

Original Research

Drought Enhanced the Allelopathy of Goldenrod on the Seed Germination and Seedling Growth Performance of Lettuce

Ruimin Wu, Bingde Wu, Huiyuan Cheng, Shu Wang, Mei Wei, Congyan Wang*

Institute of Environment and Ecology & School of the Environment and Safety Engineering,
Jiangsu University, Zhenjiang 212013, P. R. China

Received: 13 March 2020

Accepted: 21 May 2020

Abstract

Invasive alien species (IAS) can distinctly inhibit seed germination and seedling growth performance (SGeSGrP) of indigenous species *via* the allelopathy. The progressively increased drought stress can potentially affect the allelopathy of IAS. Thus, it is significant to illustrate the allelopathy of IAS on SGeSGrP of indigenous species under drought stress to obtain a deeper elucidation for the main driving mechanism attributed to the successful invasion. This study attempts to identify the allelopathy of IAS *Solidago canadensis* L. (goldenrod; using leaf extracts) on SGeSGrP of the indigenous species *Lactuca sativa* L. (lettuce) under drought stress [mimicked by Polyethylene glycol-6000 (PEG 6000)]. Goldenrod leaf extracts (low concentration) obviously reduced seed germination performance of lettuce but goldenrod leaf extracts (high concentration) notably reduced seedling growth performance of lettuce. Goldenrod leaf extracts (low concentration) also interestingly awarded an optimistic effect on the competitive ability for sunlight acquisition as well as water and inorganic salt acquisition, plant growing ability, and plant water content of lettuce. PEG 6000 dramatically inhibited the competitive ability for sunlight acquisition as well as water and inorganic salt acquisition of lettuce. PEG 6000 also noticeably enhanced the allelopathy of goldenrod leaf extracts on the germination speed and vitality, competitive ability for sunlight acquisition as well as water and inorganic salt acquisition, leaf photosynthetic area, and plant growing ability of lettuce. Thus, drought stress may be advantageous to the advance of goldenrod invasion process mainly *via* the oppressed SGeSGrP of indigenous species mediated by the enhanced allelopathy.

Keywords: invasive alien species, *Lactuca sativa* L., leaf extracts, Polyethylene glycol-6000, *Solidago canadensis* L.

Introduction

Presently, invasive alien species (IAS) have triggered remarkable effects on the ecosystem services and the corresponding stability of indigenous ecosystems [1-7]. Hence, plant ecologists are particularly interested in estimating the mechanism driving the successful invasion over the years. Previous results presented that numerous IAS can markedly prevent the growth performance of the surrounding plant species (mainly indigenous species) *via* the allelopathy triggered by the allelochemicals originated from litter residues and/or root exudates [1, 2, 11, 12, 13]. For instance, the allelopathy of the infamous IAS *Solidago canadensis* L. (goldenrod) occupy a decisive position in the process of effective establishment and flourishing expansion as well as the finally successful invasion [2, 8-10, 12, 13]. This fact is even more important as the allelopathy employed by IAS observably suppressed seed germination and seedling growth performance (SGeSGrP) of indigenous species [2, 8-10, 12-14]. SGeSGrP constitute the core competence of plant life history, which determines the success of subsequently growth performance of the individuals and recruitment potential of the population [1, 14]. Hence, the shifts in SGeSGrP of indigenous species imposed by the allelopathy of IAS can have a marked effect on their growth competitiveness and fitness within a certain range [1, 8-10, 12, 13]. Therefore, it is important to take into consideration the allelopathy recruited by IAS on SGeSGrP of indigenous species to better illuminate the successful mechanism of plant invasion.

In addition, the arid and semi-arid regions cover nearly forty percent of the earth [15-17]. Meanwhile, the area of arid and semi-arid regions is anticipated to grow rapidly as the intensity and frequency of climate change rise mostly due to the progressively increase in intra annual precipitation variability [18-20]. Furthermore, the occurrence ratio and sustained intensity of drought events will upsurge as time advances triggered by anthropic activities presumably soon [15, 16]. In addition, the gradually enhanced drought stress can pose significantly adverse impacts on plant morphological and physiological performance [21-24] as well as on SGeSGrP [25-28]. Further, the soil-water condition can trigger a noteworthy impact on the invasiveness of IAS [23, 25, 29]. Specifically, it is expected that drought stress potentially affects secondary metabolisms of IAS and the corresponding invasiveness especially *via* the variations in the secretion of allelochemicals and the corresponding allelopathy on SGeSGrP of indigenous species. Thus, the combined effects between drought stress and biological invasion have garnered much attention by plant ecologists. Accordingly, it is significant to illustrate the allelopathy of IAS on SGeSGrP of indigenous species under drought stress to gain a deeper illumination for the main driving mechanism attributed to the successful invasion.

The purpose of the study is to explore the allelopathy of goldenrod (using leaf extracts) on SGeSGrP of the indigenous species *Lactuca sativa* L. (lettuce) under a gradient level of drought stress. Goldenrod and lettuce can cohabit in the same habitat, mainly in cropland. In addition, both goldenrod and lettuce are members of Composite, which comprises the highest species number of IAS in China at the family level currently [30, 31]. As a perennial herb, goldenrod is originated in North America (mainly Canada) and first appeared in China as an ornamental plant in the beginning of Nineteen Thirties. But, goldenrod has become known as one of the maximum destructive IAS in China at present [23, 32]. Further, the seedlings of lettuce, one of the most common plant species in the area occupied by goldenrod, can prompt response to the allelopathy and the indigenous species has a wide application as a bioindicator in the aspect of allelopathy research [8-10, 12, 13].

This study verified the following hypotheses: (I) firstly, goldenrod leaf extracts pose undesirable effects on SGeSGrP of lettuce and the undesirable effects remarkably rise with the growing concentration of goldenrod leaf extracts; (II) secondly, the combined drought stress and goldenrod leaf extracts can generate a synergic effect on SGeSGrP of lettuce.

