

## PHYTOTOXICITY OF ROOT EXUDATES OF INVASIVE *SOLIDAGO CANADENSIS* ON CO-OCCURRING NATIVE AND INVASIVE PLANT SPECIES

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### Abstract

The mechanisms underlying the dominance of *Solidago canadensis* in invaded communities are unclear. We conducted a multi-species experiment to test whether the root exudates of *S. canadensis* inhibited both the native species and the invasive species in the invaded communities. The results showed that the root exudates from *S. canadensis* had significant phytotoxic effects on the root length, plant height, basal diameter, and the root, stem, leaf, and total biomass of seven plant species. The inhibition rate of root exudates on the plant height, basal diameter, root length, and total biomass was dose-dependent and species dependent. Species origin (native vs. invasive) had no significant effect on response to root exudates. Root exudates from *S. canadensis* had similar inhibition effects on the growth of native plants and invasive plants in the low concentration treatment, while the effects on the growth of native plants were greater than those on invasive plants in the high concentration treatment. These results indicated that the phytotoxic root exudates of *S. canadensis* might play an important role in the allelopathic capacities of this species.

**Key words:** Phytotoxicity, Root exudate, *Solidago canadensis*, Invasive plants, Native plants.

### Introduction

Plant invasion is one of the major threats to natural ecosystems and is considered a challenge worldwide (Alpert, 2006; Chen *et al.*, 2013). After a plant invades a novel range, the introduction of invasive plants may lead to a strong inhibitory effect on native plant species by reducing native plants richness or diversity, possibly resulting in limited diversity in many parts of its invaded range (Thorpe *et al.*, 2010; Dong *et al.*, 2015). For example, invasive *Centaurea maculosa*, *Solidago canadensis*, and *Alternanthera philoxeroides* all have this similar ecological consequence in invaded communities (Thorpe *et al.*, 2010; Chen *et al.*, 2013; Dong *et al.*, 2015). However, the mechanisms underlying this dominance are unclear (MacDougall & Turkington, 2004).

Allelopathy is one of the hypotheses postulated to explain the dominance of invasive plants in invaded communities (Callaway & Aschehoug, 2000; Callaway & Ridenour, 2004). For instance, *C. maculosa*, a species native to Europe and introduced into North America approximately 120 years ago, has created uniform, non-diverse communities in western North America by producing the allelopathic root exudate ( $\pm$ )-catechin (Thorpe *et al.*, 2010). *Centaurea diffusa*, a noxious invasive plant in North America, has much stronger negative effects on native plants in invaded communities (North America) than on closely related native plants in native communities, and these effects are mediated by allelochemicals (Callaway & Aschehoug, 2000). *Alliaria petiolata*, a Eurasian species that has invaded understories of North American forests, has inhibitory effects on the native plants by producing a toxic allelochemical (Lankau, 2010). The role of allelochemicals has been intensively studied with regard to the inhibiting effects of invasive plants on native plants (e.g., Callaway & Aschehoug, 2000; Prati & Bossdorf, 2004; Stinson *et al.*, 2006; Lankau, 2010). However, in an invaded community, invasive plants encounter both native plants and co-

occurring invasive plants or exotic non-invasive plants. However, few studies have investigated the allelopathic effect of invasive plants on the co-occurring invasive plants in an invaded region.

