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RESEARCH ARTICLE

Phenological changes in secondary metabolites and mineral nutrition of *Solidago canadensis* and their impact on the rhizosphere soil ecosystem

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Abstract

A comprehensive study of the impact of *Solidago canadensis* on the soil ecosystem using the example of monodominant communities of this species located on the exposition plot 'Steppes of Ukraine' of the M.M. Gryshko National Botanical Garden of the NAS of Ukraine (Kyiv) is presented. The research was conducted during the growing seasons of 2023–2024. The content of macro- and microelements, secondary metabolites in leaves and soil, allelopathic activity, organic and mineral carbon content, and laccase activity were assessed, and the functional structure of soil microbial communities was determined.

It has been established that *S. canadensis* actively regulates the absorption of nutrients, which serves as an adaptive mechanism to environmental changes. The capacity of *S. canadensis* to reduce soil contamination with toxic metals such as Mn, Zn, Co, Cr, Fe, Pb, and Ti has been shown. For Mn and Zn, *S. canadensis* acts as a phytoextractor, and for Co, Cr, Fe, Pb, and Ti, it acts as a phytostabilizer.

Significant phenological fluctuations in allelopathic activity, the content of biologically active secondary metabolites, and the functional structure of the rhizosphere microbiota in *S. canadensis* have been shown. The successful spread of *S. canadensis* outside its natural range may be associated with the ability of this plant to produce and release into the environment a number of secondary metabolites of phenols, terpenoids, saponins, etc., which are responsible for its high resistance to abiotic and biotic stress factors, allelopathic activity, inhibit the development of harmful bacteria and stimulate the development of actinomycetes, which participate in the restoration of soil fertility and are antagonists of phytopathogens.

Keywords: *Solidago canadensis*, mineral nutrition, allelopathic activity, secondary metabolites, rhizosphere soil, microbial communities, phytoremediation

Authors' contributions: Zaimenko N. conceived and designed the experiments. Kharytonova I. and Malashchuk O. performed agrochemical analysis of soil. Yunosheva O. performed microbiological analysis. Pavliuchenko N. performed allelopathic analysis of soil. Chernikova N. and Didyk N. performed biochemical analysis of soil and plant material. Zakrasov O. determined laccase activity. Chernikova N. and Didyk N. wrote the manuscript draft. Zaimenko N. critically revised the manuscript.

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Introduction

Climate change and urbanization promote the spread of invasive species of plants and animals altering biodiversity and the functioning of natural and seminatural ecosystems. According to EU Regulation 1143/2014 (EU 2014), invasive species are alien species of plants or animals whose introduction or spread threatens or negatively affects biodiversity and ecosystem services (Skočajić & Nešić, 2020).

Goldenrod (*Solidago canadensis* L.) is classified as an invasive plant, which was introduced to Europe as an ornamental from North America in the early 17th century (Radusiene et al., 2015). Since that time, *S. canadensis* has spread rapidly in local seminatural and natural ecosystems, which resulted in its tremendous expansion and displacement of native flora, especially in various disturbed environments, predominantly along roadsides and railways, urban settings, abandoned fields, and grasslands, forest edges, roadsides, and meadows. Presently, it is considered one of the most aggressive invaders, and is defined by the European and Mediterranean Plant Protection Organization as an invasive species having a high potential for spread and posing an important threat to the environment and biodiversity in the region (EPPO) (Radusiene et al., 2015). The EPPO (2024) recommends taking control measures and raising awareness due to *S. canadensis* high potential to alter natural ecosystems and shift ecosystem services.

Some authors indicated that *S. canadensis* provides several benefits to its new habitats, such as attraction of pollinators, forage production, and storing carbon (Gallardo et al., 2019). Besides, *S. canadensis* was shown to stabilize increased (compared with natural) concentrations of Pb and Zn in the soil (Bielecka & Królak, 2019; Bielecka et al., 2020). At the same time, it also accumulated Zn in the above-ground parts, which allowed authors (Bielecka & Królak, 2019; Bielecka et al., 2020) to assume the possibility of using this plant for phytoextraction of soils contaminated with this metal. In addition, phytosanitary properties of *S. canadensis* root secretions were demonstrated, suppressing the growth of phytopathogenic microorganisms such as *Botrytis cinerea* (Liu et al., 2016), *Fusarium* sp.,

Phytophthora infestans, etc. (Anžlovar & Koce, 2014). Taking into account such traits of *S. canadensis* as a wide range of tolerance to soil physicochemical conditions and climatic factors, ability to colonize contaminated soils, and production of high biomass of above-ground parts, an extensive underground system makes this species a promising plant for utilization for phytoremediation and phytosanitation of contaminated soils with toxic metals/phytopatogens (Bielecka & Królak, 2019).