Materials and Methods

Goldenrod Leaf Extracts Solutions Preparation

The mature goldenrod leaves were harvested from Zhenjiang (32.16°N, 119.53°E), China in September 2018. The climate conditions of Zhenjiang were provided in our previous reports (i.e., the annual mean temperature: $\approx 16.1^{\circ}\text{C}$; the annual precipitation $\approx 1,150.6$ mm; the annual sunshine time: $\approx 1,986.9$ h) [5, 6, 9, 33]. The collected goldenrod leaves were washed adequately and air-dried thoroughly at approximately 25°C . The dried goldenrod leaves were soaked with sterile distilled water in flasks at nearly 25°C . Subsequently, the impurities (for instance: solid material) in goldenrod leaf extracts were filtered executed by cheesecloth and filter paper (two layers). The crafted goldenrod leaf extracts solutions were refrigerated at 4°C . Specifically, a gradient level of goldenrod leaf extracts [control (sterile distilled water: 0 g L^{-1} ; mimicked the condition without goldenrod invasion); SCL (goldenrod leaf extracts with low concentration: 7.5 g L^{-1} ; mimicked the condition with light degree of goldenrod invasion); SCH (goldenrod leaf extracts with high concentration: 15 g L^{-1} ; represented the condition with heavy degree of goldenrod invasion)] were created by adding sterile distilled water with different amounts in the solutions to simulate the allelopathy of goldenrod.

Polyethylene Glycol-6000 (PEG 6000) Solutions Preparation

A gradient level of drought stress were prepared by using PEG 6000 (Reagent grade: BC; Purity: $\geq 99.0\%$; Manufacturer: Sangon Biotech Co., Ltd., Shanghai, China) solutions with a gradient concentration, specifically, control (0 mg L⁻¹, sterile distilled water; represented the condition without drought stress), PEL (PEG 6000 with low concentration: 25 g L⁻¹; represented the condition with light drought stress), and PEH (PEG 6000 with high concentration): 50 g L⁻¹; represented the condition with heavy drought stress). PEG has been categorized within the substances list with non-ionic, non-toxic, and inert; and this substance also thought not to be able to enter plant cells [34-36]. Currently, PEG is often taken as an osmotic agent to simulate drought stress during plant cultivation mainly due to the fact that PEG can imitate the condition with water deficits in vitro *via* the improved osmotic pressure which can lead to water deficit stress for plant grow [21, 22, 34].

Summary of Bioassay Design

The bioassay in this study comprises the following nine treatment groups: (I) control; (II) SCL; (III) SCH; (IV) PEL; (V) PEH; (VI) PELSCL, the combined PEL and SCL; (VII) PELSCH, the combined PEL and SCH; (VIII) PEHSCL, the combined PEH and SCL; (IX) PEHSCH, the combined PEH and SCH. Each bioassay treatment group was achieved in quintuplicates (i.e., five replicates per bioassay treatment group).

Determination of SGeSGrP Parameters of Lettuce

SGeSGrP experiments of lettuce were executed using the incubation method in the Petri dishes in mid-January 2019. The incubation method of lettuce in Petri dishes was provided in our earlier studies [8, 9]. The amount of germinated seeds (radicle exposed) of lettuce was recorded per day after incubation.

After eight days of incubation, ten lettuce seedlings of lettuce per Petri dish (i.e., fifty seedlings of lettuce per bioassay treatment group) were chosen randomly to assess SGeSGrP parameters of lettuce, namely, germination percentage (represents the germination ability) [3, 9, 10, 13], germination potential (represents the germination capacity and uniformity) [3, 9, 10, 13], germination index (represents the germination speed and vitality) [37-39], germination rate index (represents the germination speed and vitality) [40-42], germination vigor index (represents the germination speed and vitality) [39, 43, 44], promptness index (represents the robust response capability of seedling's germination) [45-47], seedling height (represents the competitive ability for sunlight acquisition) [3, 9, 10, 13, 33], root length (represents the competitive ability for water and inorganic salt acquisition) [3, 9, 10, 13], leaf length and

width (represents the competitive ability for sunlight acquisition) [3,6, 8-10, 13, 33, 48], green leaf area (represents leaf photosynthetic area) [49-51], single-plant fresh and dry weights (represents plant growing ability) [3, 9, 10, 13, 24, 33, 48] and plant moisture content (represents plant water content) [3, 9, 10, 13, 33].

Statistical Analysis

Deviations from normality and homogeneity of the variances were assessed by Shapiro-Wilks's test and Bartlett's test, respectively. Differences in the values of SGeSGrP parameters of lettuce were tested with an analysis of variance (ANOVA) among different treatment groups followed by the Tukey's honestly significant difference post hoc test for multiple comparisons. Two-way ANOVA tests were performed to assess the effects of the concentration of goldenrod leaf extracts and the concentration of PEG 6000 on SGeSGrP parameters of lettuce. The partial eta-squared (η^2) values were also estimated to evaluate the effect size of each factor for use in the Two-way ANOVA. Statistically significant differences were set at $P < 0.05$. The statistical analyses were operated using IBM SPSS Statistics (version 25.0; IBM Corp., Armonk, NY, USA).

Results

Effects of Goldenrod Leaf Extracts on SGeSGrP Parameters of Lettuce

SCL markedly reduced germination potential (18.391% lower), germination index (31.596% lower), germination rate index (37.890% lower), and promptness index (23.311% lower) of lettuce but notably enhanced root length (22.685% higher), leaf length (73.754% higher), leaf width (33.649% higher), green leaf area (132.139% higher), and seedling biomass (fresh weight) (32.981% higher) of lettuce comparison with control ($P < 0.05$; Fig. 1). SCH signally restrained seedling height (24.874% lower) and root length (26.423% lower) of lettuce but dramatically improved leaf length (40.063% higher) and green leaf area (59.999% higher) of lettuce comparison with control ($P < 0.05$; Fig. 1). SCH did not notably affect seed germination parameters of lettuce comparison with control ($P > 0.05$; Fig. 1).