Thorpe *et al.*, (2010) found that phytotoxic effects of ( $\pm$ )-catechin may be stronger on some North American species than on some European species. Mallik & Pellissier (2000) conducted experiments comparing the effects of leaves, leaf extracts, and humus from native *Vaccinium myrtillus* on *Picea mariana* (an exotic North American neighbor) and *Picea abies* (a long-term co-occurring native neighbor), and found that *V. myrtillus* generally had stronger biochemical effects on the exotic plant than on the native one, supporting a coevolutionary aspect to allelopathy (Rabotnov, 1982). The novel weapon hypothesis and co-evolutionary experiences between plants suggests that if the co-occurring invasive plants already exist within a habitat but do not have eco-evolutionary history, they might be experienced with the allelochemicals exuded by the newly invading species (Saul *et al.*, 2013). Previous research has suggested that the selection pressures caused by one species can change in the presence of other species in a plant community (Inouye & Stinchcombe, 2001; Callaway *et al.*, 2005; Bughio *et al.*, 2013; Ning *et al.*, 2016). Thus, it is important to explore the inhibiting effect of notorious invasive plants on co-occurring plant species in the invaded communities to predict the potential evolutionary direction of the invaded communities under the selection pressures of invasion.

The allelochemicals produced by plants are complex (Inderjit *et al.*, 2006). Many previous allelopathic experiments have used the extracts of organs (Zhang *et al.*, 2009; Uddin *et al.*, 2012; 2017; Kato-Noguchi *et al.*, 2015), residue decomposition (Uddin *et al.*, 2014), and the addition of activated carbon (Ridenour & Callaway, 2001; Callaway *et al.*, 2005). Root exudates, namely, the chemicals secreted into the soil by plant roots, occupy 5% to 21% of all photosynthetically fixed carbon being transferred to the rhizosphere (Marschner, 1995; Walker *et al.*, 2003). Inderjit *et al.* (2011) reported that root exudates

are a potential source of allelochemicals, and there has been an increased interest in the evaluation of the allelopathic effect of root exudates from invasive plants to address the allelopathic effects in environments more similar to natural settings (Qin *et al.*, 2006; Uddin *et al.*, 2014).

*Solidago canadensis*, native to North America, is a notorious invasive plant that has spread worldwide. It has strong allelopathic effects (Sun *et al.*, 2006) that cause a reduction of the growth of native plant species (Sun *et al.*, 2006; Yang *et al.*, 2007) and an inhibition of the root mycorrhizal colonization of native plant species and soil borne pathogens (Zhang *et al.*, 2009) in the invaded communities. The invasion success of *S. canadensis* may be partly attributed to the release of allelopathic compounds in the invaded range (Abhilasha *et al.*, 2008; Yuang *et al.*, 2012). Previous studies on *S. canadensis*, conducted on the ethanol extract of various plant tissues (Yang *et al.*, 2007; Zhang *et al.*, 2009; Yuan *et al.*, 2013), water extract of organs (Butcko & Jensen, 2002), and activated carbon (Abhilasha *et al.*, 2008), have shown strong phytotoxic effects on germination, growth, and physiology of native plant species. To our knowledge, there is no published report on the phytotoxic effects of *S. canadensis* root exudates on both native and invasive plants.

Here we present results from a multi-species experiment to test the phytotoxic effects of the root exudates of *S. canadensis*. We aimed to determine: 1) whether the root exudates of *S. canadensis* inhibit both the native and invasive plants in the invaded communities; 2) if the inhibition effect is dose-dependent or species-dependent; and 3) if there are interactive effects between species origin and concentration.

## Materials and Methods

**Study site and species:** To compare several species, a common garden experiment was conducted at the Jiaojiang Campus of Taizhou University, Jiaojiang District, Taizhou City, Zhejiang Province, China (121.1639 °E, 28.8813 °N). The climate is subtropical monsoon with a mean annual precipitation ranging from 1,185–2,029 mm, mean annual temperature of 17°C, and mean annual sunshine of 1,800 to 2,037 h. Six native/invasive annual species co-occurring with invasive *S. canadensis* and within the Compositae family, including native *Xanthium sibiricum*, *Eclipta prostrata*, and *Gnaphalium affine*, and invasive *Celosia argentea*, *Conyza canadensis*, *Sesbania cannabina*, and *Aster subulatus*, were selected for this study (Table 1).

