

Research Article

Cite this article: Ghosh RK, Price AJ, Maity A (2025). Allelopathic effects of horseweed (*Erigeron canadensis*) on germination and growth of seven common weeds of the southern United States. *Weed Sci.* **73**(e63), 1–12. doi: [10.1017/wsc.2025.10034](https://doi.org/10.1017/wsc.2025.10034)

Received: 19 December 2024

Revised: 18 April 2025

Accepted: 10 June 2025

Associate Editor:

Caio Brunharo, Penn State University

Keywords:

Allelopathy; *Conyza canadensis*; weed dynamics; seed germination; phenolics

Corresponding author:

Aniruddha Maity; Email: a.maity@auburn.edu

Allelopathic effects of horseweed (*Erigeron canadensis*) on germination and growth of seven common weeds of the southern United States

Rakesh Kumar Ghosh¹, Andrew J. Price² and Aniruddha Maity³ 

¹Postdoctoral Research Associate, Department of Crop, Soil, and Environmental Sciences, Auburn University, Auburn, AL, USA; ²Plant Physiologist, USDA-ARS National Soil Dynamics Lab, Auburn, AL, USA and ³Assistant Professor, Department of Crop, Soil, and Environmental Sciences, Auburn University, Auburn, AL, USA

Abstract

Horseweed [*Erigeron canadensis* L.; syn.: *Conyza canadensis* (L.) Cronquist ($2n = 18$), family: Asteraceae] is known as one of the 10 most troublesome and most commonly occurring weeds in 12 categories of broadleaf crops, fruits, and vegetables and is present in 2,540 counties across the United States. Wide phenotypic plasticity coupled with highly adaptive traits and reported allelopathy might have resulted in its rapid spread and extensive presence across the United States, presumably by altering the composition of local plant community. This study for the first time revealed the allelopathic effect of *E. canadensis* leaf aqueous extract (10%) on seed germination and seedling growth of seven common weeds, namely, Palmer amaranth (*Amaranthus palmeri* S. Watson), smooth pigweed (*Amaranthus hybridus* L.), prickly sida (*Sida spinosa* L.), and pitted morningglory (*Ipomoea lacunosa* L.), which are native to North America, and non-native lambsquarters (*Chenopodium album* L.), curly dock (*Rumex crispus* L.), and barnyardgrass [*Echinochloa crus-galli* (L.) P. Beauv.]. *Erigeron canadensis* aqueous extract significantly ($P < 0.05$) reduced the seed germination and seedling growth of *A. hybridus*, *A. palmeri*, *R. crispus*, and *S. spinosa*, but showed nonsignificant impacts on *I. lacunosa*, *C. album*, and *E. crus-galli*. Based on synthetical allelopathic effects ($SE < 0$), the order of inhibition from highest to lowest was as follows: *A. hybridus* (−0.580), *R. crispus* (−0.464), *A. palmeri* (−0.409), *S. spinosa* (−0.248), *C. album* (−0.143), *I. lacunosa* (−0.035), and *E. crus-galli* (0.009). Liquid chromatography of the *E. canadensis* aqueous extract identified a total of 38 compounds with previously known allelopathy, including piperidine, choline, 4-hydroxybenzaldehyde, acetonecyanohydrin, gallic acid, 2-furoic acid, genistein, and gentisic acid. The current study, utilizing a petri dish bioassay, explains *E. canadensis*'s invasive potential and mechanisms for affecting the succession of commonly occurring native and non-native weed species in the southern United States. These results establish a solid foundation for understanding the mechanisms driving the successful invasion of *E. canadensis* in its native range and provide a valuable theoretical framework for early-warning systems assessing ecological risks.

Introduction

The quest for food security has never been easy, being a war against various biotic and abiotic factors acting in production fields. Evolutionarily, weeds have emerged as one of the major biotic factors posing immense threats to agricultural production, causing economic losses at the tune of US\$33 billion in the United States (WSSA 2024), A\$3.3 billion in Australia (Llewellyn et al. 2016), and US\$11 billion in India (Gharde et al. 2018). Weed phenotypic plasticity coupled with adaptive trait diversity and the development of 533 unique reported cases of herbicide-resistant weeds covering 273 species, including 156 dicots and 117 monocots, in 101 crops across 72 countries have made weeds one of the greatest threats to intensive agricultural production systems globally (Heap 2024).

Among several problematic weeds in the United States, horseweed [*Erigeron canadensis* L.; syn.: *Conyza canadensis* (L.) Cronquist ($2n = 18$), family: Asteraceae], also known as marehail or Canadian fleabane, is known as 1 out of 10 most troublesome and most commonly occurring weeds in 12 categories of broadleaf crops, fruits, and vegetables (WSSA 2017). *Erigeron canadensis* has become one of the predominant weeds in 40 crops across 70 countries (Holm et al. 1997), especially under reduced tillage and no-till conditions (Steckel and Culpepper 2006). It can cause yield losses to the tune of 68% to 92% in soybean [*Glycine max* (L.) Merr.] and cotton (*Gossypium hirsutum* L.) (Byker et al. 2013; Silva et al. 2014; Trezzi et al. 2015) and 28% to 64% in sugar beet (*Beta vulgaris* L.) and grapes (*Vitis vinifera* L.) (Holm et al. 1997; Shrestha et al. 2010). *Erigeron canadensis* is a C_3 , invasive species native to North America. It exhibits high fecundity

© The Author(s), 2025. Published by Cambridge University Press on behalf of Weed Science Society of America. This is an Open Access article, distributed under the terms of the Creative Commons Attribution-NonCommercial-NoDerivatives licence (<https://creativecommons.org/licenses/by-nc-nd/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided that no alterations are made and the original article is properly cited. The written permission of Cambridge University Press must be obtained prior to any commercial use and/or adaptation of the article.



(230,000 seeds per plant) (Weaver 2001), efficient long-distance seed dispersal (from 500 m to 772 km from the source plant) (Dauer et al. 2007; Shields et al. 2006), germination under wide range of environmental conditions (Loux et al. 2006; Waggoner et al. 2011), luxurious growth and adaptability to harsh environments (Tozzi et al. 2014), and propensity for herbicide-resistance development (Heap 2014). These adaptive traits may have played a significant role in the spread of *E. canadensis* to a wide range of geographic landscapes across various countries of Asia, Africa, Europe, and Oceania (Bajwa et al. 2016; Tilley 2012).

Multiple reports have indicated that several invasive plants, including *E. canadensis* (Bhowmik and Bekech 1993; Shaukat et al. 2003; Shields et al. 2006), release numerous allelochemicals, the secondary metabolites, in leachates during the process of biomass decomposition or through volatilization from living biomass into the local ecosystem, affecting population dynamics and community composition of native plants (Callaway and Aschehoug 2000; Dorning and Cipollini 2006; Inderjit et al. 2008). Although the persistence of these allelochemicals in soil may be short-lived, they can still influence plant succession depending on the continuity of supply of these compounds from live or dead plants (Rice 1979).

Erigeron canadensis has been reported to contain various allelochemicals (Queiroz et al. 2012; Shaukat et al. 2003). The distribution of these allelochemicals and their impact on native plant communities vary depending on geographic locations. For example, gallic acid, vanillic acid, catechol, and syringic acid were main constituents of *E. canadensis* collected from Karachi, Pakistan, and inhibited the growth of tomato (*Solanum lycopersicum* L.), radish (*Raphanus sativus* L.), wheat (*Triticum aestivum* L.), corn (*Zea mays* L.), millet (*Pennisetum* spp.), and mungbean [*Vigna radiata* (L.) R. Wilczek] (Shaukat et al. 2003). Around 42 compounds, including some phenols, ketones, and acids, were identified as allelopathic in *E. canadensis* collected from China (Zhang 2010); whereas *p*-coumaric, ferulic, *p*-hydroxybenzoic, vanillic, and syringic acids were predominant compounds in *E. canadensis* collected in Belgrade, Serbia, with allelopathic effects on orchardgrass (*Dactylis glomerata* L.) and red clover (*Trifolium pratense* L.) (Djurdjević et al. 2011). Interestingly, (4Z)-lachnophyllum lactone was the major allelopathic compound isolated from *E. canadensis* in Mississippi, USA, with phytotoxicity on creeping bentgrass (*Agrostis stolonifera* L.) and lettuce (*Lactuca sativa* L.) (Queiroz et al. 2012). Shah et al. (2014) reported negative relationships between abundance of *E. canadensis* and richness of native species in non-native ranges of Europe, China, and India. But there existed either positive or no relationships in the native North American range which might be due to stronger allelopathic effect in non-native ranges.

Erigeron canadensis is present in 2,540 counties out of 3,244 counties in the United States, covering 78.29% of the total geographic area (Swearingen and Barger 2016). Although previous reports indicated wide variation in the allelopathic compositions among *E. canadensis* populations and their effects on native or non-native plants, there is no information available on the allelopathy of native *E. canadensis* on the dominant southern U.S. weeds, including four native weeds (Palmer amaranth [*Amaranthus palmeri* S. Watson], smooth pigweed [*Amaranthus hybridus* L.], prickly sida [*Sida spinosa* L.], and pitted morningglory [*Ipomoea lacunosa* L.]) and three non-native weeds (lambsquarters [*Chenopodium album* L.], curly dock [*Rumex crispus* L.], and barnyardgrass [*Echinochloa crus-galli* (L.) P. Beauv.]). *A. palmeri*, *I. lacunosa*, *C. album*, and *E. crus-galli* rank among the top 10 most troublesome and widespread weeds across the United States (WSSA 2017). In addition, *A. hybridus*,

S. spinosa, and *R. crispus* present significant threats to agricultural lands in the U.S. Southeast, particularly in states like Alabama (Buchanan et al. 1977; da Silva et al. 2022; Jones and Davis 1963). The objective of this study was to evaluate the allelopathic potential of *E. canadensis* on various parameters of seed germination and seedling growth of seven selected common native and non-native weed species of the southern United States. This study also aimed to identify the allelochemicals present in the *E. canadensis* aqueous extract and discuss its allelopathic effects on studied weed species.