Seedling height (17.069% lower), root length (40.028% lower), leaf length (19.390% lower), leaf width (14.539% lower), green leaf area (31.076% lower), and seedling biomass (fresh weight) (17.573% lower) of lettuce under SCH were markedly lower than those under SCL but contrary to germination index (28.134% higher) and germination rate index (39.355% higher) of lettuce ($P < 0.05$; Fig. 1).

Two-way ANOVA results presented that the concentration of goldenrod leaf extracts notably affected all present SGeSGrP parameters of lettuce (except single-plant dry weight) ($P < 0.05$; Table S1).

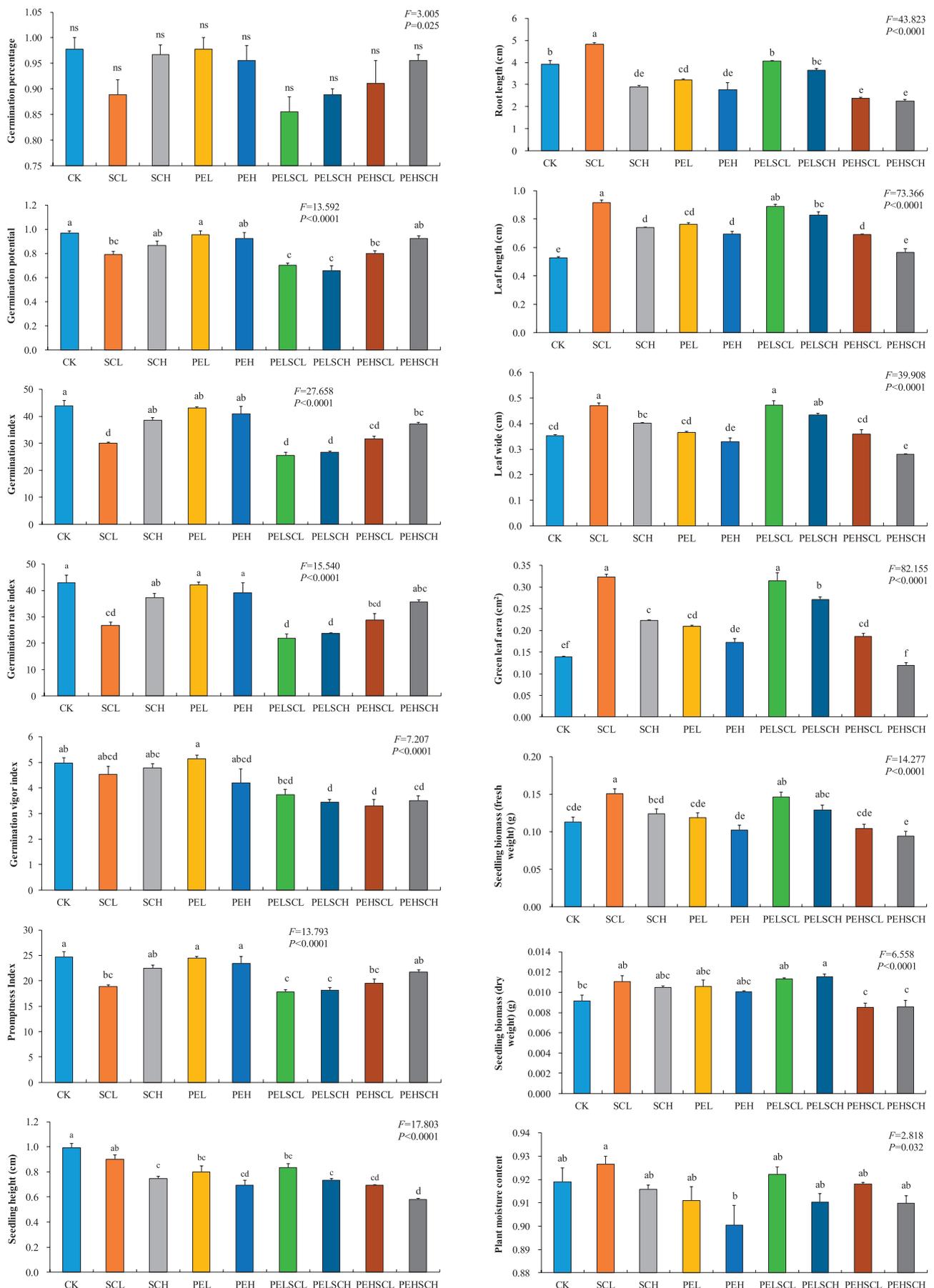


Fig. 1. Seed germination and seedling growth parameters of lettuce. Bars (means and standard error) with different lowercase letters indicate a significant difference ($P < 0.05$). "ns" means no significant difference ($P > 0.05$).

Table S1. Two-way ANOVA on the effects of the concentration of goldenrod leaf extracts and the concentration of Polyethylene glycol-6000 on seed germination and seedling growth performance parameters of lettuce.