The extraction of new products from the invasive species presents a viable approach aimed at their valorisation. In recent years, significant attention has been focused on phytochemicals of *Solidago* species, including *S. canadensis* (Poljuha et al., 2024). The latter was shown to contain a diverse array of bioactive compounds with antioxidant, antimicrobial, anticancer, anti-inflammatory, and hepatoprotective activity. Phytochemicals of *S. canadensis* can be used in pharmacy, agriculture, medicine, cosmetics, production of natural dyes, cellulose, biopesticides, etc. (Poljuha et al., 2024).

Solidago canadensis exhibits strong allelopathic effects, inhibiting the growth and development of native species, thereby reducing biodiversity. The allelochemicals responsible for the described effects identified are chlorogenic acid, rutin (quercetin-3-O-rutinoside), kaempferol-3-O-D-glucoside, and quercitrine released through root exudates, plant residue decomposition, and leachates, which alter soil microbial communities and inhibit arbuscular mycorrhizal fungi, vital for nutrient and water uptake in native plants (Likhanov et al., 2021; Kato-Noguchi & Kato, 2022; Zhu et al., 2022). These exometabolites enhance species invasiveness and present promise as potential natural herbicides (Yang & Li, 2022).

Many scientific papers are devoted to the impact of *S. canadensis* on biodiversity decline (Wang et al., 2018a, 2018b, 2019, 2021; Gallardo et al., 2019). While there is a lack of comprehensive information on *S. canadensis* effect on soil chemical and physical properties, biochemical and allelopathic regime as well as on how *S. canadensis* allelochemicals alter soil microbial communities.

This study aimed to conduct a complex assessment of *S. canadensis* effects on the

soil ecosystem, including metal cations, biologically active secondary metabolites, soil microbial community, allelopathic regime, and organic carbon deposition.

Material and methods

The research objects are rhizosphere soil and *S. canadensis* plants growing in the 'Steppes of Ukraine' exposition plot of the M.M. Gryshko National Botanical Garden of the NAS of Ukraine (Kyiv). Sampling was made during the period of *S. canadensis* shoot development (early June), flowering (end of July), and the seed maturation stage (middle of September) in 2023–2024. As the control, we used the soil collected from the rhizosphere of the surrounding forb meadow communities dominated by indigenous species *Elytrigia intermedia* (Host) Nevski, *Adonis vernalis* L., and *Paeonia tenuifolia* L. A comparative analysis of the content of chemical elements in the soil and in the above-ground parts of plants was carried out, the functional structure of soil microbial communities was determined, and the allelopathic activity of the above-ground parts and rhizosphere soil was assessed. Soil samples were taken with a drill at 10–20 cm depth, sieved through a sieve with openings of 1–2 mm.

Agronomic soil analysis

To determine the pH of the soil solution, a portion of the sieved and dry soil was placed in a porcelain beaker and poured with 25 ml of 1 N KCl (pH 5.5–6.0) and kept for 12 h, after which measurements were performed using the MW 402 TDS Meter (Milwaukee, Hungary).

The preparation of the soil samples for the analysis of the content of macro- and microelements was carried out according to Zaimenko et al. (2021). Acid-soluble forms of metal cations and other chemical elements were extracted using a 1.0 N solution of nitric acid (HNO₃). Preparation of plant samples for analysis was done by wet ashing with a solution of high-purity nitric acid using Speedwave Xpert DAP-60X (Berghof, Germany), a special system for microwave decomposition of samples. The concentrations of chemical elements in the solution were measured using an ICAP 6300 DUO plasma emission spectrometer (Thermo Fisher

Scientific, USA). The relative uncertainty ranged from 7% to 12% for different chemical elements. Laccase activity was determined spectrophotometrically using the color reaction with syringaldazine according to Dzyuba et al. (2021) using a SPECORD 200 instrument (Analytik Jena, Germany).