**Preparation of root exudates:** The production of *S. canadensis* root exudates was achieved by growing *S. canadensis* in water culture (Uddin *et al.*, 2014; Vives-Peris *et al.*, 2018). Six live rhizomes (60 cm height) of *S. canadensis* were cultured in 5 L glass beakers filled with sterile deionized water. Root exudates were collected and stored at -20°C after one week of exudation. Then, the rhizomes were cultured in a 5 L glass beaker again for one week to obtain the second batch of root exudates. Five cycles were used for the production of root exudates following the above procedure. All root exudates were combined and filtered with 0.22 µm syringe filters to remove microbes. The root exudates were stored at -20°C until use.

**Transplanting of seedlings:** On April 20, 2014, seedlings with similar plant height (10 cm) were transplanted into pots that had an upper diameter of 33 cm, lower diameter of 21 cm, and height of 26 cm. The pots were filled with a mixed matrix composed of soil, sand, and peat soil in a 6:3:1 ratio with a final pH of 6.80±0.10, an organic matter content of 27.66±1.19 g/kg, a total nitrogen content of 361.00±33.00 mg/kg, an available phosphorus content of 8.00±1.14 mg/kg, and an available potassium content of 12.00±1.00 mg/kg. Root exudates were diluted using sterile deionized water and four concentrations, 25%, 50%, 75%, and 100%, were used for the treatments. Twenty milliliters of root exudates was irrigated around the roots every week. Twenty milliliters of sterile deionized water was used as the control. Tap water was added daily to maintain the soil moisture at level of 75% ± 5% as determined by daily gravimetric measurement (Li *et al.*, 2016). Five replicates were used for every treatment. On August 20, 2014, plant height was measured with a ruler to an accuracy of 0.1 cm. The number of leaves and the number of flowers (for *S. cannabina*) or inflorescences (for the other six plant species) were recorded. The base diameter of the stem was measured using a Vernier caliper to an accuracy of 0.1 mm. Then, plants were harvested and divided into leaves, stems, roots, and flowers. The root length was measured using a ruler. Plant materials were oven-dried (at 105 °C for 1 h and then at 80 °C until a constant weight was achieved). The leaf, stem, and root biomasses were weighed separately using a balance with a precision of 0.0001 g (Shanghai Jingtian Electronic Instrument Co., Ltd, Shanghai, China). Total biomass was calculated as the sum of leaf, stem, and root biomass.

**Table 1. Information of the seven plant species in this study.**

No.	Plant species	Family	Genus	Origin	Distribution
1.	<i>Xanthium sibiricum</i>	Asteraceae	<i>Xanthium</i>	Native	Widespread in Asia
2.	<i>Celosia argentea</i>	Amarantaceae	<i>Celosia</i>	Alien invasive	India and other tropical area
3.	<i>Conyza canadensis</i>	Asteraceae	<i>Conyza</i>	Alien invasive	North America
4.	<i>Sesbania cannabina</i>	Asteraceae	<i>Sesbania</i>	Alien invasive	Tropical and subtropical area
5.	<i>Eclipta prostrata</i>	Asteraceae	<i>Eclipta</i>	Native	Widespread in the world
6.	<i>Aster subulatus</i>	Asteraceae	<i>Aster</i>	Alien invasive	North America
7.	<i>Gnaphalium affine</i>	Asteraceae	<i>Gnaphalium</i>	Native	Widespread in East Asia

**Statistical analysis:** Data were shown in mean  $\pm$  standard deviation (SD). A one-way ANOVA was used to test the effect of the concentration on the growth of the seven investigated species, and the least significant difference (LSD) method was used for the post hoc test. The semi-inhibition concentration was calculated following the method described by Wan *et al.*, (2017). The inhibition rate was calculated as  $(X_i - X_0)/X_0$ , where  $X_i$  is the value of the tested plant in a treatment, and  $X_0$  is the mean value of the tested plant in the control (Li *et al.*, 2012). Two-way ANOVAs were used to test the main effect of species origin (invasive or native), concentration, interactive effect between species origin, and exudate concentration on the inhibition rate of root length, plant height, basal diameter, and total biomass of *S. canadensis*. Species origin and concentration were used as fixed factors, while species nested in the species origin was used as a random factor. All statistical analyses were conducted using SPSS 16.0 software (SPSS Inc. Chicago, US).

