **0.0106** | 0.2259 |
| | Germination index | 1 | 4.4213 | **0.0453** | 0.1453 |
| | Germination rate index | 1 | 2.7669 | 0.1082 | 0.0962 |
| | Germination vigor index | 1 | 1.2975 | 0.2651 | 0.0475 |
| | Promptness index | 1 | 1.6195 | 0.2144 | 0.0586 |
| | Seedling height | 1 | 0.9865 | 0.3298 | 0.0366 |
| | Root length | 1 | 0.6812 | 0.4167 | 0.0255 |
| | Leaf length | 1 | 0.2486 | 0.6222 | 0.0095 |
| | Leaf width | 1 | 0.6676 | 0.4213 | 0.0250 |
| | Green leaf area | 1 | 0.1868 | 0.6692 | 0.0071 |
| | Seedling biomass (fresh weight) | 1 | 0.0029 | 0.9577 | 0.0001 |
| | Seedling biomass (dry weight) | 1 | 0.2366 | 0.6307 | 0.0090 |
| | Plant moisture content | 1 | 0.9432 | 0.3404 | 0.0350 |
| EC | Germination percentage | 1 | 4.3781 | **0.0463** | 0.1441 |
| | Germination potential | 1 | 13.6543 | **0.0010** | 0.3443 |
| | Germination index | 1 | 16.7135 | **0.0004** | 0.3913 |
| | Germination rate index | 1 | 11.8298 | **0.0020** | 0.3127 |
| | Germination vigor index | 1 | 90.6955 | **< 0.0001** | 0.7772 |
| | Promptness index | 1 | 8.4610 | **0.0073** | 0.2455 |
| | Seedling height | 1 | 50.2901 | **< 0.0001** | 0.6592 |
| | Root length | 1 | 119.3995 | **< 0.0001** | 0.8212 |
| | Leaf length | 1 | 183.9342 | **< 0.0001** | 0.8762 |
| | Leaf width | 1 | 63.6336 | **< 0.0001** | 0.7099 |
| | Green leaf area | 1 | 115.2610 | **< 0.0001** | 0.8159 |
| | Seedling biomass (fresh weight) | 1 | 126.3511 | **< 0.0001** | 0.8293 |
| | Seedling biomass (dry weight) | 1 | 3.3276 | 0.0796 | 0.1135 |
| | Plant moisture content | 1 | 83.6527 | **< 0.0001** | 0.7629 |
| GL | Germination percentage | 2 | 0.8650 | 0.4328 | 0.0624 |
| | Germination potential | 2 | 3.3356 | 0.0513 | 0.2042 |
| | Germination index | 2 | 5.6194 | **0.0094** | 0.3018 |
| | Germination rate index | 2 | 3.0789 | 0.0631 | 0.1915 |
| | Germination vigor index | 2 | 16.6980 | **< 0.0001** | 0.5623 |
| | Promptness index | 2 | 3.9009 | **0.0330** | 0.2308 |
| | Seedling height | 2 | 11.5835 | **0.0003** | 0.4712 |
| | Root length | 2 | 11.2584 | **0.0003** | 0.4641 |
| | Leaf length | 2 | 13.9920 | **< 0.0001** | 0.5184 |
| | Leaf width | 2 | 5.3826 | **0.0111** | 0.2928 |
| | Green leaf area | 2 | 9.7524 | **0.0007** | 0.4286 |
| | Seedling biomass (fresh weight) | 2 | 29.9139 | **< 0.0001** | 0.6971 |
| | Seedling biomass (dry weight) | 2 | 3.5060 | **0.0449** | 0.2124 |
| | Plant moisture content | 2 | 19.5951 | **< 0.0001** | 0.6012 |
| ID * EC | Germination percentage | 1 | 5.2936 | **0.0297** | 0.1692 |
| | Germination potential | 1 | 2.3860 | 0.1345 | 0.0841 |
| | Germination index | 1 | 4.6350 | **0.0408** | 0.1513 |
| | Germination rate index | 1 | 5.0476 | **0.0334** | 0.1626 |
| | Germination vigor index | 1 | 0.0136 | 0.9080 | 0.0005 |
| | Promptness index | 1 | 3.7605 | 0.0634 | 0.1264 |