		Type III Sum of Squares	df	Mean Square	F	P	η^2
The concentration of goldenrod leaf extracts	Germination percentage	0.033	2	0.017	8.060	0.003	0.472
	Germination potential	0.164	2	0.082	29.353	<0.0001	0.765
	Germination index	846.299	2	423.150	79.708	<0.0001	0.899
	Germination rate index	1109.830	2	554.915	44.834	<0.0001	0.833
	Germination vigor index	4.736	2	2.368	11.295	0.0007	0.557
	Promptness index	136.519	2	68.259	42.736	<0.0001	0.826
	Seedling height	0.108	2	0.054	21.199	<0.0001	0.702
	Root length	3.009	2	1.505	30.438	<0.0001	0.772
	Leaf length	0.137	2	0.069	94.839	<0.0001	0.913
	Leaf width	0.035	2	0.017	54.816	<0.0001	0.859
	Green leaf area	0.049	2	0.024	125.378	<0.0001	0.933
	Single-plant fresh weight	0.003	2	0.001	15.746	0.0001	0.636
	Single-plant dry weight	<0.001	2	<0.001	0.509	0.6093	0.054
	Plant moisture content	<0.001	2	<0.001	5.980	0.0102	0.399
The concentration of PEG 6000	Germination percentage	0.007	2	0.004	1.820	0.1906	0.168
	Germination potential	0.069	2	0.035	12.412	0.0004	0.580
	Germination index	171.465	2	85.732	16.149	<0.0001	0.642
	Germination rate index	213.322	2	106.661	8.618	0.0024	0.489
	Germination vigor index	5.519	2	2.760	13.164	0.0003	0.594
	Promptness index	17.005	2	8.502	5.323	0.0153	0.372
	Seedling height	0.228	2	0.114	44.586	<0.0001	0.832
	Root length	10.223	2	5.112	103.413	<0.0001	0.920
	Leaf length	0.141	2	0.071	97.504	<0.0001	0.915
	Leaf width	0.053	2	0.026	82.904	<0.0001	0.902
	Green leaf area	0.052	2	0.026	133.906	<0.0001	0.937
	Single-plant fresh weight	0.006	2	0.003	34.954	<0.0001	0.795
	Single-plant dry weight	<0.001	2	<0.001	16.727	<0.0001	0.650
	Plant moisture content	<0.001	2	<0.001	4.144	0.0331	0.315
The concentration of PEG 6000 * The concentration of Goldenrod leaf extracts	Germination percentage	0.009	4	0.002	1.070	0.400	0.192
	Germination potential	0.071	4	0.018	6.301	0.002	0.583
	Germination index	156.855	4	39.214	7.387	0.001	0.621
	Germination rate index	215.526	4	53.882	4.353	0.012	0.492
	Germination vigor index	1.832	4	0.458	2.184	0.112	0.327
	Promptness index	22.718	4	5.679	3.556	0.026	0.441
	Seedling height	0.028	4	0.007	2.713	0.063	0.376
	Root length	4.097	4	1.024	20.720	<0.0001	0.822
	Leaf length	0.146	4	0.037	50.561	<0.0001	0.918
	Leaf width	0.014	4	0.003	10.956	0.0001	0.709
	Green leaf area	0.027	4	0.007	34.668	<0.0001	0.885
	Single-plant fresh weight	0.001	4	0.000	3.203	0.038	0.416
	Single-plant dry weight	<0.001	4	<0.001	4.499	0.011	0.500
	Plant moisture content	<0.001	4	<0.001	0.574	0.685	0.113

P values equal to or less than 0.05 are shown in bold.

Effects of PEG 6000 on SGeSGrP Parameters of Lettuce

PEG 6000 regardless of the concentration observably declined seedling height (19.328% and 30.084% lower under PEL and PEH, respectively) and root length (18.182% and 29.227% lower under PEL and PEH, respectively) of lettuce but markedly accelerated leaf length (44.479% and 31.546% higher under PEL and PEH, respectively) of lettuce comparison with control ($P<0.05$; Fig. 1). PEL also outstandingly promoted green leaf area (49.937% higher) of lettuce comparison with control ($P<0.05$; Fig. 1). PEG 6000 regardless of the concentration did not observably affect seed germination parameters of lettuce comparison with control ($P>0.05$; Fig. 1). No remarkable difference was observed in SGeSGrP parameters of lettuce between PEL and PEH ($P>0.05$; Fig. 1).

Two-way ANOVA results exhibited that the concentration of goldenrod leaf extracts notably affected all present SGeSGrP parameters of lettuce (except germination percentage) ($P<0.05$; Table S1).

The Combined PEG 6000 and Goldenrod Leaf Extracts on SGeSGrP Parameters of Lettuce

Germination index (42.933%, 39.312%, 28.058%, and 15.183% lower, respectively) and seedling height (15.630%, 26.050%, 30.084%, and 41.681% lower, respectively) of lettuce markedly decreased under all treatment groups of the combined PEG 6000 and goldenrod leaf extracts comparison with control ($P<0.05$; Fig. 1). Meanwhile, germination potential (27.586%, 32.184%, and 17.241% lower, respectively), germination rate index (49.139%, 44.962%, and 32.876% lower, respectively), and promptness index (27.703% 26.689%, and 20.946% lower, respectively) of lettuce observably reduced but leaf length (68.139%, 57.098%, and 30.599% higher, respectively) and green leaf area (125.879%, 94.321%, and 33.644% higher, respectively) of lettuce signally facilitated under PELSCL, PELSCH, and PEHSCL comparison with control ($P<0.05$; Fig. 1). Further, leaf width (34.123% higher) and seedling biomass (fresh weight) (29.130% higher) of lettuce dramatically increased under PELSCL comparison with control ($P<0.05$; Fig. 1); germination vigor index (33.892% lower) and root length (39.507% lower) of lettuce visibly reduced under PELSCH comparison with control ($P<0.05$; Fig. 1); leaf width (23.697% higher) and seedling biomass (dry weight) (25.818% higher) of lettuce distinctly enhanced under PEHSCL ($P<0.05$; Fig. 1); germination vigor index (29.428% lower), root length (42.566% lower), and leaf width (20.379% lower) of lettuce clearly degraded under PEHSCH comparison with control ($P<0.05$; Fig. 1).