Allelopathic analysis

Water-soluble allelochemicals from freshly harvested crushed leaves of *S. canadensis* were extracted with distilled water (1:100) for 4 hours. This concentration corresponds to the observed levels of goldenrod allelochemicals in its monodominant communities in the field (Yuan et al., 2013). The allelopathic activity of the extracts was assessed by bioassay on radish (*Raphanus sativus* L. var. *sativus*) root growth (Pavliuchenko et al., 2021; Pavliuchenko & Young, 2021). The allelopathic activity of *S. canadensis* rhizosphere soil was assessed by direct bioassay using watercress (*Lepidium sativum* L.) as a test plant (Pavliuchenko et al. 2021; Pavliuchenko & Young, 2021). The percentage of root growth inhibition was measured by the given formula:

$$GI = 100 \times (PC - PT) / PC, \text{ where}$$

GI – growth inhibition, in %,

PT – length of roots of seedlings grown with extracts (treatment group), in cm,

PC – length of the roots of seedlings in the control group, in cm.

Microbiological analysis

The functional structure of microbial communities was assessed by seeding soil samples on selective media. In particular, micromycetes were determined on Čapek's medium, actinomycetes on starch-ammonia agar (KAA), ammonifiers on meat-peptone agar (MPA), and microorganisms that consume mainly mineral nitrogen compounds on KAA. The growth of nitrogen-fixing microorganisms was taken into account by the percentage of soil clods fouling on the Ashby medium (Ellanska et al., 2021).

The number of microorganisms was determined by direct colony counting in Petri dishes. The results were expressed in colony-forming units (CFU) per 1 g of soil. A sample dilution was analyzed to obtain reliable data,

in which 10 to 150 colonies were formed on a nutrient medium in a Petri dish (Ellanska et al., 2021).

The number of microorganisms was calculated per 1 g of dry soil. To do this, the moisture content was first determined: a sample weighing 10 g was placed in a pre-weighed metal box and dried in a drying oven at 105 °C for 3 hours.

The number of microorganisms was calculated using the formula:

$$a = b / (c \times d \times f), \text{ where}$$

a – the number of cells in 1 g of dry soil;

b – the average number of colonies from one Petri dish;

c – the dilution from which the culture was made, in ml;

d – the volume of suspension that was applied to the nutrient medium, in ml;

f – the mass of soil that was taken for analysis, in g.

Biochemical analysis of plant material and soil

Low molecular weight phenolic compounds were extracted from plant material first with distilled water and then with 80% ethanol. The content was determined spectrophotometrically using a color reaction with Folin-Ciocalteu reagent (Pavliuchenko et al., 2021; Pavliuchenko & Young, 2021). Flavonoids were extracted with 70% ethanol; the quantitative content was determined spectrophotometrically using a color reaction with 10% AlCl₃ solution (Pavliuchenko et al., 2021; Pavliuchenko & Young, 2021). Tannins were extracted with boiling distilled water. The quantitative content was determined by titration with 0.1% potassium permanganate solution in the presence of indigocarmine (Mardar & Serdyuk, 2008). Triterpenoids and saponins were extracted with 96% ethanol, and the quantitative content was determined spectrophotometrically using a color reaction with vanillin reagent (Pavliuchenko et al., 2021; Pavliuchenko & Young, 2021).

The free phenolic compounds are isolated from the soil by ion exchange (desorption) with the use of ion exchanger KU-2-8 (H⁺) as a model of the root system with dissolving and absorbing ability in relation to mobile organic compounds (Pavliuchenko et al., 2021; Pavliuchenko & Young, 2021). All

spectrophotometric measurements were performed using the instrument SPECORD 200 (Analytik Jena, Germany).

Statistical analysis

The results are presented as mean ± standard error (m ± SE). The reliability of the difference (P < 0.05) between the obtained data was determined by the method of variance analysis (one-factor variance analysis) using Tukey's a posteriori test using MS Excel and Statistica 10.0 software (Stat-Soft Inc., USA) for the data processing.

Results and discussion

Comparative analysis of the content of chemical elements in soil and plants *S. canadensis* indicated good ability of this species to regulate exchange of macro- and microelements with the soil environment (Tables 1 & 2). Of practical interest is the ability of *S. canadensis* to significantly reduce the level of such toxic metals as Co, Cr, Fe, Mn, Pb, Ti, and Zn in the soil. While the content of Al and P in the rhizosphere of *S. canadensis* increased 3.8 and 2 times from the beginning to the end of the vegetation season.