## Results

Root length, plant height, basal diameter, and the root, stem, leaf, flower, and total biomass were significantly decreased in the 25% root exudate treatment for the native *X. sibiricum* (LSD post hoc test,  $p < 0.05$ ; Figs. 1–2). Based on the total biomass, the exudate concentration causing 50% inhibition was 45.6%.

In the native *E. prostrata*, the 25% root exudate treatment significantly decreased the root length and basal diameter (LSD post hoc test,  $p < 0.05$ ; Figs. 1–2), while the 50% root exudate treatment significantly decreased the plant height. The 75% root exudate treatment significantly

decreased the root, stem, leaf, flower, and total biomass of native *E. prostrata* (LSD post hoc test,  $p < 0.05$ ; Figs. 1–2). Based on the total biomass, the exudate concentration causing 50% inhibition was 75.1%.

In the invasive *C. argentea*, the 25% root exudate treatment significantly decreased the root length, plant height, basal diameter, and the root, stem, leaf, and total biomass (LSD post hoc test,  $p < 0.05$ ; Figs. 1–2). The 75% root exudate treatment significantly decreased the flower biomass (LSD post hoc test,  $p < 0.05$ ; Figs. 1–2). Based on the total biomass, the exudate concentration causing 50% inhibition was 69.6%.

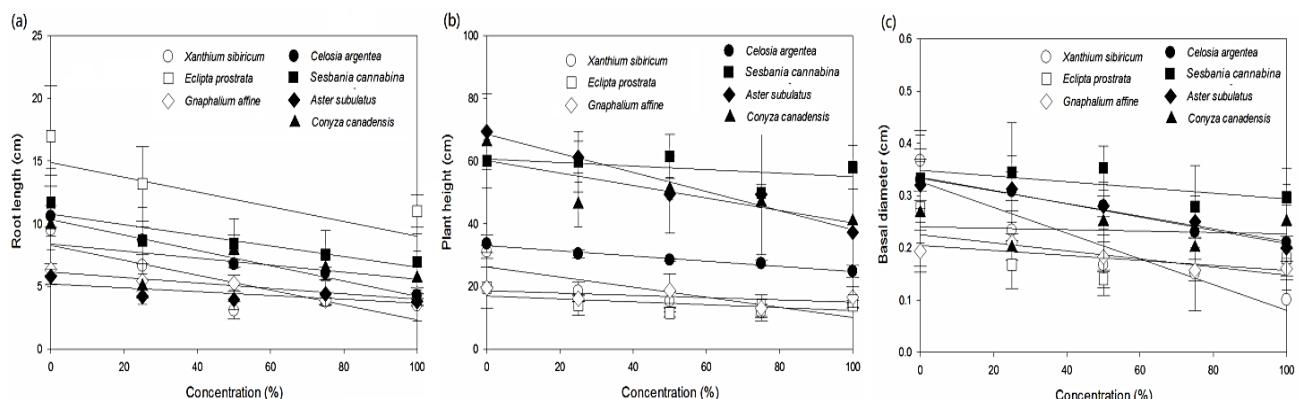
Different root exudate concentrations had no significant effect on the growth of the native *G. affine* and invasive *S. cannabina* (LSD post hoc test,  $p > 0.05$ ; Figs. 1–2). Based on the total biomass, the exudate concentration predicted to cause 50% inhibition was 212.5% and 242.9% for *G. affine* and *S. cannabina*, respectively.