PEG 6000 regardless of the concentration dramatically impacted allelopathy triggered by goldenrod leaf extracts on SGeSGrP of lettuce (Fig. 1).

Root length of lettuce was approximately 15.720% lower under PELSCL comparison with SCL ($P<0.05$; Fig. 1). Germination index (17.920% lower) and germination vigor index (31.249% lower) of lettuce under PELSCH were notably lower than those under SCH ($P<0.05$; Fig. 1). Seedling height (18.367% lower), root length (24.100% lower), leaf length (9.486% lower), and green leaf area (16.291% lower) of lettuce under PEHSCL were signally lower than those under SCL ($P<0.05$; Fig. 1). Seedling height (22.371% lower), leaf length (23.423% lower), leaf width (30.290% lower), green leaf area (46.572% lower), and seedling biomass (fresh weight) of lettuce under PEHSCH were dramatically lower than those under SCH ($P<0.05$; Fig. 1).

Two-way ANOVA results presented that the interaction between the concentration of goldenrod leaf extracts and the concentration of PEG 6000 sharply affected germination potential, germination index, germination rate index, promptness index, root length, leaf length, leaf width, green leaf area, and single-plant fresh and dry weights ($P<0.05$; Table S1).

Discussion

The allelopathy of IAS, especially on SGeSGrP of indigenous species, have been extensively regarded as a key driver for explaining why IAS are so successful in their colonial ecosystems [2, 8,-10, 12-14]. This study revealed that SCL markedly reduced the germination capacity and uniformity, germination speed and vitality, and robust response capability of seedling's germination of lettuce. Further, SCH signally restrained the competitive ability for sunlight acquisition as well as water and inorganic salt acquisition of lettuce. Hence, light degree of goldenrod invasion triggered appreciable effects on the seed germination performance of lettuce but heavy degree of goldenrod invasion posed remarkable effects on the seedling growth performance of lettuce. Thus, SGeSGrP performance of indigenous species will inevitably come down under the pressure from the allelopathy refereed by goldenrod, mostly due to the secretion of allelochemicals chiefly created from litter residues and/or root exudates [1, 11]. Hence, the results are in accordance with previous studies [2, 8-10, 12-14]. Further, as expected, SCH triggered a higher level of allelopathy on the competitive ability for sunlight acquisition as well as water and inorganic salt acquisition, leaf photosynthetic area, and plant growing ability of lettuce than SCL in this study. The chief reason may be probably attributed to the fact that more allelochemicals have been secreted into the environment with growing invasion degree of IAS and thereby induce strongly allelopathy on the growth performance of indigenous species. Zhang et al. [52] also revealed that the allelochemicals of goldenrod can from accumulation in soil with a rising degree of goldenrod invasion. Nevertheless, SCH also activated less levels of allelopathy on the germination speed and vitality of

lettuce than SCL. Probably the most important factor for the positive effects of SCL on the seedling growth performance of lettuce may be due to the hormonal effects [53-56]. Consequently, SCH generated more allelopathy on the seedling growth performance of lettuce but SCL mediated more allelopathy on the seed germination performance of lettuce. Thus, these results partially validated the first hypothesis.

SCL interestingly awarded a positive effect on the sunlight acquisition as well as water and inorganic salt acquisition, plant growing ability, and plant water content of lettuce. Hence, SCL promoted the seedling growth performance of indigenous species to some extent. The most likely factor may be the induced reactive oxygen molecules in plant cell extension mediated by the allelochemicals recruited by SCL which can stimulate the seedling growth performance of lettuce [53-56]. Thus, goldenrod with light invasion degree could instigate slight pressure on the growth performance of indigenous species and thereby cause an optimistic drive for their seedling growth performance [8, 9, 57]. Currently, this phenomenon is mainly ascribed to hormonal effects which thought to be the chief driving force of the response strategies of plant species to exterior stress [53, 54, 56].

Several studies have shown that drought stress not only notably affect plant morphological and physiological performance [21-24, 58] but also dramatically restrain SGeSGrP of plant species [25-28]. Similar outcomes were obtained in this study, i.e., PEG 6000 dramatically reduced the competitive ability for sunlight acquisition as well as water and inorganic salt acquisition of lettuce. Hence, drought stress remarkably inhibited the seedling growth performance of lettuce. The inhibited effects mediated by drought stress on the seedling growth performance of lettuce most likely because of the gradually enhanced osmotic pressure generated by water deficit situations. While the advanced water deficit situations can enable the nutrient absorption efficiency of plant species tends to decrease. However, PEG 6000 dramatically improved the competitive ability for sunlight acquisition and leaf photosynthetic area of lettuce. Drought stress augmented leaf length and green leaf area of lettuce, in turn, could exacerbate the negative effects of drought stress mainly due to the uplifted leaf transpiration (losing water) with growing leaf length and green leaf area.

Drought stress has occurred frequently in recent years and is anticipated to rise in future decades. Thus, the allelopathy of IAS may be shifted and even consolidated under drought stress. This study presented that drought stress distinctly strengthened the allelopathy of goldenrod leaf extracts on SGeSGrP of lettuce, especially award a synergic effect on the germination speed and vitality, competitive ability for sunlight acquisition as well as water and inorganic salt acquisition, leaf photosynthetic area, and plant growing ability of lettuce. Two-way ANOVA results also

