Effects of different plant parts of invasive *Solidago* species on the germination and growth of native grassland plant species

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Allelopathy is an important factor influencing whether an invasive plant species can become successfully established in a new range through disrupting the germination and growth of native plant species. Goldenrods (*Solidago* species) are one of the most widespread invasive taxa in Central Europe of North American origin. Owing to their high environmental impact and wide distribution range, invasive *Solidago* species should be controlled in Europe, and the areas invaded by them should be restored. Numerous studies have reported the allelopathic effects of *Solidago gigantea* and *Solidago canadensis*, but the results are inconsistent regarding differences in the allelopathic effects of particular plant parts and in the sensitivity to *Solidago* allelopathic effects among native species as well as between the two invasive species themselves. In this study, we aimed to analyse the effect of water extracts from *S. canadensis* and *S. gigantea* parts (roots, rhizomes, stems, leaves, and inflorescences) on the germination and initial growth of seedlings of 13 grassland species that typically grow in Central Europe. The tested grassland species differed in susceptibility to *Solidago* allelopathy, with the most resistant species being *Daucus carota*, *Leucanhemum vulgare*, *Lolium perenne* and *Trifolium pratense*. The inhibitory effect of 10% water extracts from leaves and flowers was stronger than those from rhizomes, roots, and stems without leaves, regardless of the *Solidago* species. Our study results imply that reducing the allelopathic effect of *Solidago* during habitat restoration requires removal of the aboveground parts, including fallen leaves. The allelopathic effects of roots and rhizomes seem to be of secondary importance.

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Abstract

Allelopathy is an important factor influencing whether an invasive plant species can become successfully established in a new range through disrupting the germination and growth of native plant species. Goldenrods (*Solidago* species) are one of the most widespread invasive taxa in Central Europe of North American origin. Owing to their high environmental impact and wide distribution range, invasive *Solidago* species should be controlled in Europe, and the areas invaded by them should be restored. Numerous studies have reported the allelopathic effects of *Solidago gigantea* and *Solidago canadensis*, but the results are inconsistent regarding differences in the allelopathic effects of particular plant parts and in the sensitivity to *Solidago* allelopathic effects among native species as well as between the two invasive species themselves. In this study, we aimed to analyse the effect of water extracts from *S. canadensis* and *S. gigantea* parts (roots, rhizomes, stems, leaves, and inflorescences) on the germination and initial growth of seedlings of 13 grassland species that typically grow in Central Europe. The tested grassland species differed in susceptibility to *Solidago* allelopathy, with the most resistant species being *Daucus carota*, *Leucanhemum vulgare*, *Lolium perenne* and *Trifolium pratense*. The inhibitory effect of 10% water extracts from leaves and flowers was stronger than those from rhizomes, roots, and stems without leaves, regardless of the *Solidago* species. Our study results imply that reducing the allelopathic effect of *Solidago* during habitat restoration requires removal of the aboveground parts, including fallen leaves. The allelopathic effects of roots and rhizomes seem to be of secondary importance.

Key words: allelopathy, grassland restoration, inhibition, goldenrods, land reclamation, plant invasion, semi-natural grasslands

Introduction

Allelopathy involves the production of secondary metabolite biochemical substances by one plant that stimulate or inhibit the germination, growth, and development of adjoining or neighbouring organisms (Rice, 1984; Cheema, Farooq & Khaliq, 2013; Bachheti et al., 2020; Li et al., 2021). The allelochemicals are present in various plant tissues, primarily inside the cells composing the various plant parts, such as leaves, stems, pollen, flowers, fruits, and roots (Begum et al., 2019; Macías, Mejías & Molinillo, 2019; Bachheti et al., 2020). Allelochemicals can be released to the environment through leaching from leaves and other aboveground plant parts, volatilization, root exudation, and litter decomposition (Uddin & Robinson, 2017; Wang et al., 2021).

Allelopathy plays a significant role in both natural and agricultural ecosystems by influencing seed germination and the growth of seedlings (Chon, Kim & Lee, 2003; Mushtaq & Siddiqui, 2018). The inhibition of plant growth caused by allelopathy differs based on the plant tissue (e.g., leaves, stems, roots) from which the allelopathic compounds are released (Begum et al., 2019; Kato-Noguchi & Kato, 2022). Most research shows that leaf extracts have stronger effects than those from flowers, stems, and roots (Turk & Tawaha, 2003; Siddiqui, Bhardwaj & Meghvanshi, 2009; Sodaeizadeh et al., 2009; Meiners, 2014; Debnath, Debnath & Paul, 2016; Mushtaq & Siddiqui, 2018; Mangao et al., 2020), however, it is not absolute and the effect of belowground parts can sometimes be stronger (Li & Jin, 2010; Zivanai, Ronald & Nester, 2019). The sensitivity to allelochemicals differs considerably among plant species (Debnath, Debnath & Paul, 2016; Sekutowski et al., 2019; Mangao et al., 2020) and even among genotypes within a species (Meiners, 2014; Appiah, Amoatey & Fujii, 2015). Most allelopathy studies have focused on the interactions between weeds and crops and have described the negative impacts of weeds on crops (Turk & Tawaha, 2003; Mangao et al., 2020). Allelopathy studies have also focused on aspects of eco-friendly agriculture such as the synthesis of agrochemicals to control pests and diseases, especially in weed management as an alternative to synthetic herbicides (Chon, Kim & Lee, 2003; Macías, Mejías & Molinillo, 2019; Bachheti et al., 2020; Mangao et al., 2020; Li et al. 2021; Motmainna et al., 2021, Ullah, Khan & Khan, 2021).