Materials and Methods

Collection of *Erigeron canadensis* Biomass

Aboveground parts of mature but green *E. canadensis* plants were collected from natural areas in Auburn, AL, USA (32.6442°N, 85.52265°W). The fresh leaves were separated from the stems, followed by washing under tap water to remove adhered dirt, and then removing excess water by soaking onto tissue paper/blotting paper. The cleaned leaves were stored in a freezer maintained at -80 °C and used to prepare *E. canadensis* aqueous extract for different experiments within the present study.

Preparation of Aqueous Extract from *Erigeron canadensis* Biomass

One hundred grams of *E. canadensis* leaf was weighed and macerated with a porcelain mortar and pestle. The resulting paste was mixed with 400 ml of double-distilled water in a 1,000-ml Erlenmeyer flask and was agitated over an orbital shaker (Innova 4000, New Brunswick Scientific, Hauppauge, New York, USA) at 150 rpm for 48 h under 25 ± 1 °C. The primary leachate was collected by filtering the materials of the flask with a double-layer of cheesecloth, followed by centrifugation (Megafuge ST4R Plus-MD, Thermo Fisher Scientific, Langensfeld, Hesse, Germany) at 3,000 rpm for 30 min at 25 ± 1 °C. The supernatant was collected in a glass bottle, marked as "25% w/v basis" (100 g of leaves in 400 ml of water), and stored at 4 ± 1 °C for use in various experiments. Further, this primary stock solution was diluted to prepare a 10% aqueous extract with double-distilled water and used in various studies.

Seed Germination Assay

Screening studies were conducted to understand the effect of *E. canadensis* extracts (0% and 10%) on seed germination of seven common weed species, including broadleaves, namely, *A. palmeri*, *A. hybridus*, *S. spinosa*, *R. crispus*, *I. lacunosa*, and *C. album*, and one grass, *E. crus-galli*. The seeds (procured from Azlin Seed Service, Leland, MS, USA) were collected in 2022 and placed in permeable paper bags for storage under laboratory conditions at 20 ± 2 °C in the dark until commencement of the experiment. A preliminary viability test was conducted to ensure adequate seed viability before the experiment.

Twenty-five seeds in triplicates per population were placed on two layers of Whatman No.1 filter paper (supplied by VWR International, Radnor, Pennsylvania, USA) in a series of 9-cm-diameter petri dishes. Twelve milliliters of 10% *E. canadensis* extract was added to each petri dish to evaluate the allelopathic effect of *E. canadensis* extract on various weed seeds. Preliminary studies indicated that a 12-ml volume of either water or *E. canadensis* extract was sufficient for conducting 21-d

germination studies under present incubation conditions of light/dark (12/12-h, 25/18 °C) at 60% relative humidity. Water levels (for control) or *E. canadensis* extract levels (for treatments) were regularly monitored throughout the 21-d experiment, and only double-distilled water was added to petri dishes as needed to maintain the initial solution levels for both control and *E. canadensis* treatments, compensating for evaporation and concentration changes in the solutions. Petri dishes with control and *E. canadensis* treatment were incubated for 21 d under a controlled environment of light/dark (12/12-h, 25/18 °C) and relative humidity of 60% by randomly distributing the petri dishes between the shelves of a growth chamber (ISTA 2024). Seed germination was recorded every 2 d up to 10 d and thereafter at 14 and 21 d (Maity et al. 2025). All experiments were repeated three times under the same experimental conditions. At the conclusion of the germination test, the viability of nongerminated seeds that appeared intact was assessed by gently tapping the seeds with forceps to check for the presence of a turgid embryo. The seeds that exhibited blackened, decayed tissues or were empty were classified as dead. The healthy nongerminated seeds were longitudinally dissected and immersed in a 1% solution of 2,3,5-triphenyl tetrazolium chloride for 24 h at 25 ± 1 °C. Seeds with red-stained embryos were considered viable. All viable but nongerminated seeds were categorized as dormant (Supplementary Figure 1). Germination-associated parameters, such as germination percentage (G%), inhibited germination (IG%), relative inhibited germination (RIG%), speed of germination (SG), and mean germination time (MGT) were calculated using the following equations.

$$G\% = (\text{Number of normal seedling/number of seeds}) \times 100 \quad [1]$$

$$IG\% = 100 - G\% \quad [2]$$

$$RIG\% = [(IG\% \text{ at treatment} - IG\% \text{ at control}) / (100 - IG\% \text{ at control})] \times 100 \quad [3]$$

$$SG = n_1/d_1 + n_2/d_2 + n_3/d_3 + \dots \quad [4]$$

$$MGT = (n_1 \times d_1 + n_2 \times d_2 + n_3 \times d_3 + \dots) / \text{total number of days} \quad [5]$$

where n represents the number of germinated seeds on the d th day.

At the end of the germination test (21 d), seedling shoot and root lengths were measured, which served as an indicator of seed vigor. The allelopathic effects of *E. canadensis* extracts were measured by calculating the allelopathic response index (RI) as described by Williamson and Richardson (1988).

$$RI = 1 - (C/T)(T > C) \text{ or } RI = (T/C) - 1(T < C) \quad [6]$$

where C and T represent the corresponding index values for control and treatment. The RI ranges from +1 to −1. If $RI > 0$, it indicated there was a promoting effect, otherwise $RI < 0$ indicated an inhibiting effect, and the absolute value of RI depicted the strength of the allelopathy. The synthetical allelopathic effects (SE) were assessed based on the average RI value of five parameters including germination percentage (G%), speed of germination (SG), mean germination time (MGT), shoot height (S), and root length

(R) (Dai et al. 2022; Wang et al. 2022). SE was calculated using the following equation:

$$SE = [RI(P_1) + RI(P_2) + RI(P_3) + \dots RI(P_n)]/n \quad [7]$$

where $RI(P_1)$, $RI(P_2)$, $RI(P_3)$, and $RI(P_n)$ represent response index (RI) values until the n th parameter (P). The SE ranges from +1 to −1, with positive values indicating treatment-induced stimulation and negative values indicating inhibition relative to the controls. SE values close to zero indicate no or low effect of the treatment. All measurements were taken from the same receptor seeds subjected to the same treatment.

Identification of Compounds in *Erigeron canadensis* Extract with Reverse-Phase Liquid Chromatography–Mass Spectrometry (LC–MS)

For reverse-phase analysis, 100 µl of sample was mixed with 500 µl ice-cold methanol with 15 min of freezing time followed by centrifugation at 16,000 × g (g denotes the relative centrifugal force or g -force) for 5 min to precipitate protein. The supernatant was concentrated on a Thermo Savant DNA 120 vacuum centrifuge at 300 × g on medium heat for 2 h. The sample was re-dissolved with 100 µl of water and analyzed. Analysis was performed on a Vanquish UHPLC system (Thermo Fisher Scientific, Waltham, Massachusetts, USA) coupled with a quadrupole orbitrap mass spectrometer (Orbitrap Exploris 120, Thermo Fisher Scientific, Waltham, Massachusetts, USA) with electrospray ionization (H-ESI) switching between positive or negative modes using Xcalibur software (v. 4.4.16.14). Injection of 10 µl of the sample was made on a C18 column (Accucore RP-MS 100 × 2.1 mm with 2.6-µm particles; Thermo) held at 40 °C with a 200 µl min^{−1} flow rate of mobile phase solution A (99.9% water with 0.1% formic acid) and solution B (100% acetonitrile). The gradient began at 0% B, was held for 2 min, followed by a linear ramp to 95% B in 11 min, was held at 95% B for 1 min, and decreased to 0%B in 1 min, then was held for 5 min for a total analysis time of 20 min. The flow was diverted to waste for the first minute and a half of analysis and after 15 min.

For mass spectrometry, the scan range was 50 to 500 m/z with resolution of 120,000, 70% radio frequency (RF) lens, maximum injection time auto, with EASY-IC run-start on. The spray voltage was 3,300 V in positive and 2,100 V in negative mode, the ion transfer tube temperature was 320 °C, and the vaporizer temperature was 275 °C. Data-dependent acquisition on singly charged precursors only was used with dynamic exclusion on auto, with an intensity threshold of 50,000, the window was 2 Da, the higher-energy collisional dissociation (HCD) was set to 40% normalized, the tandem mass spectrometry (MS/MS) resolution was 15,000, and the automatic gain control (AGC) was set to standard for the four dependent scans. A targeted mass exclusion list was created based on a blank injection and apex detection was set to 30%.

The LC-MS results were used in Compound Discoverer v. 3.2 to align retention times; detect compounds; merge features; group compounds; search mzCloud; search ChemSpider with BioCyc, ChEBI, and ChEMBL databases with tolerance of 5 ppm; search mass lists, including the Arita Lab Flavonoid Structure Database, EFS HRAM compound Database, and the Endogenous Metabolites database; and predict compositions automatically. The LC-MS analysis indicated the presence of several compounds in the

E. canadensis extract. The “top 38” compounds were selected based on the relative abundance or % area contribution of a particular compound in the total ion chromatogram (TIC) of the LC-MS analysis. It was determined as follows:

$$\% \text{ Area} = \left(\frac{\text{Area under the peak of a particular compound}}{\text{total area of all peaks in the total ion chromatogram}} \right) \times 100$$

[8]

Data Analysis

For all germination and seedling growth data, deviations from normality and the homogeneity of the variances were evaluated in RStudio (v. 3.0.1; Ritz et al. 2015) by using a Shapiro-Wilk test and Bartlett's test, respectively. Differences in the values of various parameters of seed germination and seedling growth for all studied weed species were measured using a one-way ANOVA with Student's *t*-test JMP PRO v. 18 (1989–2023, SAS Institute, Cary, NC, USA). Means were separated using Tukey's honest significant difference (HSD) for comparing among treatments, whereas Student's *t*-test was used to compare between two treatments at a significance level of $\alpha = 0.05$. Data presented in this paper indicated mean value \pm SE of various parameters for different weed species. For developing the regression curves for germination percentage recorded over the entire period of germination test, a third-order

polynomial function was used based on the best R^2 value using the *LINEST* function in Microsoft® Excel (Redmond, WA, USA).