implied that the interaction between the concentration of goldenrod leaf extracts and the concentration of PEG 6000 notably affected the germination capacity and uniformity, germination speed and vitality, robust response capability of seedling's germination, competitive ability for sunlight acquisition as well as water and inorganic salt acquisition, leaf photosynthetic area, and plant growing ability. This result may be because the independent PEG 6000 and goldenrod leaf extracts (especially high concentration) all posed noteworthy inhibition on SGeSGrP of lettuce, and therefore the combination of the two treatment processes produced a synergic effect. Another and maybe equally important reason might be that leaf size and green leaf area of lettuce obviously aggrandized under the combined PEG 6000 and goldenrod leaf extracts (especially low concentration) which can enhance the intensity of transpiration and then promoted the level of water deficits. Thirdly, this phenomenon may be due to the enhanced contents of secondary metabolites (such as anthocyanin, flavonoids, phenol, and phenylalanine ammonia lyase activity) of plant species under drought stress [24]. Interestingly, the combined PEL and goldenrod leaf extracts regardless of the concentration exert more negative effects on the seed germination performance (including germination capacity and uniformity, germination speed and vitality, and robust response capability of seedling's germination) of lettuce than the combined PEH and goldenrod leaf extracts with equal concentration; But by contrast, the combined PEH and goldenrod leaf extracts regardless of the concentration exert more negative effects on the seedling growth performance (including the competitive ability for sunlight acquisition as well as water and inorganic salt acquisition, leaf photosynthetic area, and plant growing ability) of lettuce than the combined PEL and goldenrod leaf extracts with equal concentration. It seems to indicate that the seed germination performance of lettuce was more sensitive to light drought stress than seedling growth performance of lettuce but the seedling growth performance of lettuce was more sensitive to heavy drought stress than the seed germination performance of lettuce under the allelopathy induced by goldenrod leaf extracts. Consequently, drought stress may be advantageous to the invasion process of goldenrod largely through the oppressed SGeSGrP of indigenous species. Thus, the results did not entirely verify the second hypothesis.

Conclusions

This study firstly estimated the allelopathy of goldenrod (using leaf extracts) under a gradient level of drought stress. Goldenrod leaf extracts (low concentration) significantly reduced seed germination performance of lettuce but goldenrod leaf extracts (high concentration) notably decreased seedling growth performance of lettuce. PEG 6000 dramatically

inhibited the competitive ability for sunlight acquisition as well as water and inorganic salt acquisition of lettuce. PEG 6000 also noticeably reinforced the allelopathy of goldenrod leaf extracts on the germination speed and vitality, competitive ability for sunlight acquisition as well as water and inorganic salt acquisition, leaf photosynthetic area, and plant growing ability of lettuce. Thus, drought stress may be advantageous to the advance of goldenrod invasion process mainly via the oppressed SGeSGrP of indigenous lettuce mediated by the enhanced allelopathy.

Acknowledgements

This study was supported by Jiangsu Collaborative Innovation Center of Technology and Material of Water Treatment and Student Scientific Research Project, Jiangsu University. We are very grateful to the anonymous reviewer for the insightful and constructive comments that greatly improved this manuscript.

Conflict of Interest

The authors declare no conflict of interest.

References

- SVENSSON J.R., NYLUND G.M., CERVIN G., TOTH G.B., PAVIA H. Novel chemical weapon of an exotic macroalga inhibits recruitment of native competitors in the invaded range. *J Ecol* **101**, 140, **2013**.
- YUAN Y.G., WANG B., ZHANG S.S., TANG J.J., TU C., HU S.J., YONG J.W.H., CHEN X. Enhanced allelopathy and competitive ability of invasive plant *Solidago canadensis* in its introduced range. *J Plant Ecol* **6**, 253, **2013**.