The phenological dynamics of the content of the metal cations in the leaves of *S. canadensis* are mainly due to phenological changes in physiological processes associated with active vegetative growth, flowering, and seed formation, as well as weather conditions (high temperature and drought in mid-summer and early autumn). In particular, the concentration of Ca, which is known to enhance plant tolerance towards abiotic stress (Gupta et al., 2023), reached maximum values in September and was 3.1 times higher compared to the initial phase of plant development. The concentration of P, essential for flower and seed development, was minimal during the vegetative phase and reached a maximum at full flowering. The presence of vanadium in the leaves in the absence of detectable concentrations of this element in the soil.

The decrease in Mn and Zn concentrations in the soil correlated with the increase in the accumulation of these toxic metals in the above-ground parts of *S. canadensis*, which indicates the possibility of using this

Table 1. Phenological changes in the content of chemical elements in the rhizosphere soil of *Solidago canadensis* and meadow forbs, mg/kg (averages for 2023–2024).

Element	<i>S. canadensis</i>			Meadow forbs		
	Shoot development	Flowering	Seed maturation	Shoot development	Flowering	Seed maturation
Al	1067.0±53.1	7028.0±315.3	4047.0±196.3	11995.0±132.8	13440.0±41.5	17070.0±148.2
B	9.5±0.5	7.09±0.4	1.4±0.09	7.1±0.6	7.2±0.6	11.3±1.1
Ba	76.6±3.5	79.3±3.5	35.5±1.8	67.3±2.9	43.3±2.1	39.267.3±2.4
Ca	3250.0±152.6	2328.0±113.5	2456.0±120.6	3104.0±273.5	3628.8±161.8	3373.7±221.8
Co	4.0±0.2	3.4±0.2	1.4±0.1	5.6±0.9	5.1±0.4	4.2±0.6
Cr	14.0±0.7	11.8±0.4	4.4±0.2	24.1±1.1	22.9±1.2	38.3±1.6
Cu	15.4±0.7	15.5±0.8	9.4±0.4	15.8 ±1.2	24.4 ±2.1	21.5±1.7
Fe	7086.0±348.2	5763.0±282.4	2967.0±141.83	2563±129.1	2465.8±137.3	2257.4±122.2
K	2379.0±155.3	1239.0±59.8	557.3±26.3	116.4±65.6	174.2±77.1	128.4±46.1
Mg	1492.0±74.5	903.8±44.3	516.8±24.3	828.7±39.5	1258.0±54.1	378.8±42.7
Mn	532.9±25.2	271.0±12.9	119.4±5.9	503.2±19.3	477.0±28.5	416.6±32.1
Na	64.8±3.2	50.3±2.5	32.4±1.6	89.0±2.6	59.8±3.4	55.2±2.1
Ni	8.2±0.4	9.0±0.4	4.4±0.2	9.9±0.5	7.1±0.5	6.8±0.4
P	3.7±0.2	8.4±0.4	7.4±0.3	9.2±0.1	15.3±0.3	12.2±0.1
S	703.0±33.3	557.0±24.8	887.8±41.2	188.6±28.6	143.4±32.5	156.3±20.1
Pb	74.6±0.7	68.7±3.3	34.5±1.6	122.9±2.7	118.5±2.4	109.4±3.2
Si	1002.0±48.8	399.9±18.9	132.5±5.9	1438.0±98.4	1062.0±92.3	837.0±33.6
Sr	16.7±0.8	10.4±0.5	14.5±0.7	19.6±0.8	16.9±0.2	15.0±0.4
Ti	331.0±15.7	129.2±6.0	15.5±0.7	556.4±12.2	495.0±7.1	432.9±5.3
Zn	41.4±1.7	4.8±2.0	21.3±1.1	47.0 ±2.3	30.0 ±1.9	46.0 ±2.5

invasive species for phytoextraction of these pollutants from the soil. Also, *S. canadensis* is promising for phytostabilization of toxic metals, such as Co, Cr, Fe, Pb, and Ti, the concentrations of which were reduced in the soil but did not increase in the above-ground parts. The potential of *S. canadensis* to adsorb Pb and Zn from the surrounding soil was shown by Bielecka & Królak (2019). The authors demonstrated the good ability of this plant to actively transport metals through the membranes of root cells, chelate them using organic acids, flavonoids, and phenolic compounds, and store metal chelates in cell vacuoles to minimize toxic effects. The high resistance of *S. canadensis* to heavy metal contamination (zinc and lead) was also shown by Czortek et al. (2020).