Results and Discussion

Effect of *Erigeron canadensis* Aqueous Extract on Seed Germination of Weed Species

The effect of *E. canadensis* aqueous extract (10%) on studied weed species varied significantly (Table 1). At the end of a 21-d germination study, it was observed that application of *E. canadensis* aqueous extract resulted in 33.33%, 41.03%, 60.71%, and 65.22% decrease in germination for *S. spinosa*, *A. palmeri*, *A. hybridus*, and *R. crispus*, respectively, with respect to the control treatments ($P < 0.05$) (Figure 1). SG values decreased by 39.35%, 48.39%, 64.78%, and 82.01% for *S. spinosa*, *A. palmeri*, *R. crispus*, and *A. hybridus*, respectively, in response to *E. canadensis* aqueous extract treatment over the control; whereas MGT values were reduced by 25.65%, 41.44%, 65.26% and 69.58% for *S. spinosa*, *A. palmeri*, *R. crispus*, and *A. hybridus*, respectively, under *E. canadensis* aqueous extract treatment over the control. However, there was no significant difference ($P < 0.05$) in seed germination of *C. album*, *I. lacunosa*, and *E. crus-galli* with *E. canadensis* aqueous extract over the control (Figure 2), and SG and MGT values remained lower ($<4.04\%$) or not affected with *E. canadensis* aqueous extract.

Table 1. Effect of aqueous extract of *Erigeron canadensis* (HW) on the germination and growth parameters of various weeds^a

Treatments	G(%)	RI(G)	SG	RI(SG)	MGT	RI(MGT)
<i>Amaranthus hybridus</i>						
0.0% HW	74.67 a (± 0.267)	—	13.24a (± 0.698)	—	53.02 a (± 0.286)	—
10% HW	16.00 b (± 0.533)	−0.606 D (± 0.040)	2.38b (± 0.365)	−0.817 D (± 0.035)	16.13b (± 0.984)	−0.696 E (± 0.019)
<i>Chenopodium album</i>						
0.0% HW	34.67 a (± 0.267)	—	2.85 a (± 0.162)	—	20.79 a (± 0.124)	—
10% HW	32.00 a (± 1.386)	−0.094 AB (± 0.207)	3.39 a (± 0.526)	0.127 A (± 0.122)	20.38 a (± 3.851)	−0.039 AB (± 0.174)
<i>Sida spinosa</i>						
0.0% HW	48.00 a (± 0.462)	—	6.48 a (± 0.248)	—	31.94 a (± 0.715)	—
10% HW	37.33 b (± 0.706)	−0.223 BC (± 0.056)	3.93 b (± 0.415)	−0.394 B (± 0.058)	23.75 b (± 2.353)	−0.258 BC (± 0.063)
<i>Amaranthus palmeri</i>						
0.0% HW	52.00 a (± 0.462)	—	11.14 a (± 0.250)	—	37.92 a (± 1.353)	—
10% HW	30.67 b (± 0.267)	−0.406 CD (± 0.049)	5.75 b (± 0.584)	−0.481 BC (± 0.065)	22.21 b (± 0.894)	−0.412 CD (± 0.039)
<i>Rumex crispus</i>						
0.0% HW	30.67 a (± 0.267)	—	3.75 a (± 0.168)	—	20.75 a (± 0.825)	—
10% HW	10.67 b (± 0.267)	−0.655 D (± 0.030)	1.32 b (± 0.185)	−0.650 CD (± 0.038)	7.21 b (± 1.033)	−0.655 DE (± 0.038)
<i>Echinochloa crus-galli</i>						
0.0% HW	28.00 a (± 0.462)	—	2.23 a (± 0.102)	—	16.97 a (± 1.095)	—
10% HW	30.67 a (± 0.267)	0.083 A (± 0.083)	2.14 a (± 0.237)	−0.046 A (± 0.093)	17.32 a (± 1.059)	0.015 A (± 0.092)
<i>Ipomoea lacunosa</i>						
0.0% HW	86.67 a (± 0.266)	—	25.45 a (± 0.746)	—	66.40 a (± 0.894)	—
10% HW	82.67 a (± 0.266)	−0.046 AB (± 0.001)	24.98 a (± 0.549)	−0.002 A (± 0.019)	64.71 a (± 1.019)	−0.039 AB (± 0.006)

^aAt the end of a 21-d germination test. G(%), % germination; RI(G%), response index for G(%); SG, speed of germination; RI(SG), response index for SG; MGT, mean germination time; RI(MGT), response index for MG. Different lowercase letters following mean values within a species in columns G (%), SG, and MGT indicate significant differences between the treatments within a species at $P < 0.05$. Different uppercase letters following mean values in columns RI(G), RI(SG), and RI(MGT) indicate significant differences in the respective parameter among the species at $P < 0.05$.

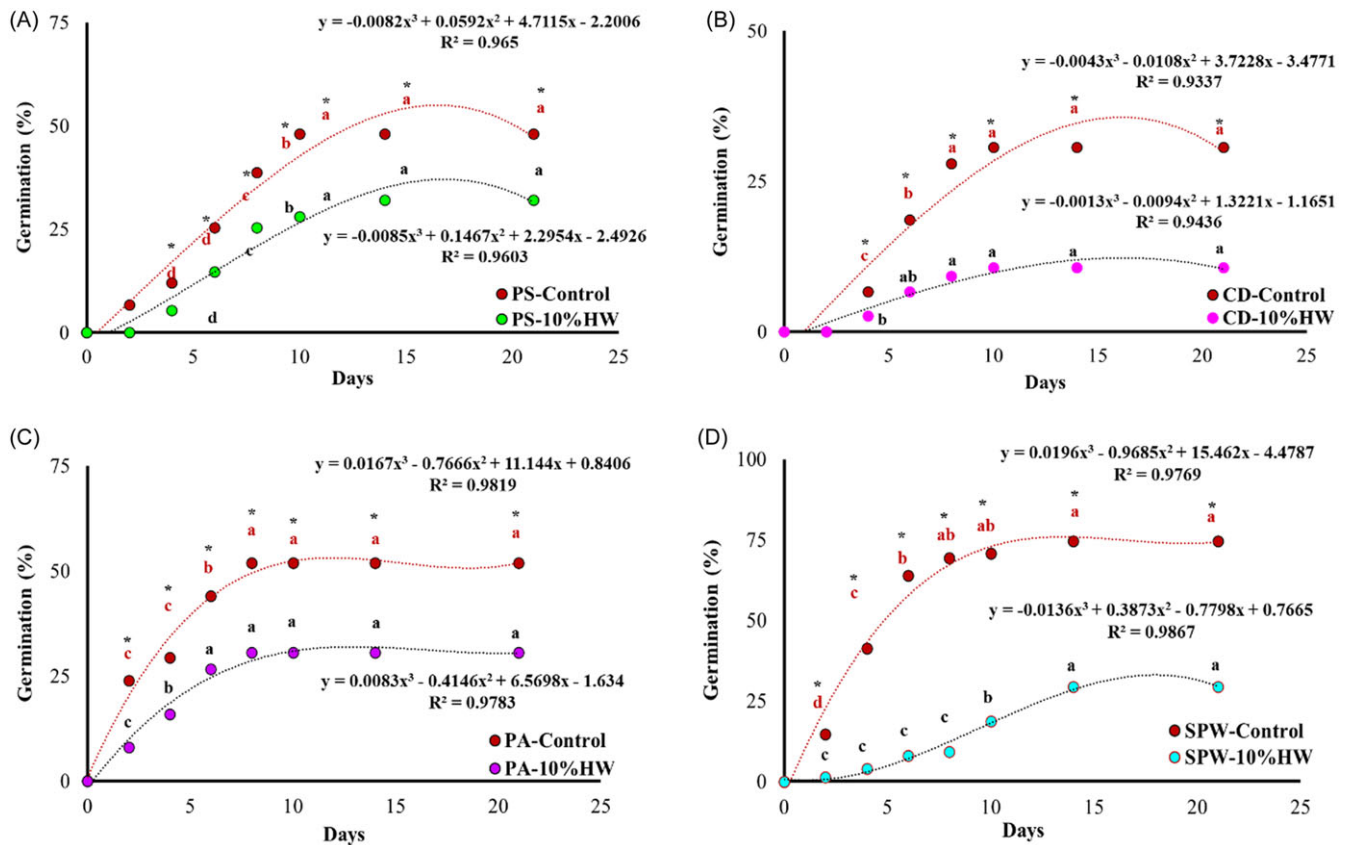


Figure 1. Seed germination of (A) *Sida spinosa* (PS), (B) *Rumex crispus* (CD), (C) *Amaranthus palmeri* (PA), and (D) *Amaranthus hybridus* (SPW), in response to 10% aqueous extracts of *Erigeron canadensis* (HW) at the end of a 21-d germination test. In panels, different letters on the data points indicate significant difference ($P < 0.05$) among observation timings in response to a specific treatment (0% or control in brown and 10% HW in other colors). Asterisks (*) indicate significant difference ($P < 0.05$) between two treatments for a given day. Third-order regression curves were based on the best R^2 value using the *LINEST* function in Microsoft® Excel.