**Table 2** continued

| | Dependent variable | df | *F* | *P* | $\eta^2$ |
|---|---|---|---|---|---|
| | Seedling height | 1 | 0.6524 | 0.4266 | 0.0245 |
| | Root length | 1 | 0.4263 | 0.5195 | 0.0161 |
| | Leaf length | 1 | 6.2153 | **0.0194** | 0.1929 |
| | Leaf width | 1 | 1.8189 | 0.1891 | 0.0654 |
| | Green leaf area | 1 | 4.2022 | 0.0506 | 0.1391 |
| | Seedling biomass (fresh weight) | 1 | 3.5822 | 0.0696 | 0.1211 |
| | Seedling biomass (dry weight) | 1 | 3.7861 | 0.0626 | 0.1271 |
| | Plant moisture content | 1 | 0.1715 | 0.6821 | 0.0066 |
| ID* GL | Germination percentage | 2 | 1.3238 | 0.2835 | 0.0924 |
| | Germination potential | 2 | 2.0631 | 0.1474 | 0.1370 |
| | Germination index | 2 | 0.4517 | 0.6415 | 0.0336 |
| | Germination rate index | 2 | 0.1261 | 0.8821 | 0.0096 |
| | Germination vigor index | 2 | 8.3815 | **0.0016** | 0.3920 |
| | Promptness index | 2 | 0.1074 | 0.8985 | 0.0082 |
| | Seedling height | 2 | 1.7250 | 0.1979 | 0.1171 |
| | Root length | 2 | 20.3878 | **< 0.0001** | 0.6106 |
| | Leaf length | 2 | 27.8969 | **< 0.0001** | 0.6821 |
| | Leaf width | 2 | 10.7179 | **0.0004** | 0.4519 |
| | Green leaf area | 2 | 17.6649 | **< 0.0001** | 0.5761 |
| | Seedling biomass (fresh weight) | 2 | 18.3183 | **< 0.0001** | 0.5849 |
| | Seedling biomass (dry weight) | 2 | 0.0841 | 0.9196 | 0.0064 |
| | Plant moisture content | 2 | 14.5262 | **< 0.0001** | 0.5277 |
| EC* GL | Germination percentage | 2 | 5.3309 | **0.0115** | 0.2908 |
| | Germination potential | 2 | 5.5590 | **0.0098** | 0.2995 |
| | Germination index | 2 | 3.2027 | 0.0571 | 0.1977 |
| | Germination rate index | 2 | 4.1680 | **0.0269** | 0.2428 |
| | Germination vigor index | 2 | 5.7154 | **0.0088** | 0.3054 |
| | Promptness index | 2 | 2.3989 | 0.1106 | 0.1558 |
| | Seedling height | 2 | 4.4652 | **0.0215** | 0.2557 |
| | Root length | 2 | 3.9808 | **0.0310** | 0.2344 |
| | Leaf length | 2 | 3.6720 | **0.0394** | 0.2203 |
| | Leaf width | 2 | 0.3298 | 0.7220 | 0.0247 |
| | Green leaf area | 2 | 0.7709 | 0.4729 | 0.0560 |
| | Seedling biomass (fresh weight) | 2 | 4.1393 | **0.0275** | 0.2415 |
| | Seedling biomass (dry weight) | 2 | 0.3522 | 0.7065 | 0.0264 |
| | Plant moisture content | 2 | 5.9862 | **0.0073** | 0.3153 |
| ID* EC* GL | Germination percentage | 2 | 4.9998 | **0.0145** | 0.2778 |
| | Germination potential | 2 | 6.7766 | **0.0043** | 0.3427 |
| | Germination index | 2 | 8.9481 | **0.0011** | 0.4077 |
| | Germination rate index | 2 | 7.5520 | **0.0026** | 0.3675 |
| | Germination vigor index | 2 | 10.4731 | **0.0005** | 0.4462 |
| | Promptness index | 2 | 5.3772 | **0.0111** | 0.2926 |
| | Seedling height | 2 | 5.7379 | **0.0086** | 0.3062 |
| | Root length | 2 | 1.8899 | 0.1713 | 0.1269 |
| | Leaf length | 2 | 16.9853 | **< 0.0001** | 0.5665 |
| | Leaf width | 2 | 7.4211 | **0.0028** | 0.3634 |
| | Green leaf area | 2 | 9.8962 | **0.0006** | 0.4322 |
| | Seedling biomass (fresh weight) | 2 | 4.4537 | **0.0217** | 0.2552 |