The 50% root exudate treatment significantly decreased the root length, plant height, and stem biomass in the invasive *A. subulatus* (LSD post hoc test,  $p < 0.05$ ; Figs. 1–2). The 100% root exudate treatment significantly decreased the basal diameter, and root, leaf, and total biomass (LSD post hoc test,  $p < 0.05$ ; Figs. 1–2). Based on the total biomass, the exudate concentration causing 50% inhibition was 75.1%.

The 25% root exudate treatment significantly decreased the root length, plant height, and the root, stem, leaf, and total biomass of invasive *C. canadensis* (LSD post hoc test,  $p < 0.05$ ; Figs. 1–2). Based on the total biomass, the exudate concentration causing 50% inhibition was 81.6%.

**Table 2. Mean and standard deviation of the deleterious effect of root exudation of *Solidago canadensis* at different concentrations based on the root length, plant height, basal diameter, and total biomass of native plants or invasive plants. Different small letters indicate a significant difference among different root exudation concentrations of native plants or invasive plants.**

Species origin	Concentration	Root length	Plant height	Basal diameter	Total biomass
Native	0	0a	0a	0a	0a
	25%	-0.2431 $\pm$ 0.1898b	-0.3182 $\pm$ 0.1252b	-0.2410 $\pm$ 0.2764b	-0.2022 $\pm$ 0.6680a
	50%	-0.4315 $\pm$ 0.2409c	-0.2946 $\pm$ 0.2762b	-0.3342 $\pm$ 0.2675b	-0.2694 $\pm$ 0.6095a
	75%	-0.4749 $\pm$ 0.1232c	-0.4241 $\pm$ 0.2240b	-0.3501 $\pm$ 0.2519b	-0.3827 $\pm$ 0.5781a
Invasive	100%	-0.4267 $\pm$ 0.1678c	-0.3142 $\pm$ 0.2082b	-0.3967 $\pm$ 0.2677b	-0.4150 $\pm$ 0.3990a
	0	0a	0a	0a	0a
	25%	-0.2083 $\pm$ 0.2358b	-0.0988 $\pm$ 0.1463b	-0.0653 $\pm$ 0.2132b	-0.2036 $\pm$ 0.3862b
	50%	-0.2345 $\pm$ 0.1892b	-0.1307 $\pm$ 0.1707b	-0.0374 $\pm$ 0.1605b	-0.2315 $\pm$ 0.2966b
	75%	-0.2897 $\pm$ 0.1834b	-0.2148 $\pm$ 0.2035c	-0.2371 $\pm$ 0.1663c	-0.4073 $\pm$ 0.2908c
	100%	-0.3958 $\pm$ 0.2434c	-0.2430 $\pm$ 0.2261c	-0.2527 $\pm$ 0.2175c	-0.4965 $\pm$ 0.2843c



**Fig. 1.** The linear curve of the phytotoxic effect of *S. canadensis* root exudate on the root length (a), plant height (b), and basal diameter (c) of seven plant species. The data are shown in mean  $\pm$  standard deviation (SD).