Analysis of the allelopathic activity of aqueous extracts from freshly collected

material and rhizosphere soil of *S. canadensis* revealed the presence of inhibitors of growth processes of acceptor plants both in the leaves and in the roots of the donor plant (Fig. 1). The phenological changes in the accumulation of inhibitors in plants had a parabolic character with a maximum in July (flowering phase) and a minimum in September (seed ripening phase). Meanwhile, the phenological dynamics of soil allelopathic activity had a U-shaped pattern, with a maximum during vegetative growth, a sharp drop in the flowering phase, and a subsequent rise in autumn. The allelopathic activity of aqueous extracts from leaves and rhizosphere soil of *S. canadensis* was positively correlated with the content of low-molecular phenolic substances (Table 3), which indicates the important role of these substances in the formation of the allelopathic potential of *S. canadensis*.

Strong inhibitory effect of *S. canadensis* allelochemicals to native flora was shown in many studies (Zhu et al., 2022; Kato-Noguchi & Kato, 2022; Yang & Li, 2022). The allelopathic effect of *S. canadensis* is associated with phenolic acids (ferulic, p-coumaric, caffeic, chlorogenic acid, etc.), flavonoids (kaempferol, quercitrin, and rutin), fatty acids, terpenes, polyphenols, and saponins (Likhhanov et al., 2021; Zhu et al., 2022; Kato-Noguchi & Kato, 2022). The results of our research confirm the opinion of other authors that the allelopathy of *S. canadensis* may contribute to its increasing competitive ability and make the plant invasive.

Analysis of the secondary metabolites of *S. canadensis* showed a high content of biologically active compounds related to phenols and terpenoids, indicating its powerful adaptive potential and ecological plasticity. Flavonoids are potent antioxidants that neutralize reactive oxygen species (ROS) and protect cells from oxidative stress (Mierziak et al., 2014). The high content of flavonoids in the leaves of *S. canadensis* indicates its ability to effectively counteract abiotic stress factors, such as drought, high temperatures, or UV radiation. Some flavonoids exhibit allelopathic effects, inhibiting the growth of other plants, which may explain the invasive ability of goldenrod in phytocenoses (Mierziak et al., 2014).

Tannins can bind proteins, making the plant less attractive to herbivores and insect pests

Table 2. Phenological changes in the content of chemical elements in *Solidago canadensis* leaves, mg/kg (average for 2023–2024).

Element	Phenological stage		
	Shoot development	Flowering	Seed maturation
Al	295.7±14.78	120.3±5.87	215.8±9.96
B	33.8±1.45	42.9±2.03	45.8±2.14
Ba	6.01±0.27	11.27±0.51	9.63±0.42
Ca	5705±279.3	8799±421.7	18080±892.8
Co	0.34±0.01	0.33±0.01	0.34±0.01
V	5.51±0.24	6.08±10.29	6.41±0.31
Cr	1.65±0.08	1.55±0.08	1.40±0.07
Cu	10.81±0.52	9.62±0.46	9.99±0.48
Fe	256.2±12.77	130.2±6.43	209.9±10.35
K	23910±1147	12330±587	9828±493
Mg	1880±95.2	1798±87.4	2153±103.6
Mn	69.74±3.51	68.05±3.42	80.24±3.87
Na	37.70±1.75	28.39±1.42	55.77±2.69
Ni	2.12±0.11	2.18±0.10	1.37±0.06
P	20.58±1.03	43.9±2.11	34.7±1.69
S	2300±109.7	755±35.9	1819±89.7
Pb	2.47±0.12	1.83±0.08	1.10±0.05
Si	1369±67.5	441.6±22.1	733.1±35.9
Sr	6.16±0.29	15.75±0.76	26.33±1.28
Ti	11.93±0.52	2.46±0.12	6.76±0.32
Zn	18.53±0.88	37.38±1.83	38.92±0.91

