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

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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.

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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 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 synergetic 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: ≈16.1ºC; the annual precipitation =1,150.6 mm; the annual sunshine time: ≈1,986.9 h) [5, 6, 9, 33]. The collected goldenrod leaves were washed adequately and air-dried thoroughly at approximately 25ºC. The dried goldenrod leaves were soaked with sterile distilled water in flasks at nearly 25ºC. 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 4ºC. 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: ≥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 in vitro that PEG can imitate the condition with water deficits in planta. PEG has been used as a 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 in vitro that PEG can imitate the condition with water deficits in plant cells [34-36].

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) PELSCL, 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-Wilk’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 ($\eta^2$) 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 $P\leq0.05$. 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), and green leaf area (59.999% 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) (32.981% higher) of lettuce under SCH were markedly lower than those under SCL but contrary to germination index (28.134% lower) 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.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Type III Sum of Squares</th>
<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>P</th>
<th>$\eta^2$</th>
</tr>
</thead>
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<tr>
<td>Germination percentage</td>
<td>0.033</td>
<td>2</td>
<td>0.017</td>
<td>8.060</td>
<td>0.003</td>
<td>0.472</td>
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<td>Germination potential</td>
<td>0.164</td>
<td>2</td>
<td>0.082</td>
<td>29.353</td>
<td>&lt;0.0001</td>
<td>0.765</td>
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<td>Germination index</td>
<td>846.299</td>
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<td>423.150</td>
<td>79.708</td>
<td>&lt;0.0001</td>
<td>0.899</td>
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<td>Germination rate index</td>
<td>1109.830</td>
<td>2</td>
<td>554.915</td>
<td>44.834</td>
<td>&lt;0.0001</td>
<td>0.833</td>
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<td>Germination vigor index</td>
<td>4.736</td>
<td>2</td>
<td>2.368</td>
<td>11.295</td>
<td>0.0007</td>
<td>0.557</td>
</tr>
<tr>
<td>Promptness index</td>
<td>136.519</td>
<td>2</td>
<td>68.259</td>
<td>42.736</td>
<td>&lt;0.0001</td>
<td>0.826</td>
</tr>
<tr>
<td>Seedling height</td>
<td>0.108</td>
<td>2</td>
<td>0.054</td>
<td>21.199</td>
<td>&lt;0.0001</td>
<td>0.702</td>
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<td>Root length</td>
<td>3.009</td>
<td>2</td>
<td>1.505</td>
<td>30.438</td>
<td>&lt;0.0001</td>
<td>0.772</td>
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<td>0.069</td>
<td>94.839</td>
<td>&lt;0.0001</td>
<td>0.913</td>
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<td>Leaf width</td>
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<td>0.017</td>
<td>54.816</td>
<td>&lt;0.0001</td>
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<td>0.024</td>
<td>125.378</td>
<td>&lt;0.0001</td>
<td>0.933</td>
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<td>Single-plant fresh weight</td>
<td>0.003</td>
<td>2</td>
<td>0.001</td>
<td>15.746</td>
<td>0.0001</td>
<td>0.636</td>
</tr>
<tr>
<td>Single-plant dry weight</td>
<td>&lt;0.001</td>
<td>2</td>
<td>&lt;0.001</td>
<td>0.509</td>
<td>0.6093</td>
<td>0.054</td>
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<td>&lt;0.001</td>
<td>2</td>
<td>&lt;0.001</td>
<td>5.980</td>
<td>0.0102</td>
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<td>2</td>
<td>0.004</td>
<td>1.820</td>
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<td>Germination potential</td>
<td>0.069</td>
<td>2</td>
<td>0.035</td>
<td>12.412</td>
<td>0.0004</td>
<td>0.580</td>
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<td>Germination index</td>
<td>171.465</td>
<td>2</td>
<td>85.732</td>
<td>16.149</td>
<td>&lt;0.0001</td>
<td>0.642</td>
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<tr>
<td>Germination rate index</td>
<td>213.322</td>
<td>2</td>
<td>106.661</td>
<td>8.618</td>
<td>0.0024</td>
<td>0.489</td>
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<td>Germination vigor index</td>
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<td>2</td>
<td>2.760</td>
<td>13.164</td>
<td>0.0003</td>
<td>0.594</td>
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<td>2</td>