Hu and Zhang (2013) reported 79.8%, 85.5%, and 93.8% reduction in germination of broadleaf plantain [*Plantago major* L.; syn.: *Plantago asiatica* L.], large crabgrass [*Digitaria sanguinalis* (L.) Scop.], and Oriental false hawkbeard [*Youngia japonica* (L.) DC.] in response to 20% aqueous extract of aboveground parts of *E. canadensis* without any autotoxicity in southern China. Other studies also reported negative impacts of *E. canadensis* extract alone (Wang et al. 2017) or in combination of other plants like Canada goldenrod [*Solidago canadensis* L.] (Wei et al. 2020) on germination and growth of allelochemical-sensitive lettuce [*L. sativa*] in China. Shah et al. (2014) reported mostly negative relationships between abundance of *E. canadensis* and richness of native species in non-native ranges of Europe (Queen Anne's lace [*Daucus carota* L.], heath false brome [*Brachypodium pinnatum* (L.) P. Beauv.], orchardgrass [*D. glomerata*], purple moor-grass [*Molina caerulea* (L.) Moench], and codlins-and-cream [*Epilobium hirsutum* L.], China (dwarf daylily [*Heimerocallis minor* L.], Chinese motherwort [*Leonurus tataricus* L.], tidal marsh flat sedge [*Cyperus serotinus* Rottb.], yellow avens [*Geum aleppicum* Jacq.], redroot pigweed [*A. retroflexus*], and patience dock [*Rumex patientia* L.], and India (Himalayan rhubarb [*Rheum australe* D. Don], prickly lettuce [*Lactuca serriola* L.], and nodding Carpesium [*Carpesium cernuum* L.]). But they observed either positive or no relationships in the native North American range (large-leaved avens [*Geum macrophyllum* Willd.], Great Basin wildrye [*Elymus cinereus* Scribn. & Merr.], slender cinquefoil [*Potentilla gracilis* Douglas ex Hook.], and nettleleaf giant hyssop [*Agastache urticifolia* (Benth.)

Kuntze]), suggesting the presence of biogeographic differences. Differential inhibition of weed germination in the current study resonates this biogeographic difference. Wang et al. (2017) reported higher inhibitory effect of *E. canadensis* on lettuce [*L. sativa*] at higher latitudes in Shenyang, China (41.82°N, 123.46°E) due to production of more allelochemicals in a cold temperate climate compared with lower latitudes in Zhenjiang, China (32.20°N, 119.51°E) with a subtropical monsoon climate. Production of higher concentrations of allelochemicals in *E. canadensis* collected from higher-latitude areas in Jiangsu (31°57'N to 32.15°N, 118°54'E to 120°53'E) compared with lower-latitude areas in Hubei (30°21'N to 30°6'N, 114°21'E to 115°21'E) and Anhui (30°37'N to 31°22'N, 117°32'E to 118°23'E) in China was also reported by Cheng et al. (2021). Similar reports of production of higher concentrations of allelochemicals at higher latitudes were also made earlier for other plants like goat weed [*Ageratum conyzoides* L.] (Hu and Kong 2002) and western waterweed [*Elodea nuttallii* (Planch.) H. St. John] (Erhard and Gross 2005).

Effect of *Erigeron canadensis* Aqueous Extract on Seedling Growth

The effect of *E. canadensis* aqueous extract on root and shoot lengths of seedlings varied across the studied weed species (Table 2; Figure 3). The root lengths decreased significantly ($P < 0.05$) at 34.6%, 48.77%, and 68.35% for *C. album*, *A. hybridus*, and *A. palmeri*, respectively, over the control treatments, but no significant reduction in root

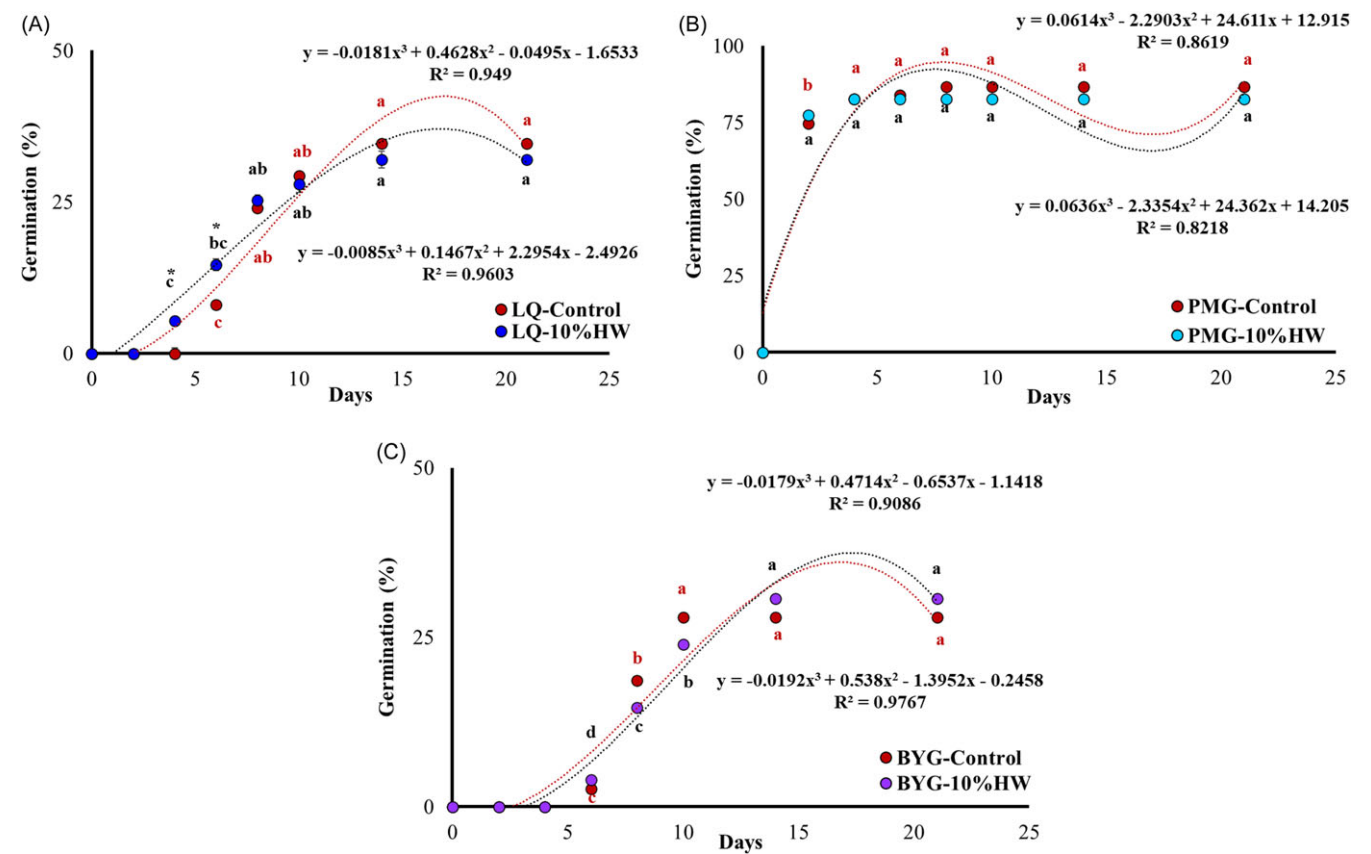


Figure 2. Seed germination patterns of (A) *Chenopodium album* (LQ), (B) *Ipomoea lacunosa* (PMG), and (C) *Echinochloa crus-galli* (BYG) in response to 10% aqueous extracts of *Erigeron canadensis* (HW) at the end of a 21-d germination test. In panels, different letters on the data points indicate significant difference ($P < 0.05$) among observation timings in response to a specific treatment (0% or control in brown and 10% HW in other colors). Asterisks (*) indicate significant difference ($P < 0.05$) between two treatments for a given day. Third-order regression curves were based on the best R^2 value using the *LINEST* function in Microsoft® Excel.

Table 2. Effect of aqueous extract of *Erigeron canadensis* on the seedling growth parameters of various weeds^a

Treatments	R	RI(R)	S	RI(S)
	mm		mm	
<i>Amaranthus hybridus</i>				
0.0% HW	24.40 a (± 0.961)	—	17.43 a (± 0.464)	—
10% HW	12.50 b (± 1.323)	−0.490 D (± 0.038)	12.28 b (± 1.120)	−0.292 AB (± 0.081)
<i>Chenopodium album</i>				
0.0% HW	36.83 a (± 0.733)	—	20.32 a (± 2.644)	—
10% HW	24.09 b (± 0.753)	−0.345 C (± 0.030)	12.70 b (± 0.733)	−0.364 B (± 0.044)
<i>Sida spinosa</i>				
0.0% HW	38.10 a (± 1.466)	—	14.39 a (± 1.120)	—
10% HW	34.10 a (± 1.845)	−0.090 AB (± 0.014)	11.43 a (± 0.733)	−0.192 AB (± 0.096)
<i>Amaranthus palmeri</i>				
0.0% HW	30.06 a (± 1.120)	—	16.51 a (± 1.466)	—
10% HW	17.85 b (± 0.737)	−0.403 CD (± 0.043)	10.58 b (± 0.423)	−0.344 B (± 0.085)
<i>Rumex crispus</i>				
0.0% HW	31.75 a (± 2.200)	—	15.24 a (± 1.466)	—
10% HW	26.25 a (± 0.423)	−0.167 B (± 0.046)	12.28 a (± 1.120)	−0.194 AB (± 0.014)
<i>Echinochloa crus-galli</i>				
0.0% HW	35.56 a (± 1.466)	—	22.01 a (± 1.526)	—
10% HW	35.14 a (± 1.526)	−0.012 A (± 0.012)	22.44 a (± 1.526)	0.002 A (± 0.130)
<i>Ipomoea lacunosa</i>				
0.0% HW	83.82 a (± 2.644)	—	52.49 a (± 2.575)	—
10% HW	81.28 a (± 3.880)	−0.021 A (± 0.063)	48.68 a (± 2.240)	−0.066 AB (± 0.086)

^aAt the end of a 21-d germination test. R, root length (mm); RI(R), response index for R; S, shoot length (mm); RI(S), response index for S. Different lowercase letters following mean values within a species in columns R (mm), and S (mm) indicate significant differences between the treatments within a species at $P < 0.05$. Different uppercase letters following values in columns RI(R), and RI(S) indicate significant differences in respective parameter among the species at $P < 0.05$.