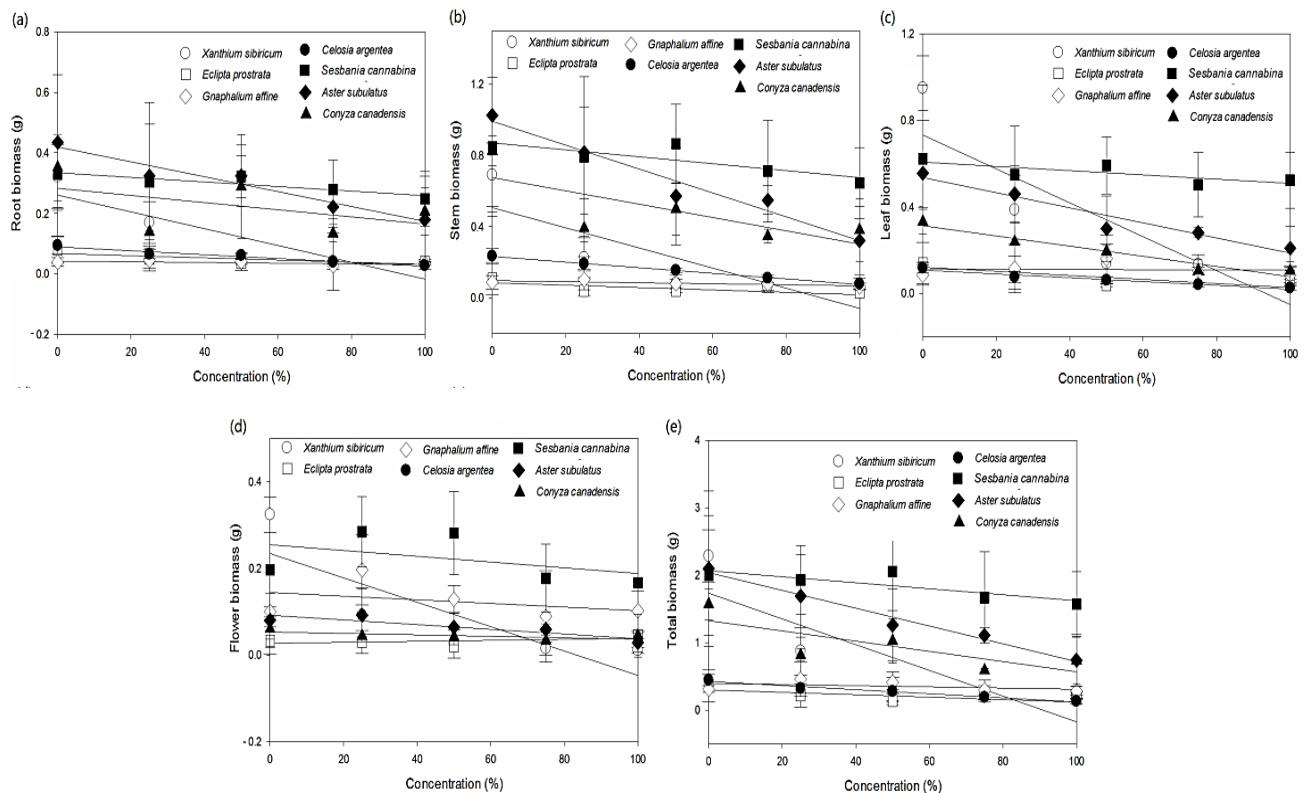


Fig. 2 The linear curve of the phytotoxic effect of *S. canadensis* root exudate on the root biomass (a), stem biomass (b), leaf biomass (c), flower biomass (d), and total biomass (e) of seven plant species. The data are shown in mean  $\pm$  standard deviation (SD).

**Table 3. The main effect of species origin (O), concentration of root exudates (C), interactive effect OxC, and the random effect of species (nested in species origin) (S) on root length, plant height, basal diameter, and total biomass tested by the general linear model.**

Factors	Root length	Plant height	Basal diameter	Total biomass
Concentration (C)	27.152***	18.180***	18.306***	10.868***
Species origin (O)	0.852	1.892	2.214	0.001
OxC	2.341	2.795*	2.860*	0.182
Species nested in origin (S)	9.860***	12.533***	14.137***	17.571***

\*, \*\*\* Indicated significant effect at 0.05 and 0.001 levels

With the increasing root exudate concentration, the deleterious effect of root exudates on plant height, basal diameter, root length, and total biomass increased (Table 2). The general linear model indicated that species (nested in species origin) had a significant effect on the deleterious effect of root exudates based on the root length, plant height, basal diameter, and total biomass (Table 3). Though species origin had no significant effect on the root length, plant height, basal diameter, and total biomass, a significant interactive effect of species origin and concentration was found based on plant height and basal diameter (Table 3).