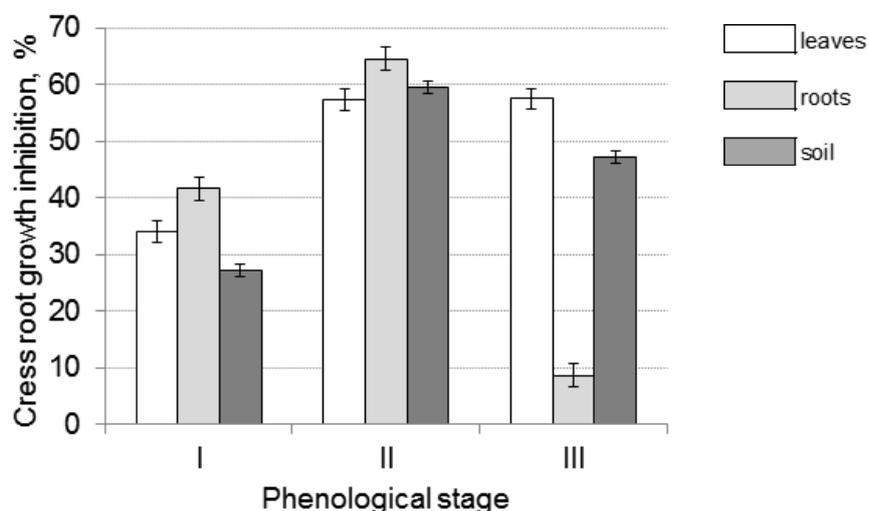


Figure 1. Phenological changes in allelopathic activity of 1% aqueous extracts from leaves and roots of *Solidago canadensis* (bioassay for radish root growth) and rhizosphere soil (cress root growth), growth inhibition in %. Phenological stages: I – shoot development, II – flowering, III – seed maturation.

Table 3. Content of secondary metabolites in leaves and the rhizosphere soil of *Solidago canadensis*, mg/g DW.

Secondary metabolites	Phenological stage		
	Shoot development	Flowering	Seed maturation
Leaves			
Total phenolics	41.3±3.4	77.4±3.3	54.2±2.7
Flavonoids	22.6±2.8	56.6±3.4	42.3±2.9
Tannins	49.8±2.9	76.2±3.4	111.3±3.5
Saponins	4.7±0.2	12.2±0.7	9.5±0.9
Triterpenoids	6.5±0.6	13.8±0.8	17.6±1.1
Rhizosphere soil			
Triterpenoids	1.9±0.2	2.6±0.1	1.8±0.1
Saponins	1.2±0.1	1.8±0.2	1.7±0.1
Total phenolics	58.73±1.9	24.8±2.2	71.9±4.8
Control soil			
Triterpenoids	1.6±0.1	2.1±0.1	1.4±0.1
Saponins	1.4±0.2	1.6±0.1	1.3±0.1
Total phenolics	51.4±3.5	67.2±3.1	78.6±2.2

(Barbehenn & Constabel, 2011). Their high concentration in the leaves of *S. canadensis* may be a key factor in the formation of resistance to phytopathogens. The high concentration of saponins and triterpenoids in the leaves may also be a defense mechanism against phytophagous organisms (Mathur et al., 2025).

The antimicrobial activity of *S. canadensis* is thought to be due to the terpenoids present in the root essential oils and soluble phenolic and polyphenolic compounds (Anžlovar & Koce, 2014). The results of our studies showed the presence of biologically active concentrations of saponins, triterpenoids, and especially phenolics in the rhizosphere soil of *S. canadensis* throughout the growing season, with maximums in July (for triterpenoids) and September (for phenolics).

Solidago canadensis phytotoxic allelochemicals not only suppress other plants' growth, but also alter the community structure of soil microbiota (Table 4).

Comparison of the results of the assessment of the biochemical regime of the *S. canadensis* rhizosphere soil with the changes in the functional structure of microbial communities showed that a 2.9-fold increase in the content of low-molecular-weight phenolics in the

rhizosphere soil was accompanied by a 1.7-fold decrease in the number of ammonifiers, and an increase in the number of actinomycetes and micromycetes by 2 and 1.14 times, respectively. This trend is consistent with the findings of other authors that phenolic allelochemicals inhibit the development of soil bacteria but stimulate the growth of microfungi and actinomycetes (Zhou et al., 2012; Badri et al., 2013).