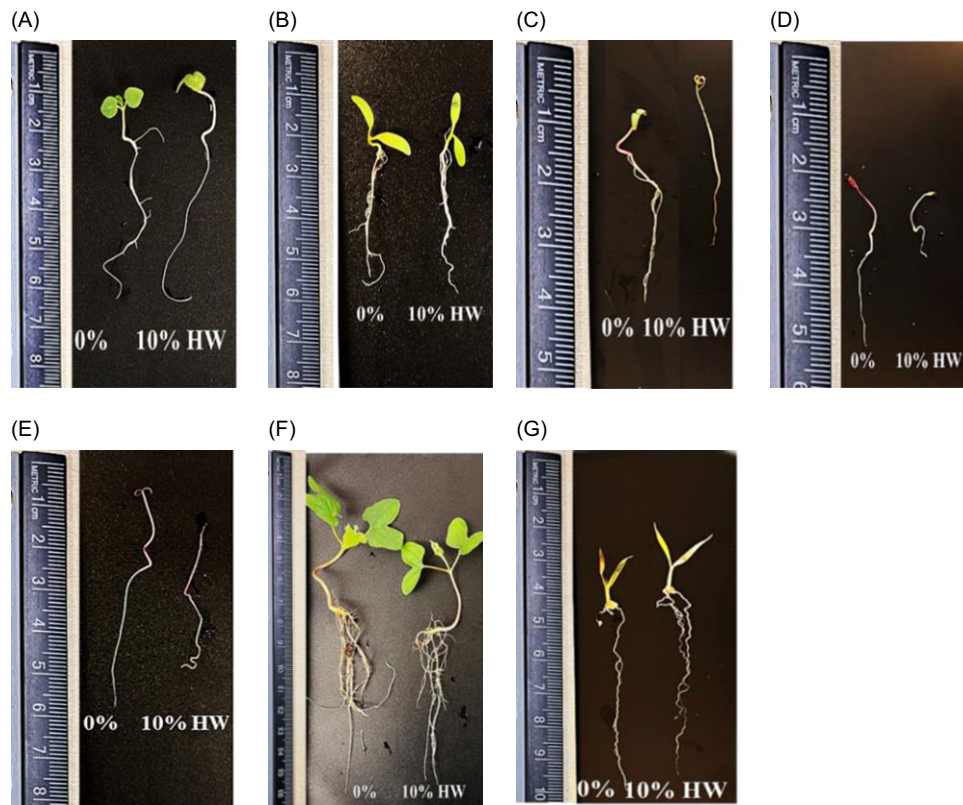


Figure 3. Seedling growth of (A) *Sida spinosa*, (B) *Rumex crispus*, (C) *Amaranthus palmeri*, (D) *Amaranthus hybridus*, (E) *Chenopodium album*, (F) *Ipomoea lacunosa*, and (G) *Echinochloa crus-galli* in response to 10% aqueous extracts of *Erigeron canadensis* (HW) at the end of a 21-d germination test.

lengths was observed in *S. spinosa*, *R. crispus*, *E. crus-galli*, and *I. lacunosa*. A similar trend was observed with a significant reduction ($P < 0.05$) in shoot length at 29.57%, 35.90%, and 37.50% for *A. hybridus*, *A. palmeri*, and *C. album*, respectively, in *E. canadensis* aqueous extract treatments over the respective control, while other weed seedlings' shoot length remained less or not affected. Shaukat et al. (2003) reported significant reduction of root and shoot lengths of tomato [*S. lycopersicum*], radish [*R. sativus*], wheat [*T. aestivum*], corn [*Z. mays*], millet [*Pennisetum* spp.], and mungbean [*V. radiata*] with aqueous extract of *E. canadensis* in Karachi, Pakistan. Djurdjević et al. (2011) reported 68.06% to 77.53% and 72.95% to 95.37% reduction in root and shoot lengths of orchardgrass [*D. glomerata*] and white clover [*Trifolium repens* L.], respectively, under 25% aqueous extract of areal parts of *E. canadensis* in Belgrade, Serbia. The allelopathic chemicals released by plants can influence the physiological processes of neighboring plants in several ways (Dadkhah 2015; Macías et al. 2019; Rice 1984), with growth retardation being the most observed response (Cordeau et al. 2016; Rice 1974, 1979; Singh et al. 2022).

Allelopathy of *Erigeron canadensis* Extract

The allelopathic potential of *E. canadensis* aqueous extract was evaluated based on various seed germination parameters (G%, SG, and MGT) and seedling growth measures (R and S) of studied weed species. The RI was calculated for each parameter (Dai et al. 2022; Williamson and Richardson 1988) (Tables 1 and 2). Generally, RI ranges from -1 to $+1$, where positive values indicate stimulation by the treatments, and negative values signify inhibition in comparison with the controls. The absolute value indicates the strength of

allelopathic effect. RI close to zero indicates no or low effect from the treatment. The order for germination inhibition [RI(G)] with *E. canadensis* extract was *R. crispus* (-0.655) \geq *A. hybridus* (-0.606) $>$ *A. palmeri* (-0.406) $>$ *S. spinosa* (-0.223); whereas low/no inhibition of germination was noted for *C. album* (-0.094), *I. lacunosa* (-0.046), and *E. crus-galli* (0.083) with RI(G) values close to zero. The order for inhibition of speed of germination [RI(SG)] was *A. hybridus* (-0.817) $>$ *R. crispus* (-0.65) $>$ *A. palmeri* (-0.481) \geq *S. spinosa* (-0.394), with low/no effect on *I. lacunosa* (-0.002), *E. crus-galli* (-0.046), and *C. album* (0.127). The order for inhibition of mean germination time [RI(MGT)] was *A. hybridus* (-0.696) \geq *R. crispus* (-0.655) $>$ *A. palmeri* (-0.412) $>$ *S. spinosa* (-0.258), with low/no effect on *I. lacunosa* (-0.039), *E. crus-galli* (0.015), and *C. album* (0.039). The order for inhibition of root [RI(R)] was *A. hybridus* (-0.49) $>$ *A. palmeri* (-0.403) $>$ *C. album* (-0.345) $>$ *R. crispus* (-0.167), with no effect on *S. spinosa* (-0.090), *I. lacunosa* (-0.021), and *E. crus-galli* (-0.012). The order for inhibition of shoot [RI(S)] was *C. album* (-0.364) $>$ *A. palmeri* (-0.344) $>$ *A. hybridus* (-0.292) $>$ *R. crispus* (-0.194) \geq *S. spinosa* (-0.192), with low/no effect on *I. lacunosa* (-0.066) and *E. crus-galli* (0.002). The study indicated that the allelopathic effect of *E. canadensis* extract impacted different parameters of seed germination and seedling growth of studied weed species. Overall germination parameters like G%, SG, and MGT were inhibited with 10% *E. canadensis* extract in *A. hybridus*, *R. crispus*, *A. palmeri*, and *S. spinosa*, while other weeds like *C. album*, *I. lacunosa*, and *E. crus-galli* remained low/not affected. Weed species like *A. hybridus* and *A. palmeri* that showed inhibition of various germination parameters with *E. canadensis* extract also showed inhibition of seedling growth parameters. Although

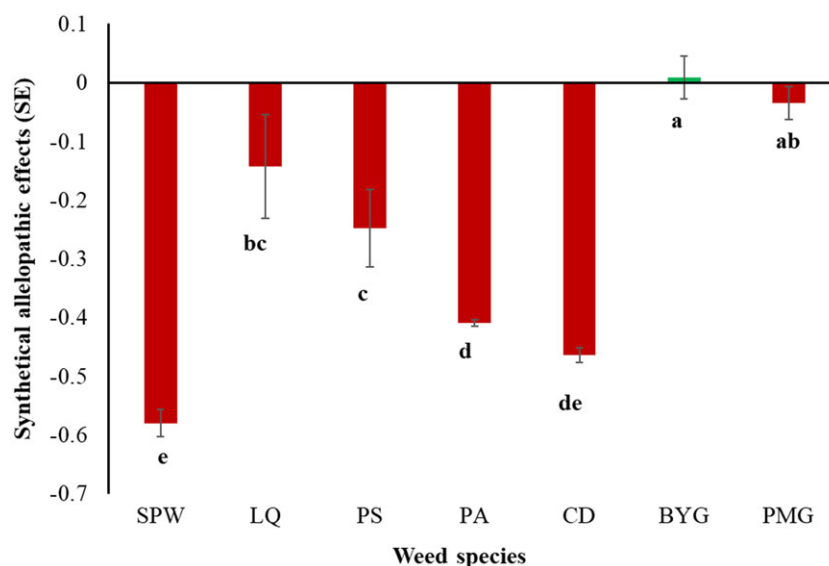


Figure 4. The synthetic allelopathic effects (SE) of aqueous extract of *Erigeron canadensis* (HW) on different weed species: *Amaranthus hybridus* (SPW), *Chenopodium album* (LQ), *Sida spinosa* (PS), *Amaranthus palmeri* (PA), *Rumex crispus* (CD), *Echinochloa crus-galli* (BYG), and *Ipomoea lacunosa* (PMG). Different letters below bars indicate significant difference ($P < 0.05$) in SE values among weed species treated with 10% HW aqueous extract.

E. canadensis extract produced low/no inhibition of germination parameters (as indicated by low RI values, ranging from -0.094 to 0.127) for *C. album*, seedling root and shoot lengths were inhibited (RI values ranged from -0.364 to -0.345). *Erigeron canadensis* extract had no inhibitory effects on seed germination and seedling growth of *I. lacunosa* and *E. crus-galli*. Similar reports on differential RI values for various germination and growth parameters of sensitive plants were also reported for extracts of wolf poison [*Stellera chamaejasme* L.] (Liu et al. 2019), coastal plain yellowtops [*Flaveria bidentis* (L.) Kuntze] (Dai et al. 2022), and barrelclover [*Medicago truncatula* Gaertn.] (Wang et al. 2022).