<td>8.502</td>
<td>5.323</td>
<td>0.0153</td>
<td>0.372</td>
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<td>Seedling height</td>
<td>0.228</td>
<td>2</td>
<td>0.114</td>
<td>44.586</td>
<td>&lt;0.0001</td>
<td>0.832</td>
</tr>
<tr>
<td>Root length</td>
<td>10.223</td>
<td>2</td>
<td>5.112</td>
<td>103.413</td>
<td>&lt;0.0001</td>
<td>0.920</td>
</tr>
<tr>
<td>Leaf length</td>
<td>0.141</td>
<td>2</td>
<td>0.071</td>
<td>97.504</td>
<td>&lt;0.0001</td>
<td>0.915</td>
</tr>
<tr>
<td>Leaf width</td>
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<td>2</td>
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<td>82.904</td>
<td>&lt;0.0001</td>
<td>0.902</td>
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<td>Green leaf area</td>
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<td>2</td>
<td>0.026</td>
<td>133.906</td>
<td>&lt;0.0001</td>
<td>0.937</td>
</tr>
<tr>
<td>Single-plant fresh weight</td>
<td>0.006</td>
<td>2</td>
<td>0.003</td>
<td>34.954</td>
<td>&lt;0.0001</td>
<td>0.795</td>
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<tr>
<td>Single-plant dry weight</td>
<td>&lt;0.001</td>
<td>2</td>
<td>&lt;0.001</td>
<td>16.727</td>
<td>&lt;0.0001</td>
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<td>&lt;0.001</td>
<td>4.144</td>
<td>0.0331</td>
<td>0.315</td>
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<td>Germination percentage</td>
<td>0.009</td>
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<td>0.002</td>
<td>1.070</td>
<td>0.400</td>
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<tr>
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<td>0.071</td>
<td>4</td>
<td>0.018</td>
<td>6.301</td>
<td>0.002</td>
<td>0.583</td>
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<td>Germination index</td>
<td>156.855</td>
<td>4</td>
<td>39.214</td>
<td>7.387</td>
<td>0.001</td>
<td>0.621</td>
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<td>Germination rate index</td>
<td>215.526</td>
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<td>53.882</td>
<td>4.353</td>
<td>0.012</td>
<td>0.492</td>
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<tr>
<td>Germination vigor index</td>
<td>1.832</td>
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<td>0.458</td>
<td>2.184</td>
<td>0.112</td>
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<tr>
<td>Promptness index</td>
<td>22.718</td>
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<td>5.679</td>
<td>3.556</td>
<td>0.026</td>
<td>0.441</td>
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<td>Seedling height</td>
<td>0.028</td>
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<td>2.713</td>
<td>0.063</td>
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<td>0.918</td>
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<td>0.0001</td>
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<td>&lt;0.0001</td>
<td>0.885</td>
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<td>0.038</td>
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<td>&lt;0.001</td>
<td>4.499</td>
<td>0.011</td>
<td>0.500</td>
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<tr>
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<td>&lt;0.001</td>
<td>0.574</td>
<td>0.685</td>
<td>0.113</td>
</tr>
</tbody>
</table>

* 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 in comparison with control ($P<0.05$; Fig. 1). PEL also outstandingly promoted green leaf area (49.937% higher) of lettuce in comparison with control ($P<0.05$; Fig. 1). PEG 6000 regardless of the concentration did not observably affect seed germination parameters of lettuce in 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 in 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 in 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 in 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 PELSCL in 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 in 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 in 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 signal 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 SCH markedly reduced the germination capacity and uniformity, germination speed and vitality, and robust response capability of seedling’s germination of lettuce. Further, SCH signal 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 referred 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
lettuces 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, 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’s germination, and seedling growth performance 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.

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Conflict of Interest

The authors declare no conflict of interest.

References

8. WANG C.Y., JIANG K., WU B.D., ZHOU JW., 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.
23. DU L.S., LIU H.Y., GUAN W.B., LI J.M., LI J.S. Drought affects the coordination of belowground and aboveground