Actinomycetes are also known for their ability to produce and release into the environment phenolic secondary metabolites with diverse biological activity (Golińska & Dahm, 2011). Therefore, the autumn increase in phenolic content in *S. canadensis* rhizosphere soil could result from the intensification of actinomycetes metabolic activity, among which many antibiotic compounds are produced. Today, actinomycetes are recognized as noteworthy antibiotic producers, making 40% of the 160 microbial-based antibiotics (Raut et al., 2023). Actinomycetes are also an important component of the soil ecosystem because of their ability to decompose many complex compounds, such as proteins, pectins, cellulose, hemicellulose, lignins, and chitin (Golińska & Dahm, 2011).

The ecological outcome of microbiological

Table 4. The number of microorganisms belonging to different functional groups in the rhizosphere soil of *Solidago canadensis* and meadow forbs.

Plants	Phenological stage	Micromycetes, thousands CFU per g DW soil	Actinomycetes, millions CFU per g DW soil	Ammonifiers, millions CFU per g DW soil	Microorganisms that consume mineral nitrogen, millions CFU per g DW soil	Mineralization coefficient
<i>S. canadensis</i>	Flowering	34.7±2.9	0.7±0.07	6.1±0.2	6.3±0.1	1.0
	Seed maturation	39.7±1.5	1.4±0.2	3.5±0.1	6.1±0.1	1.7
Meadow forbs	Flowering	58.4±1.1	1.34±0.1	7.8±0.1	8.8±0.2	1.4
	Seed maturation	43.9±1.3	1.15±0.1	4.6±0.2	9.4±0.1	1.8

Note. CFU – colony-forming unit.

processes was assessed by the ratio of the number of microorganisms with mineral and organic nutrition. The maximum mineralization-immobilization coefficient in the *S. canadensis* rhizosphere soil was observed at the end of the growing season. This tendency was confirmed by the results of the analysis of the content of organic carbon and laccase activity (Table 5).

The significant impact of *S. canadensis* on soil microflora has been shown in the works of other authors. In particular, Qiao et al. (2024) found that the *S. canadensis* enhanced nutrient-releasing microorganisms (Actinomycetota) and disease-resistant microorganisms (*Nocardioide*s), while decreasing N-cycling microorganisms (Nitrososphaeria and Nitrospirota). These changes in the soil microbiome create conditions that promote the effective use of *S. canadensis* resources and its aggressive invasion. The ability of *S. canadensis* to influence nitrogen-fixing bacterial communities and adapt to varying levels of heavy metals in the soil may also contribute to its invasive success (Wang et al., 2018a, 2018b, 2023).

It is known that metabolites of *S. canadensis* can inhibit the activity of microorganisms responsible for the nitrogen cycle and promote the dominance of microorganisms that are adapted to allelopathic substances (Zhu et al., 2022; Kato-Noguchi & Kato, 2022; Wang et al., 2023). Also, allelochemicals of *S. canadensis* are known for their toxicity to insect pests, affecting their nervous system, reproductive ability, and development (Benelli et al., 2019).

The content of soil organic carbon is an indicator of its fertility, health, and ability to provide ecosystem services. According to the results of our research, the content of organic carbon in the rhizosphere soil of *S. canadensis* is quite high throughout the growing season, if compared with the organic carbon level common for the meadow-steppe vegetation in our region (Vyshenska & Ivanyk, 2015; Zaimenko et al., 2022), which confirms the positive role of this plant in the deposition of atmospheric carbon dioxide in the form of soil organic carbon.

Laccases are oxidoreductase enzymes with polyphenol oxidase activity that belong to the multicopper oxidase superfamily (Aza & Camarero, 2023). After being discovered in the exudates of the oriental lacquer tree, *Toxicodendron vernicifluum* (Stokes) F.A. Barkley, laccases have been identified in fungi, bacteria, and insects (Aza & Camarero, 2023). Presently, laccases are considered promising for the remediation of water and soil environment due to their ecological safety and ability to oxidize a wide range of aromatic pollutants to less toxic derivatives (Aza & Camarero, 2023). The relatively high laccase activity in the rhizosphere of *S. canadensis* throughout the growing season explains the resistance of this plant to its own phenolic allelochemicals and other organic aromatic pollutants. It should be noted that *Solidago* plants were shown to be capable of absorbing, translocating, and accumulating in foliar tissues organic pollutants involved in the manufacturing of explosives (Groom et al., 2002).