Figure 4 presents the synthetic allelopathic effect (SE) of *E. canadensis* aqueous extract on the weed species studied. The key distinction between RI and SE is that the RI value represents the effect of a treatment on a specific parameter (either inhibition or stimulation), whereas the SE value reflects the overall inhibitory or stimulatory effect of the treatment in comparison to the control. Therefore, SE value represents the ultimate impact of treatment. All RI values of five parameters (%G, SG, MGT, S, and R) were negative, with higher absolute values for *A. hybridus*, *S. spinosa*, *A. palmeri*, and *R. crispus* (Tables 1 and 2), which resulted in higher negative SE values for *A. hybridus* (-0.580 ± 0.023), *R. crispus* (-0.464 ± 0.013), *A. palmeri* (-0.409 ± 0.006) and *S. spinosa* (-0.248 ± 0.066). In *C. album*, RI values for RI(R) and RI(S) were moderately negative, with other parameters (G, SG, MGT) close to zero, resulting in a low SE of $-0.143 (\pm 0.088)$ compared with *A. hybridus*, *S. spinosa*, *A. palmeri*, and *R. crispus*. For *I. lacunosa*, treatment with *E. canadensis* extract led to numerically smaller, but statistically nonsignificant at $P < 0.05$, values for all parameters studied. Interestingly, *E. canadensis* treatment in *E. crus-galli* resulted in statistically nonsignificant at $P < 0.05$, but numerically higher values for three parameters (G%, MTG, and S) and lower values for two parameters (R and S). This resulted in variations in the SE values for *E. crus-galli* in the range of -0.046 to 0.0782 , with a positive average of $0.009 (\pm 0.036)$, which was close to zero. Hence, in terms of overall allelopathic impact, 10% *E. canadensis*

extract showed high inhibitory effects (higher negative SE values) on *A. hybridus* and *R. crispus*, while it did not show any inhibitory effect on *I. lacunosa* and *E. crus-galli* (low SE values).

Variations in the inhibition of seed germination and seedling growth with 12.5% extract of wolf poison [*S. chamaejasme*] were reported on alfalfa (*Medicago sativa* L.) (SE = -0.35), Dahurian wildrye [*Elymus dahuricus* Turcz. ex Griseb.] (SE = -0.42), and crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.] (SE = -0.24) (Liu et al. 2019). Dai et al. (2022) reported variations in SE values for field mustard (*Brassica rapa* L.) (SE = -0.70), wheat [*T. aestivum*] (SE = -0.40), and barnyardgrass [*E. crus-galli*] (SE = -0.65) with 5% aqueous extract of coastal plain yellowtops [*F. bidentis*]. *Erigeron canadensis* shoot extracts and volatile compounds extracted from the inflorescence of the invasive flaxleaf fleabane [*Erigeron sumatrensis* (Retz.) L.; syn.: *Conyza albida* L.], a sister species of horseweed, in Athens, Greece, were reported to significantly inhibit the germination and growth of several crop species (Economou et al. 2002; Shaikat et al. 2003). Similar allelopathic effects were reported for water extracts of coastal plain yellowtops [*F. bidentis*] (Dai et al. 2022), leaf extracts of Scots pine [*Pinus sylvestris* L.] and paper mulberry [*Broussonetia papyrifera* L.] (Wang et al. 2021) and root exudates of alfalfa [*M. sativa*] (Wang et al. 2022) on other native plants.

Shajib et al. (2012) reported differential uptake and transformation of biochanin A, a major allelochemical present in red clover [*Trifolium pratense* L.] and white clover [*T. repens*], in two broadleaf weeds, namely, dove's-foot crane's-bill [*Geranium molle* L.] and night-flowering catchfly [*Silene noctiflora* L.], and a grass weed, barnyardgrass [*E. crus-galli*]. This study reported resistance of *E. crus-galli* to biochanin A due to lack of uptake, while comparatively higher uptakes were observed in broadleaf weeds studied. Within the category of broadleaf weeds, although the uptake of biochanin A was higher in *G. molle* compared with *S. noctiflora*, biotransformation of toxic biochanin A to nontoxic compounds was greater in *G. molle*, making it less susceptible to biochanin A compared with *S. noctiflora*. In the present study, the reason for differential effects of *E. canadensis* aqueous extract on various weed species could be due to differential

Table 3. Liquid chromatography–mass spectrometry (LC–MS) analysis of *Erigeron canadensis* aqueous extract (10%)^a

Sl. no.	Compound	Formula	Molecular weight	RT (min)	% Area
1	Piperidine	C ₅ H ₁₁ N	85.08907	2.408	5.322
2	Choline	C ₅ H ₁₃ NO	103.0996	1.542	4.072
3	4-Hydroxybenzaldehyde	C ₇ H ₆ O ₂	1.35	122.0369	1.884
4	4-hydroxy-2-oxo-heptanedioic acid	C ₇ H ₁₀ O ₆	190.0479	1.318	1.331
5	Betaine	C ₅ H ₁₁ NO ₂	117.079	1.471	1.321
6	Acetonecyanohydrin	C ₄ H ₇ NO	85.05266	1.425	1.201
7	Daldinise B	C ₁₅ H ₁₆ O ₈	324.0842	13.657	1.194
8	Isoleucine	C ₆ H ₁₃ NO ₂	131.0946	1.571	3.832
9	Gallic acid	C ₇ H ₆ O ₅	170.0217	2.067	1.161
10	3-Butene-1,2,3-tricarboxylic acid	C ₇ H ₈ O ₆	188.0325	1.95	1.148
11	3,5-Dioxoocanedioic acid	C ₈ H ₁₀ O ₆	202.0476	13.656	1.092
12	Valine	C ₅ H ₁₁ NO ₂	117.0789	1.292	1.087
13	2-Furoic acid	C ₅ H ₄ O ₃	112.0163	1.413	1.064
14	5-hydroxy-2,4-dioxopentanoate	C ₅ H ₆ O ₅	146.022	1.441	0.969
15	2-Hydroxyhepta-2,4-dienedioate	C ₇ H ₈ O ₅	172.0373	1.42	0.918
16	(E)-Glutaconate	C ₅ H ₆ O ₄	130.0269	1.444	0.879
17	L-Phenylalanine	C ₉ H ₁₁ NO ₂	165.079	7.634	0.845
18	[FAhydroxy(4:1/2:0)]2-hydroxy-2-butenedioic acid	C ₄ H ₄ O ₅	132.006	1.444	0.836
19	Methylmalonic acid	C ₄ H ₆ O ₄	118.0269	1.992	0.834
20	2-Hydroxyhepta-2,4-dienedioate	C ₇ H ₈ O ₅	172.0375	1.269	0.791
21	2-Oxovaleric acid	C ₅ H ₈ O ₃	116.0473	13.642	0.669
22	Methylmalonic acid	C ₄ H ₆ O ₄	118.0269	2.525	1.287
23	Indoline	C ₈ H ₉ N	119.0734	7.648	0.640
24	Isocitronensaeure	C ₆ H ₈ O ₇	192.0271	1.373	0.608
25	Acrylic acid	C ₃ H ₄ O ₂	72.02134	1.593	0.589
26	Genistein	C ₁₅ H ₁₀ O ₅	270.0528	14.366	0.588
27	Butadiene	C ₄ H ₆	54.04691	1.428	0.587
28	Benzoic acid	C ₇ H ₆ O ₂	122.0369	14.347	0.575
29	(6RS,10RS)-6,10-dimethylbicyclo[4.4.0]dec-1-en-3-one	C ₁₂ H ₁₈ O	178.1357	14.932	0.565
30	Gentisic acid	C ₇ H ₆ O ₄	154.0269	8.264	0.559
31	Pyrrrolidine	C ₄ H ₉ N			0.555
32	trans-3-Indoleacrylic acid	C ₁₁ H ₉ NO ₂	187.0634	9.312	0.546
33	(1R,2S)-1-Hydroxypropane-1,2,3-tricarboxylate	C ₆ H ₈ O ₇	192.0274	1.765	0.536
34	2-Methylbutanal	C ₅ H ₁₀ O	86.07309	1.349	0.511
35	N-Methylpyrrolidone	C ₅ H ₉ NO	99.06836	1.723	0.509
36	[FAhydroxy(4:1/2:0)]2-hydroxy-2-butenedioic acid	C ₄ H ₄ O ₅	132.006	1.77	0.500
37	2-Caffeoylisocitrate	C ₁₅ H ₁₄ O ₁₀	354.0584	9.866	0.485
38	3-Butene-1,2,3-tricarboxylic acid	C ₇ H ₈ O ₆	188.0325	1.562	0.482

^aSl. no., serial number; RT (min), retention time (in minutes) of the compound in the total ion chromatogram of LC-MS analysis; % area, area-wise contribution of a particular compound in the total ion chromatogram (TIC) of LC-MS analysis.

uptake and transformation of allelochemicals by weed species. This might have resulted in higher susceptibility of *A. hybridus*, *R. crispus*, and *A. palmeri* toward *E. canadensis* aqueous extract, while *E. crus-galli* and *I. lacunosa* showed no effect for *E. canadensis* treatment.

Identification of Allelopathic Compounds in *Erigeron canadensis* Aqueous Extract

The present study indicated allelopathic effects of *E. canadensis* aqueous extract on the native weed species of the southern United States, although the allelopathic effect varied among weed species. Allelopathy is a process whereby plants release phytotoxins into the environment to gain a competitive edge, significantly influencing plant dominance and succession within communities (Lambers et al. 1998). Allelopathic compounds with phytotoxic or fitness-reducing effects may be novel to plant competitors lacking a coevolutionary history, making them more susceptible to these chemicals in the native range (Callaway and Aschehoug 2000; Callaway and Ridenour 2004; Inderjit et al. 2008).

The LC-MS analysis indicated the presence of numerous compounds in the aqueous extract of *E. canadensis* aerial biomass, and the top 38 compounds are presented in Table 3. It was found

that the aqueous extract of *E. canadensis* contained some natural compounds with previously known allelopathic potential. Based on the % area of a peak in the TIC of LC-MS analysis, the primary allelopathic compound was piperidine (5.322%).