## Discussion

Root-mediated allelopathy has been suspected since the early 1800s and has been extensively studied in invasive plants such as *Larrea tridentata* (Mahall & Callaway, 1992), *Centaurea diffusa* (Vivanco *et al.*, 2004), *Euphorbia esula* (Qin *et al.*, 2006), *Phragmites australis* (Uddin *et al.*, 2014), and *Chrysanthemoides monilifera* subsp. *monilifera* (Harun *et al.*, 2015). Our data illustrated

that the root exudates from *S. canadensis* had significant phytotoxic effects on the root length, plant height, basal diameter, and the root, stem, leaf, and total biomass of seven different species. Previously, Mahall & Callaway (1992) showed that root exudates of invasive *Larrea tridentata* suppressed the root elongation of conspecific and interspecific neighbors. Uddin *et al.*, (2014) found that the root exudates of invasive *P. australis* had significant negative effects on the germination and growth of native *Melaleuca ericifolia* by decreasing the germination percentage, maximum root length, plant height, biomass, and stem diameter. This study provided additional evidence for the root exudate-mediated allelopathy of *S. canadensis*, supporting the strong allelopathic effects of *S. canadensis* in its invasion success.

The novel weapon hypothesis, which states that the allelochemicals of invasive plants act against native plants in the invaded communities, explains why some exotic species are so successful at invading natural plant communities (Callaway & Aschehoug, 2000). Here, we found that the root exudates of invasive *S. canadensis* had significant effects on five out of the seven investigated

species, impacting both native and invasive plants in the invaded community. However, no significant difference was found between native and invasive plants in response to the phytotoxic root exudates based on plant height, root length, basal diameter, or total biomass. The similar phytotoxic effects of the root exudates of *S. canadensis* on all native and invasive plants co-occurring in the invaded community may explain why *S. canadensis* quickly dominated in the invaded communities after colonization.

More interestingly, in the present study, we also found a significant interactive effect between species origin and concentration on the inhibition rate of the root exudates, i.e., the *S. canadensis* root exudates had similar inhibition effects on the growth of native plants and invasive plants in the low concentration treatment, while the effects on the growth of native plants were greater than those on invasive plants in the high concentration treatment, indicating that invasive plants had stronger resistance to a high concentration of root exudates of *S. canadensis*. Mallik & Pellissier (2000) found that the extracts of native *Vaccinium myrtillus* had a stronger allelopathic effect on an exotic *Picea mariana* than on a native neighbor, *Picea abies*, which had a coevolutionary history with *V. myrtillus*. The stronger resistance of invasive *A. subulatus* and *C. canadensis* to the root exudates of *S. canadensis* than on native plants might be due to the possible coevolutionary history with *S. canadensis* because these species are all native to North America.

Here, we also found that different plant species have different responses to the phytotoxic effects of *S. canadensis* root exudates. In this manuscript, compared with the other five plant species, no significant inhibitory effect of root exudates was found on the growth of the native *G. affine* or the invasive *S. cannabina*, and the predicted concentration causing a 50% inhibition was 212.5% and 242.9%, respectively. Similar species-dependent phytotoxic effects of *S. canadensis* have been reported (Huang *et al.*, 2009), suggesting a different sensitivity of plants species to the allelochemicals in the root exudates of *S. canadensis*. This might be useful in determining resistant plant species that can be used to recover communities severely invaded by *S. canadensis*.

In conclusion, the phytotoxic root exudates of *S. canadensis* might play an important role in the allelopathic capacity of this species. Although most information on root exudates has been obtained from solution-grown plants (Rovira, 1969), the reality (i.e., the root exudates in soils) may differ because of the lack of allelochemicals induced or secondarily produced by the residual matter remaining in the soil. Therefore, more studies are required, especially using root exudates extracted from soils. Additional studies focusing on the chemical identification of root exudates and their individual effects, the phytotoxic effects of root exudates on soil microbial activities, and the separation of phytotoxic effects from other competitors in natural settings are essential for understanding and predicting the successful invasion of *S. canadensis* in invaded ranges.

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