**Table 2** continued

| | Dependent variable | df | *F* | *P* | $\eta^2$ |
|---|---|---|---|---|---|
| | Seedling biomass (dry weight) | 2 | 1.0380 | 0.3684 | 0.0739 |
| | Plant moisture content | 2 | 6.7892 | **0.0042** | 0.3431 |

$P \leq 0.05$ are in boldface print

Medina-Villar et al. 2020). Specifically, the horseweed leaf extract in HBHIH activates stronger allelopathy compared to HBLIH. Hence, the allelopathy of the extract of horseweed leaves on lettuce SGe-SGr significantly increase with the degree of invasion. Thus, the performance of SGe-SGr of native species may be distinctively repressed when subjected to the horseweed allelopathy under HI conditions, which can accelerate the advance of the diffusion process. More allelochemicals may be generated by the IAPs under HI conditions compared with LI conditions (Hu and Zhang 2013; Wang et al. 2017a, 2018b, 2019c). More importantly, the allelochemicals excreted by IAPs can accumulate in the invaded habitat with the increase in the degree of invasion (Zhang et al. 2011). Thus, our observations support the first hypothesis. Unexpectedly, the stress intensity on lettuce SGe-SGr in JSLIH is obviously higher compared to JSHIH. This observation may be triggered by different allelochemical components for the allelopathic activity of IAPs under the conditions of different degrees of invasion.

Horseweed can invade plant communities across numerous regions despite differences in temperature, precipitation, and sunlight in the regions colonized by horseweed. The differences in environments may affect plant secondary metabolism, especially the production of secondary metabolites, which may subsequently affect the allelopathic activity of IAP leaf extract on the SGe-SGr of native species (Šėžienė et al. 2012; Gatti et al. 2014; Wang et al.2017a, b). There is no difference in the allelopathy of the horseweed leaf extract from the three provinces on lettuce SGe-SGr due to the similar environments of the nine cities in three provinces along the YRC (i.e., north subtropical climate). In contrast with the third hypothesis, the stress intensity of JSLIH on lettuce SGe-SGr is markedly higher compared to that of HBLIH. Additionally, there are differences in the allelopathy of the horseweed leaf extract from the three provinces on lettuce SGe-SGr in the following order: JS > HB > AH. This may be due to the high latitudes for the three cities in JS compared with the latitudes in HB and AH. Plant species located in high latitudes may allocate more biomass into leaf structure and therefore may generate more secondary metabolites compared to plants in the same species located in low latitudes (Wright et al. 2005; Reef and Lovelock 2014). There are also certain differences in the environments among the three provinces. Consequently, the allelopathy of horseweed on SGe-SGr of native species may play a more vital role in the diffusion in JS compared to the other two provinces.

In sum, this can be deduced that the allelopathy of horseweed on SGe-SGr of native species may play a key role in its spread, especially under heavy invasion conditions in high latitudes. The observations from our study can create a solid foundation for illustrating the mechanism underlying the successful invasion of horseweed and affords a powerful theoretical basis as an early warning of ecological risk. Further, these observations build a basic practical guidance for its prevention and control.

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**Authors' contributions** Congyan Wang conceived and designed this study. Huiyuan Cheng and Bingde Wu performed the experiments. Youli Yu, Shu Wang, and Mei Wei analyzed the data. Congyan Wang wrote the manuscript. Daolin Du provided editorial advice. All other authors have read the manuscript and have agreed to submit it in its current form for consideration for publication in the Journal.

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**Declarations**

**Conflict of interest** The authors affirm that they have no conflict of interest.

**Ethical approval** This article does not contain any studies with animals performed by any of the authors.

**Informed consent** Informed consent was obtained from all individual participants included in the study.

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