The aqueous extract of castor bean [*Ricinus communis* L.] containing gallic acid along with other phenolic compounds was noted to inhibit germination and growth of Spanish needles [*Bidens bipinnata* L.] (Lopes et al. 2022). The aqueous extract of dragon spurge [*Euphorbia dracunculoides* L.], which contained 2-furoic acid, was allelopathic on germination and seedling growth of chickpea [*Cicer arietinum* L.] and wheat [*T. aestivum*] (Tanveer et al. 2012). Other phenolic acids like genistein present in various plants (Shajib et al. 2012) and gentisic acid present in buffalograss [*Buchloe dactyloides* (Nutt.) J.T. Columbus] (Wu et al. 1998) were reported to have growth inhibitory activities on *E. crus-galli* and annual bluegrass (*Poa annua* L.), respectively. The phytotoxicity of *E. canadensis* aqueous extract is probably not due to the presence of any one compound; rather it could be due to the combined action of all compounds present in the aqueous extract. Similar postulations regarding the allelopathic effects of the aqueous extracts from *E. dracunculoides* on chickpea [*C. arietinum*] and wheat [*T. aestivum*] (Tanveer et al. 2012), as well as aqueous extracts from Common

gorse [*Ulex europaeus* L.] and Scotch broom [*Cytisus scoparius* (L.) Link] on *A. retroflexus* and *D. sanguinalis* (Pardo-Muras et al. 2020) have also been reported.

The present study indicated that the mechanism behind the inhibition of germination and seedling growth of selected weeds species by *E. canadensis* aqueous extract could be a combination of several mechanisms associated with compounds present in the extract (Blum et al. 1999; Reigosa et al. 1999). For example, the aqueous extract of *E. canadensis* aerial parts collected in Karachi, Pakistan, contained gallic acid, vanillic acid, catechol, and syringic acid and exhibited allelopathic effects on crops such as tomato [*S. lycopersicum*], radish [*R. sativus*], wheat [*T. aestivum*], corn [*Z. mays*], millet [*Pennisetum* spp.], and mungbean [*V. radiata*] (Shaukat et al. 2003). The aqueous extract of *E. canadensis* aerial parts, collected in Belgrade, Serbia, contained *p*-coumaric, ferulic, *p*-hydroxybenzoic, vanillic and syringic acids and demonstrated allelopathic effects on *D. glomerata* and *T. repens* (Djurdjević et al. 2011). The dichloromethane extract of *E. canadensis* aerial parts, collected in Mississippi, USA, contained (4*Z*)-lactonophyl-lum lactone, which inhibited growth of creeping bentgrass [*A. stolonifera*] and lettuce [*L. sativa*] (Queiroz et al. 2012).

Earlier reports showed that the allelopathic potential and nature of allelopathic compounds in *E. canadensis* biomass varied with geographic location. This could be the reason for the negative relationships between abundance of *E. canadensis* and richness of native species in non-native ranges of Europe, China, and India, but either positive or no relationships in native North American range (Shah et al. 2014). However, the present study did not show any trend in respect to inhibition of seed germination and seedling growth of native (*A. palmeri*, *A. hybridus*, *S. spinosa*, and *I. lacunosa*) and non-native weed species (*C. album*, *R. crispus*, and *E. crus-galli*) by the native *E. canadensis* from the southern United States. Accumulation of allelochemicals in soil needs continuous supply due to the shorter life span of these compounds; however, gradual release from decomposing biomass could cause inhibition of various physiological processes, including reduced germination, poor seedling growth, low photosynthetic efficiency, and decreased water and nutrient uptake in receptor plants, leading to a decrease in their abundance or complete elimination (Cheng et al. 2021; Djurdjević et al. 2008, 2011; Rice 1974, 1979).

A recent study by Cheng et al. (2021) examined the allelopathic effects of *E. canadensis* with varying levels of invasion in Jiangsu, Hubei, and Anhui provinces along the Yangtze River in China. The results indicated that *E. canadensis* populations from higher-latitude regions in Jiangsu produced higher concentrations of allelochemicals that had a stronger inhibitory effect on the growth of native lettuces compared with those from lower-latitude areas. *Erigeron canadensis*'s ability to survive in extreme environmental conditions (Waggoner et al. 2011), along with its dense foliage production (Tozzi et al. 2014), contributes to its ecological resilience. Additionally, the widespread distribution of *E. canadensis* across North America, along with its allelopathic impacts on both native and non-native plant species, poses a growing ecological concern. This is especially significant given the rise in herbicide resistance (Heap 2024), which complicates weed management. This research provides a foundation for further exploring the allelopathic impacts of both herbicide-resistant and herbicide-susceptible *E. canadensis* populations on various plant species and for understanding their role in the ecological process of invasion.

In conclusion, the present study indicated differential allelopathic effects of *E. canadensis* aqueous extract on the seven weed species studied. The *E. canadensis* aqueous extract showed the highest

inhibitory effects on seed germination and seedling growth of *A. hybridus*, followed by *R. crispus*, *A. palmeri*, and *S. spinosa*, without affecting *I. lacunosa*, *C. album*, or *E. crus-galli*. The *E. canadensis* aqueous extract contained several allelopathic compounds, including piperidine, choline, 4-hydroxybenzaldehyde, acetonecyanohydrin, gallic acid, 2-furoic acid, genistein, and gentisic acid. The observed variations in inhibition could be due to differential uptake and transformation of allelochemicals by weed species. The results from this preliminary laboratory study provide a robust foundation for elucidating the mechanisms driving the successful invasion of *E. canadensis* and offer a valuable theoretical framework for assessments of ecological risks.

Supplementary material. To view supplementary material for this article, please visit <https://doi.org/10.1017/wsc.2025.10034>

Acknowledgments. We are grateful to Melissa Boersma, director, Mass Spectrometry Lab, Department of Chemistry & Biochemistry, Auburn University, Auburn, AL 36849, for chromatographic analysis.

Funding statement. Startup funds provided to AM by Auburn University are gratefully acknowledged.

Competing interests. The authors declare that they have no conflicts of interest.

References

- [ISTA] International Seed Testing Association (2024) International Rules for Seed Testing. Wallisellen, Switzerland: ISTA
- [WSSA] Weed Science Society of America (2024) Weed impacts on crop yields. <https://wssa.net/resources/weed-impacts-on-crop-yields/>. Accessed: December 2, 2024
- [WSSA] Weed Science Society of America (2024) WSSA Survey Ranks Most Common and Most Troublesome Weeds in Broadleaf Crops, Fruits and Vegetables. <https://wssa.net/2017/05/wssa-survey-ranks-most-common-and-most-troublesome-weeds-in-broadleaf-crops-fruits-and-vegetables>. Accessed: December 18, 2024
- Bajwa AA, Sadia S, Ali HH, Jabran K, Peerzada AM, Chauhan BS (2016) Biology and management of two important *Conyza* weeds: a global review. *Environ Sci Pollut Res Int* 23:24694–24710
- Bhowmik PC, Bekech MM (1993) Horseweed (*Conyza canadensis*) seed production, emergence, and distribution in no-tillage and conventional-tillage corn (*Zea mays*). *Agron Trends Agric Sci* 1:67–71
- Blum U, Shafer SR, Lehman ME (1999) Evidence for inhibitory allelopathic interactions involving phenolic acids in field soils: concepts vs. an experimental model. *Crit Rev Plant Sci* 18:673–693
- Buchanan GA, Crowley RH, McLaughlin RD (1977) Competition of prickly sida with cotton. *Weed Sci* 25:106–110
- Byker HP, Soltani N, Robinson DE, Tardif FJ, Lawton MB, Sikkema PH (2013) Glyphosate-resistant Canada fleabane [*Conyza canadensis*(L.) Cronq.]: dose response to glyphosate and control with postemergence herbicides in soybean in Ontario. *Can J Plant Sci* 93:1187–1193
- Callaway RM, Aschehoug ET (2000) Invasive plant versus their new and old neighbors: a mechanism for exotic invasion. *Science* 290:521–523
- Callaway RM, Ridenour WM (2004) Novel weapons: invasive success and the evolution of increased competitive ability. *Front Ecol Environ* 2:436–443
- Cheng H, Wu B, Yu Y, Wang S, Wei M, Wang C, Du D (2021) The allelopathy of horseweed with different invasion degrees in three provinces along the Yangtze River in China. *Physiol Mol Biol Plants* 27:483–495
- Cordeau S, Triolet M, Wayman S, Steinberg C, Guillemin JP (2016) Bioherbicides: dead in the water? A review of the existing products for integrated management. *Crop Prot* 87:44–49
- da Silva A, Oliveira S, Jones Z, Li S (2022) Growing Organic Vegetables in Alabama: Know Your Weeds. ANR-2923. <https://www.aces.edu/blog/topics/crop-production/growing-organic-vegetables-in-alabama-know-your-weeds/>. Accessed: December 10, 2024