- WANG C.Y., JIANG K., LIU J., ZHOU J.W., WU B.D. Moderate and heavy *Solidago canadensis* L. invasion are associated with decreased taxonomic diversity but increased functional diversity of plant communities in East China. *Ecol Eng* **112**, 55–, **2018**.
- WANG C.Y., JIANG K., ZHOU J.W., WU B.D. *Solidago canadensis* invasion affects soil N-fixing bacterial communities in heterogeneous landscapes in urban ecosystems in East China. *Sci Total Environ* **631–632**, 702, **2018**.
- WANG C.Y., WU B.D., JIANG K., ZHOU J.W., LIU J., LV Y.N. Canada goldenrod invasion cause significant shifts in the taxonomic diversity and community stability of plant communities in heterogeneous landscapes in urban ecosystems in East China. *Ecol Eng* **127**, 504, **2019**.
- WANG C.Y., WU B.D., JIANG K., ZHOU J.W., DU D.L. Canada goldenrod invasion affect taxonomic and functional diversity of plant communities in heterogeneous landscapes in urban ecosystems in East China. *Urban For Urban Green* **38**, 145, **2019**.
- WANG C.Y., WEI M., WANG S., WU B.D., CHENG H.Y. *Erigeron annuus* (L.) Pers. and *Solidago canadensis* L. antagonistically affect community stability and community invasibility under the co-invasion condition. *Sci Total Environ* **716**, 137128, **2020**.
- WANG C.Y., JIANG K., WU B.D., ZHOU J.W., LV Y.N. Silver nanoparticles with different particle sizes enhance the allelopathic effects of Canada goldenrod on the seed germination and seedling development of lettuce. *Ecotoxicology* **27**, 1116, **2018**.
- WANG C.Y., WU B.D., JIANG K. Allelopathic effects of Canada goldenrod leaf extracts on the seed germination and seedling growth of lettuce reinforced under salt stress. *Ecotoxicology* **28**, 103, **2019**.
- WANG S., WEI M., WU B.D., CHENG H.Y., WANG C.Y. Combined nitrogen deposition and Cd stress antagonistically affect the allelopathy of invasive alien species Canada goldenrod on the cultivated crop lettuce. *Sci Horticult* **261**, 108955, **2020**.
- MACEL M., VOS R.C.H., JANSEN J.J., PUTTEN W.H., DAM N.M. Novel chemistry of invasive plants: exotic species have more unique metabolomic profiles than native congeners. *Ecol Evol* **4**, 2777, **2014**.
- LU Y.J., WANG Y.F., WU B.D., WANG S., WEI M., DU D.L., WANG C.Y. Allelopathy of three Compositae invasive alien species on indigenous *Lactuca sativa* L. enhanced under Cu and Pb pollution. *Sci Horticult* **267**, 109323, **2020**.
- WEI M., WANG S., WU B.D., CHENG H.Y., WANG C.Y. Heavy metal pollution improves allelopathic effects of Canada goldenrod on lettuce germination. *Plant Biol* Doi: 10.1111/plb.13126, **2020**.
- HU G., ZHANG Z.H. Aqueous tissue extracts of *Conyza canadensis* inhibit the germination and shoot growth of three native herbs with no autotoxic effects. *Planta Daninha* **31**, 805, **2013**.
- SAFRIEL U., ADEEL Z. Dryland Systems. In: Hasson R, Scholes R, Ash N (eds) Ecosystem Trends and Human Well Being, Current State and Trends. Island Press, Washington, **2005**.
- REYNOLDS J.F., SMITH D.M.S., LAMBIN E.F., TURNER II B.L., MORTIMORE M., BATTERBURY S.P.J., DOWNING T.E., DOWLATABADI H., FERNÁNDEZ R.J., HERRICK J.E., HUBER-SANNWALD E., JIANG H., LEEMANS R., LYNAM T., MAESTRE F.T., AYARZA M., WALKER B. Global desertification: Building a science for dryland development. *Science* **316**, 847, **2007**.
- POINTING S.B., BELNAP J. Microbial colonization and controls in dryland systems. *Nat Rev Microbiol* **10**, 551, **2012**.
- EASTERLING D.R., MEEHL G.A., PARMESAN C., CHANGNON S.A., KARL T.R., MEARNES L.O. Climate extremes: Observations, modeling, and impacts. *Science* **289**, 2068, **2000**.
- DAI A. Increasing drought under global warming in observations and models. *Nat Clim Change* **3**, 52, **2013**.
- FU Q., FENG S. Responses of terrestrial aridity to global warming. *J Geophys Res Atmos* **119**, 7863, **2014**.
- HAJIHASHEMI S., SOFO A. The effect of polyethylene glycol-induced drought stress on photosynthesis, carbohydrates and cell membrane in *Stevia rebaudiana* grown in greenhouse. *Acta Physiol Plant* **40**, 142, **2018**.
- ZHANG C.M., SHI S.L. Physiological and proteomic responses of contrasting Alfalfa (*Medicago sativa* L.) varieties to PEG-induced osmotic stress. *Front Plant Sci* **9**, 242, **2018**.
- DU L.S., LIU H.Y., GUAN W.B., LI J.M., LI J.S. Drought affects the coordination of belowground and aboveground