Table 5. C_{org} content, laccase activity, and HCO₃⁻ and electrical conductivity in the rhizosphere soil of *Solidago canadensis* and meadow forbs.

Plants	Phenological stage	Laccase activity, mV/g	C _{org} , %	HCO ₃ ⁻ , mg-eq./lH ₂ O	Electrical conductivity, µS/cm
<i>S. canadensis</i>	Shoot development	87.6±0.9	4.5±0.2	0.14±0.04	132.1±1.5
	Flowering	93.7±1.1	5.3±0.2	0.38±0.06	275.2±1.7
	Seed maturation	88.3±1.1	4.1±0.2	0.32±0.06	250.2±1.3
Meadow forbs	Shoot development	22.9±3.1	3.1±0.1	0.23±0.05	98.7±2.4
	Flowering	36.2±3.4	4.6±0.2	0.48±0.04	186.1±2.6
	Seed maturation	42.1±2.8	4.0±0.1	0.53±0.04	184.7±2.9

Conclusions

The effective spread of *S. canadensis* outside its natural range is associated with the ability of this plant to produce and release into the environment a number of secondary metabolites such as phenols, terpenoids, saponins, etc., which are responsible for its high resistance to abiotic and biotic stress factors, create favorable soil conditions for this species – reduce soil pollution with toxic metals (Mn, Zn, Co, Cr, Fe, Pb, and Ti), inhibit the development of other plant species, harmful bacteria and stimulate the development of actinomycetes, which take part in the restoration of soil fertility and are antagonists of phytopathogens. Analysis of literature data, as well as the results of our research, allows us to conclude that the use of monodominant stands of this species for phytoremediation and restoration of fertility of soils contaminated with toxic metals, aromatic organic and inorganic toxicants, bacterial phytopathogens, and insect pests is promising. Due to its high productivity and resistance, *S. canadensis* exerts a powerful influence on the chemical, biochemical, allelopathic, and microbiological characteristics of the soil throughout the growing season. The impact of soil conditions, microbiota, and specific types of anthropogenic load on the effectiveness of the phytoremediation potential of *S. canadensis*, as well as the possibility of using local flora species to control the unwanted spread of this invasive species, require further study.

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Фенологічні зміни вторинних метаболітів та мінерального живлення *Solidago canadensis* та їх вплив на ґрунтову екосистему ризосфери

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Представлено комплексне дослідження впливу життєдіяльності рослин *Solidago canadensis* на ґрунтову екосистему на прикладі монодомінантних угруповань цього виду на ділянці “Степи України” Національного ботанічного саду ім. М.М. Гришка НАН України (м. Київ). Дослідження проводили впродовж вегетаційних сезонів 2023–2024 рр. Визначили вміст макро- і мікроелементів, вторинних метаболітів у листках та ґрунті, алелопатичну активність, вміст органічного та мінерального вуглецю,

активність лакази, а також з'ясували функціональну структуру мікробних угруповань ґрунту.

Встановлено, що *S. canadensis* активно регулює поглинання поживних елементів, що слугує адаптивним механізмом до змін довкілля. Показано здатність *S. canadensis* знижувати забруднення ґрунту токсичними такими металами як Mn, Zn, Co, Cr, Fe, Pb, Ti. При цьому для Mn та Zn *S. canadensis* виступає у ролі фіто екстрактора, а для Co, Cr, Fe, Pb, Ti – фітостабілізатора.

Показано значні фенологічні коливання алелопатичної активності, вмісту біологічно активних вторинних метаболітів та функціональної структури мікробіоти ризосфери у *S. canadensis*. Успішне розповсюдження *S. canadensis* за межами його природного ареалу може бути пов'язане зі здатністю цієї рослини продукувати та виділяти у навколишнє середовище низку вторинних метаболітів фенольних, терпеноїдів сапонінів та ін., які відповідають за його високу стійкість до абіотичних і біотичних стресових чинників, алелопатичну активність, пригнічують розвиток шкідливих бактерій та стимулюють розвиток актиміцетів, які приймають участь у відновленні родючості ґрунту та є антагоністами фітопатогенів.

Ключові слова: *Solidago canadensis*, мінеральне живлення, алелопатична активність, вторинні метаболіти, ризосферний ґрунт, мікробні угруповання, фітореємедіація