- Dadkhah A (2015) Allelopathic potential of canola and wheat to control weeds in soybean (*Glycine max*). Russ Agric Sci 41:111–114
- Dai L, Wu L, Zhou X, Jian Z, Meng L, Xu G (2022) Effects of water extracts of *Flaveria bidentis* on the seed germination and seedling growth of three plants. Sci Rep 12:1–7
- Dauer JT, Mortensen DA, Vangessel MJ (2007) Temporal and spatial dynamics of long-distance *Conyza canadensis* seed dispersal. J Appl Ecol 44:105–114
- Djurdjević L, Mitrović M, Gajić G, Jarić S, Kostić O, Oberan L, Pavlović P (2011) An allelopathic investigation of the domination of the introduced invasive *Conyza canadensis* L. Flora 206:921–927
- Djurdjević L, Popović Z, Mitrović M, Pavlović P, Jarić S, Oberan L, Gajić G (2008) Dynamics of bioavailable rhizosphere soil phenolics and photosynthesis of *Arum maculatum* L. in a lime-beech forest. Flora 203:590–601
- Dorning M, Cipollini D (2006) Leaf and root extracts of the invasive shrub, *Lonicera maackii*, inhibit seed germination of three herbs with no autotoxic effects. Plant Ecol 184:287–296
- Economou G, Tzakou O, Gani A, Yannitsaros A, Bilalis D (2002) Allelopathic effect of *Conyza albida* on *Avena sativa* and *Spirodela polyrhiza*. J Agron Crop Sci 188:248–253
- Erhard D, Gross E (2005) Do environmental factors influence composition of potential allelochemicals in the submersed freshwater macrophyte *Elodea nuttallii* (Hydrocharitaceae)? Verhandlungen der IVL 29:287–291
- Gharde Y, Singh PK, Dubey RP, Gupta PK (2018) Assessment of yield and economic losses in agriculture due to weeds in India. Crop Prot 107:12–18
- Heap I (2014) Global perspective of herbicide-resistant weeds. Pest Manag Sci 70:1306–1315
- Heap I (2024) The International Herbicide-Resistant Weed Database. www.weedscience.org. Accessed: December 18, 2024
- Holm LG, Doll J, Holm E, Pancho JV, Herberger JP (1997) World Weeds: Natural Histories and Distribution. New York: Wiley. 1144 p
- Hu F, Kong C (2002) Allelopathy of *Ageratum conyzoides*. VI. Effects of meteorological conditions on allelopathy of *Ageratum conyzoides*. J Appl Ecol 13:76–80
- Hu G, Zhang ZH (2013) Aqueous tissue extracts of *Conyza canadensis* inhibit the germination and shoot growth of three native herbs with no autotoxic effects. Planta Daninha 31:805–811
- Inderjit, Seastedt TR, Callaway RM, Pollock JL, Kaur J (2008) Allelopathy and plant invasions: traditional, congeneric, and bio-geographical approaches. Biol Invasions 10:875–890
- Jones SB, Davis DE (1963) Weeds of the lower coastal plain in Alabama. Weeds 11:322–323
- Kumari S, Chander S, Kaluram, Sajana S (2017) Allelopathy and its effect on fruit crop—a review. Int J Curr Microbiol Appl Sci 6:952–960
- Lambers H, Chapin FS, Pons TL (1998) Plant Physiological Ecology. Berlin: Springer-Verlag. 540 p
- Liu YJ, Meng ZJ, Dang XH, Song WJ, Zhai B (2019) Allelopathic effects of *Stellera chamaejasme* on seed germination and seedling growth of alfalfa and two forage grasses. Acta Pratacult Sin 28:130–138
- Llewellyn RS, Ronning D, Ouzman J, Walker S, Mayfield A, Clarke M (2016) Impact of Weeds on Australian Grain Production: the cost of weeds to Australian grain growers and the adoption of weed management and tillage practices. Report for GRDC. Australia: CSIRO. 112 p
- Lopes RW, Morais EM, Lacerda JJ, Araújo FD (2022) Bioherbicidal potential of plant species with allelopathic effects on the weed *Bidens bipinnata* L. Sci Rep 12:1–12
- Loux M, Stachler J, Johnson B, Nice G, Davis V, Nordby D (2006) Biology and Management of Horseweed. The Glyphosate, Weeds and Crops Series. GWC-9. Purdue University Extension. 12 p
- Macías FA, Mejías FJ, Molinillo JM (2019) Recent advances in allelopathy for weed control: from knowledge to applications. Pest Manag Sci 75:2413–2436
- Maity A, Paul D, Rocha RL, Bagavathiannan M, Beckie HJ, Ashworth MB (2025) Intensive cropping influences the success of seed dormancy breaking methods in Australian collected *Hordeum*, *Avena*, and *Bromus* sp. Pest Manag Sci 81:2133–2143
- Pardo-Muras M, Puig CG, Souto XC, Pedrol N (2020) Water-soluble phenolic acids and flavonoids involved in the bioherbicidal potential of *Ulex europaeus* and *Cytisus scoparius*. South Afr J Bot 133:201–211
- Queiroz SC, Cantrell CL, Duke SO, Wedge DE, Nandula VK, Moraes RM, Cerdeira AL (2012) Bioassay-directed isolation and identification of phytotoxic and fungitoxic acetylenes from *Conyza canadensis*. J Agric Food Chem 60:5893–5898
- Reigosa MJ, Sanchez-Moreiras A, Gonzalez L (1999) Ecophysiological approach in allelopathy. Crit Rev Plant Sci 18:577–608
- Rice EL (1974) Allelopathy. New York: Academic Press. 353 p
- Rice EL (1979) Allelopathy – an update. Bot Rev 45:15–109
- Rice EL (1984) Allelopathy. 2nd ed. Orlando FL: Academic Press. 400 p
- Ritz C, Baty F, Streibig JC, Gerhard D (2015) Dose-response analysis using R. PLoS ONE 10:e0146021
- Shah MA, Callaway RM, Shah T, Houseman GR, Pal RW, Xiao S, Luo W, Rosche C, Reshi ZA, Khasa DP, Chen S (2014) *Conyza canadensis* suppresses plant diversity in its nonnative ranges but not at home: a transcontinental comparison. New Phytol 202:1286–1296
- Shajib MTI, Pedersen HA, Mortensen AG, Kudsk P, Fomsgaard IS (2012) Phytotoxic effect, uptake, and transformation of Biochanin A in selected weed species. J Agric Food Chem 60:10715–10722
- Shaukat SS, Munir N, Siddiqui IA (2003) Allelopathic responses of *Conyza canadensis* (L.) Cronquist: a cosmopolitan weed. Asian J Plant Sci 2:1034–1039
- Shields EJ, Dauer, JT, VanGessel, MJ, Neumann G (2006) Horseweed (*Conyza canadensis*) seed collected in the planetary boundary layer. Weed Sci 54:1063–1067
- Shrestha A, Fidelibus MW, Alcorta MF, Cathline KA (2010) Threshold of horseweed (*Conyza canadensis*) in an established ‘Thompson seedless’ vineyard in the San Joaquin Valley of California. Int J Fruit Sci 10:301–308
- Silva D, Vargas L, Agostinetto D, Mariani F (2014) Glyphosate-resistant hairy fleabane competition in RR[®] soybean. Bragantia 73:451–457
- Singh V, Segbefia W, Fuller MG, Shankle MW, Morris CJ, Meyers SL, Tseng TM (2022) Allelopathy: an ecofriendly approach to control Palmer amaranth using allelopathic sweetpotato. Front Agron 4:930378
- Steckel LE, Culpepper S (2006) Impacts and management of glyphosate-resistant weeds in the southern region. In The Fifth National IPM Conference Abstracts. St. Louis, Missouri, USA. 46 p
- Swearingen J, Barger C (2016) Invasive Plant Atlas of the United States. University of Georgia Center for Invasive Species and Ecosystem Health. <http://www.invasiveplantatlas.org/>. Accessed: December 16, 2024
- Tanveer A, Jabbar MK, Kahliq A, Matloob A, Abbas RN, Javaid MM (2012) Allelopathic effects of aqueous and organic fractions of *Euphorbia dracunculoides* Lam. on germination and seedling growth of chickpea and wheat. Chil J Agric Res 72:495–501
- Tilley D (2012) Ecology and Management of Canadian Horseweed (*Conyza canadensis*). Technical Note No. 59. Boise, ID: U.S. Department of Agriculture–Natural Resources Conservation Service, Plant Materials Center. 5 p
- Tozzi E, Beckie H, Weiss R, Gonzalez-Andujar JL, Storkey J, Cici SZH, Acker RC (2014) Seed germination response to temperature for a range of international populations of *Conyza canadensis*. Weed Res 54:178–185
- Trezzi MM, Vidal RA, Patel F, Miotto E, Debastiani F, Balbinot AA, Mosquen R (2015) Impact of *Conyza bonariensis* density and establishment period on soybean grain yield, yield components and economic threshold. Weed Res 55:34–41
- Waggoner BS, Mueller TC, Bond JA, Steckel LE (2011) Control of glyphosate-resistant horseweed (*Conyza canadensis*) with saflufenacil tank mixtures in no-till cotton. Weed Technol 25:310–315
- Wang C, Jiang K, Zhou J, Liu J (2017) Allelopathic suppression by *Conyza canadensis* depends on the interaction between latitude and the degree of the plant's invasion. Acta Bot Bras 31:212–219
- Wang C, Liu Z, Wang Z, Pang W, Zhang L, Wen Z, Zhao Y, Sun J, Wang ZY, Yang C (2022) Effects of autotoxicity and allelopathy on seed germination and seedling growth in *Medicago truncatula*. Front Plant Sci 13:908426
- Wang X, Zhang R, Wang J, Di L, Wang H, Sikdar A (2021) The effects of leaf extracts of four tree species on *Amygdalus pedunculata* seedlings growth. Front Plant Sci 11:587579

- Weaver SE (2001) The biology of Canadian weeds. 115. *Conyza canadensis*. Can J Plant Sci 81:867–875
- Wei M, Wang S, Wu B, Cheng H, Wang C (2020) Combined allelopathy of Canada goldenrod and horseweed on the seed germination and seedling growth performance of lettuce. Landscape Ecol Eng 16:299–306
- Williamson GB, Richardson D (1988) Bioassays for allelopathy: measuring treatment responses with independent controls. J Chem Ecol 14:181–187
- Wu L, Guo X, Harivandi M (1998) Allelopathic effects of phenolic acids detected in buffalograss (*Buchloe dactyloides*) clippings on growth of annual bluegrass (*Poa annua*) and buffalograss seedlings. Environ Exp Bot 39:159–167
- Zhang S (2010) Study on Invasive Biology of Alien Plant *Conyza canadensis*. M.S. dissertation. Shanghai: College of Life and Environmental Sciences, Shanghai Normal University. 264 p