- resource-related traits in *Solidago canadensis* in China. *Ecol Evol* **9**, 9948, **2019**.
24. CHAVOUSHI M., NAJAFI F., SALIMI A., ANGAJI S.A. Effect of salicylic acid and sodium nitroprusside on growth parameters, photosynthetic pigments and secondary metabolites of safflower under drought stress. *Sci Horticult* **259**, 108823, **2020**.
 25. KARIMMOJENI H., BAZRAFSHAN A.H., MAJIDI M.M., TORABIAN S., RASHIDI B. Effect of maternal nitrogen and drought stress on seed dormancy and germinability of *Amaranthus retroflexus*. *Plant Species Biol* **29**, E1–E8, **2014**.
 26. CAVALLARO V., BARBERA A.C., MAUCIERI C., GIMMA G., SCALISI C., PATANE C. Evaluation of variability to drought and saline stress through the germination of different ecotypes of carob (*Ceratonia siliqua* L.) using a hydrotime model. *Ecol Eng* **95**, 557, **2016**.
 27. ZAHER-ARA T., BOROOM N., SADAT-HOSSEINI M. Physiological and morphological response to drought stress in seedlings of ten citrus. *Trees* **30**, 985, **2016**.
 28. BORSAI O., AL HASSAN M., BOSCAIU M., SESTRAS R.E., VICENTE O. Effects of salt and drought stress on seed germination and seedling growth in *Portulaca*. *Rom Biotech Lett* **23**, 13340, **2018**.
 29. YUE M.F., YU H.X., LI W.H., YIN A.G., CUI Y., TIAN X.S. Flooding with shallow water promotes the invasiveness of *Mikania micrantha*. *Ecol Evol* **9**, 9177, **2019**.
 30. YAN X.L., LIU Q.R., SHOU H.Y., ZENG X.F., ZHANG Y., CHEN L., LIU Y., MA H.Y., QI S.Y., MA J.S. The categorization and analysis on the geographic distribution patterns of Chinese alien invasive plants. *Biodivers Sci* **22**, 667, **2014** [In Chinese].
 31. WANG C.Y., LIU J., XIAO H.G., ZHOU J.W., DU D.L. Floristic characteristics of alien invasive seed plant species in China. *An Acad Bras Ciênc* **88**, 1791, **2016**.
 32. ZHAO S.Y., SUN S.G., DAI C., GITURU R.W., CHEN J.M., WANG Q.F. Genetic variation and structure in native and invasive *Solidago canadensis* populations. *Weed Res* **55**, 163, **2015**.
 33. JIANG K., WU B.D., WANG C.Y., RAN Q. Ecotoxicological effects of metals with different concentrations and types on the morphological and physiological performance of wheat. *Ecotox Environ Safe* **167**, 345, **2019**.
 34. SEN A., ALIKAMANOGLU S. Antioxidant enzyme activities, malondialdehyde, and total phenolic content of PEG-induced hyperhydric leaves in sugar beet tissue culture. *In Vitro Cell Dev Biol Plant* **49**, 396, **2013**.
 35. RAMYA R., SINGH G.P., JAIN N., SINGH P.K., PANDEY M.K., SHARMA K. Effect of recurrent selection on drought tolerance and related morpho-physiological traits in bread wheat. *PLoS One* **11**, e156869, **2016**.
 36. Duan H.Y., Zhu Y.Q., Li J.Y., Ding W.K., Wang H.N., Jiang L.N., Zhou Y.Q. Effects of drought stress on growth and development of wheat seedlings. *Int J Agr. Biol* **19**, 1119, **2017**.
 37. SCHMER M.R., XUE Q., HENDRICKSON J.R. Salinity effects on perennial, warm-season (C4) grass germination adapted to the northern Great Plains. *Can. J Plant Sci* **92**, 873, **2012**.
 38. TAN M., LIAO F., HOU L.T., WANG J., WEI L.J., JIAN H.J., XU X.F., LI J.N., LIU L.Z. Genome-wide association analysis of seed germination percentage and germination index in *Brassica napus* L. under salt and drought stresses. *Euphytica* **213**, 40, **2017**.
 39. DING T.L., YANG Z., WEI X.C., YUAN F., YIN S.S., WANG B.S. Evaluation of salt-tolerant germplasm and screening of the salt-tolerance traits of sweet sorghum in the germination stage. *Plant Species Biol* **45**, 1073, **2018**.
 40. STEINMAUS S.J., TIMONTHY S.P., JODIE S.H. Estimation of base temperature for nine weed species. *J Exp Bot* **51**, 275, **2000**.
 41. QIU J., BAI Y.G., FU Y.B., WILMSHURST J.F. Spatial variation in temperature thresholds during seed germination of remnant *Festuca hallii* populations across the Canadian prairie. *Environ Exp Bot* **67**, 479, **2010**.
 42. MOLLARD F.P.O., NAETH M.A. Photoinhibition of germination in grass seed-Implications for prairie revegetation. *J Environ Manag* **14**, 1, **2014**.
 43. LIN W.X., KIM K.U., SMIN D.H. Rice allelopathic potential and its modes of action on barnyardgrass (*Echinochloa crus-galli*). *Allelopathy J* **7**, 215, **2000**.
 44. LI Z., PENG Y., ZHANG X.Q., MA X., HANG L.K., YAN Y.H. Exogenous spermidine improves seed germination of white clover under water stress via involvement in starch metabolism, antioxidant defenses and relevant gene expression. *Molecules* **19**, 18003, **2014**.
 45. NOREEN Z., ASHRAF M., HASSAN M.U. Inter-accessional variation for salt tolerance in pea (*Pisum sativum* L.) at germination and screening stage. *Pak J Bot* **39**, 2075, **2007**.
 46. ASCI O.O. Salt tolerance in red clover (*Trifolium pratense* L.) seedlings. *Afr J Biotechnol* **10**, 8774, **2011**.
 47. TOSCANO S., ROMANO D., TRIBULATO A., PATANE C. Effects of drought stress on seed germination of ornamental sunflowers. *Acta Physiol Plant* **39**, 184, **2017**.
 48. WU B.D., LIU J., JIANG K., ZHOU J.W., WANG C.Y. Differences in leaf functional traits between simple and compound leaves of *Canavalia maritima*. *Pol J Environ Stud* **28**, 1425, **2019**.
 49. AMANULLAH MARWAT K.B., SHAH P., MAULA N., ARIFULLAH S. Nitrogen levels and its time of application influence leaf area, height and biomass of maize planted at low and high density. *Pak J Bot* **41**, 761, **2009**.
 50. XIA T.T., MIAO Y.X., WU D.L., SHAO H., KHOSLA R., MI G.H. Active optical sensing of spring maize for in-season diagnosis of nitrogen status based on nitrogen nutrition index. *Remote Sens* **8**, 605, **2016**.
 51. HUANG S.S., SUN L.Q., HU X., WANG Y.H., ZHANG Y.J., NEVO E., PENG J.H., SUN D.F. Associations of canopy leaf traits with SNP markers in durum wheat (*Triticum turgidum* L. durum (Desf.)). *PLoS One* **13**, e206226, **2018**.
 52. ZHANG S.S., ZHU W.J., WANG B., TANG J.J., CHEN X. Secondary metabolites from the invasive *Solidago canadensis* L. accumulation in soil and contribution to inhibition of soil pathogen *Pythium ultimum*. *Appl Soil Ecol* **48**, 280, **2011**.
 53. AN M. Mathematical modelling of dose-response relationship (hormesis) in allelopathy and its application. *Nonlinear Biol Toxicol Med* **3**, 153, **2005**.
 54. VIATOR R.P., JOHNSON R.M., GRIMM C.C., RICHARD E.P. Allelopathic, autotoxic, and hormetic effects of postharvest sugarcane residue. *Agr J* **98**, 1526, **2006**.
 55. PRITHIVIRAJ B., PERRY L.G., BADRI D.V., VIVANCO J.M. Chemical facilitation and induced pathogen resistance mediated by a root-secreted phytotoxin. *New Phytol* **173**, 852, **2007**.

-
56. TAKAO L.K., RIBEIRO J.P.N., LIMA M.I.S. Allelopathic effects of *Ipomoea cairica* (L.) Sweet on crop weeds. *Acta Bot Bras* **25**, 858, **2011**.
57. HOSSAIN M.K., ANWAR S., NANDI R. Allelopathic effects of *Mikania cordata* on forest and agricultural crops in Bangladesh. *J For Res* **27**, 155, **2016**.
58. MEHRABAN A., TOBE A., GHOLIPOURI A., AMIRI E., GHAFARI A., ROSTAI M. The effects of drought stress on yield, yield components, and yield stability at different growth stages in bread wheat cultivar (*Triticum aestivum* L.). *Pol J Environ Stud* **28**, 739, **2019**.