Allelopathy also plays a significant role in the successful establishment and survival of invasive plant species in the ecosystems of new ranges owing to potential for interfering with the seed germination, seedling growth, development, and establishment of native plant species (Uddin & Robinson, 2017; Torawane & Mokat, 2020). The allopathic effect of some invasive species can be so strong that introduced has been so-called 'novel weapon hypothesis' as an explanation for invasiveness (Callaway & Ridenour, 2004). The novel weapons hypothesis explains that the invasion efficiency of an exotic plant species can involve novel biochemical weapons that act as very strong allelopathic agents against resident vegetation. These agents give the invaders an advantage that arises from differences in the coevolutionary histories of plant communities. Allelopathic substances can be relatively ineffective against natural neighbours in the native range of an invader because they are adapted to its presence; however, newly encountered plants in invaded communities lack that adaptation. The exploitation by invaders of the susceptibility of resident species to the allelopathic effect due to evolutionary inadequacy is known as the advantage against resident species hypothesis (Callaway & Ridenour, 2004; Awty-Carroll et al., 2020). The novel weapons hypothesis explains successful invasions due to allelopathy in cases such as *Centaurea diffusa*, *Centaurea maculosa*, *Mikania micrantha*, and *Alliaria petiolata* in America and China (Callaway & Ridenour, 2004; Chen et al., 2017) as well as *Solidago canadensis* in China and Europe (Chen et al., 2017; Wei et al., 2020a; Wei et al., 2020b, Wei et al., 2020c) and *Solidago gigantea* in Europe (Pal et al., 2015).

In this study, we focussed on two invasive species, *Solidago gigantea* Aiton (Giant goldenrod) and *Solidago canadensis* L. (Canadian goldenrod), which are the most widespread invasive species of North American origin in Central Europe (Meyer, 2022; Popay & Parker 2022). These *Solidago* species have strong negative environmental impacts due to competition for soil nutrients, water, and space, as well as inhibition of native plants through allelopathy (Ledger et al., 2015). Because of clonal growth, *Solidago* species form dense stands and decrease the biodiversity of plants (Pal et al., 2015; Hejda, Pyšek & Jarošík, 2009), arthropods (Moroń et al., 2009; Lenda et al., 2021), ants (Kajzer-Bonk, Szpiłyk & Woyciechowski; 2016), and birds (Skórka, Lenda & Tryjanowski, 2010). The alien *Solidago* are able to invade grasslands, especially recently abandoned once (Moroń et al., 2009; Fenesi et al., 2015; Czarniecka-Wiera et al., 2020; Szymura, Świerszcz & Szymura, 2022), strongly influencing their plant species richness and pollinators abundance (Moroń et al., 2009; Fenesi et al., 2015).

Ample evidence exists regarding allelopathic impact of *Solidago* species on crops and forage grass species. For example, *S. canadensis* extracts can inhibit seed germination and growth performance parameters of *Lactuca sativa* (Wang, Wu & Jiang, 2019; Wei et al., 2020a; Wei et al., 2020b), *Trifolium pratense* (Zandi et al., 2020), *Pterocypsela laciniata* (Wang et al., 2017), and *Festuca rubra* and *Festuca pratensis* (Karpavičiene, Daniloviene & Vykertaite, 2019). In addition, *S. gigantea* decreases the germination and growth performance parameters of *Avena sativa*, *Brassica napus* subsp. *oleifera*, and *Helianthus annuus* (Novak et al., 2018). Moreover, root extracts from *Solidago* species show inhibitory activity against microorganisms (Móricz et al., 2020; Móricz et al., 2021). Finally, the allelopathy of *S. canadensis* can reduce the biodiversity of species-rich plant communities and thus increase the susceptibility of a community to further invasion (Ledger et al., 2015; Adomako et al., 2019).

The content and type of phenolic compounds differ in plant tissues, including leaves, flowers, stem, and roots, and the characteristics can also be variable between *S. canadensis* and *S. gigantea* (Marksa et al., 2020; Kato-Noguchi & Kato, 2022; Zhu et al., 2022). Further, even in the same species, the concentration of allelochemicals can differ based on location (e.g., native vs. invasive range). For example, in the case of *S. canadensis*, samples from China had higher allelochemical contents (total phenolics, total flavones, and total saponins) and stronger allelopathic effects than samples from North America (Yuan et al., 2013).

Because of the high environmental impact, wide distribution range, and locally high abundance of invasive *Solidago* species, they should be controlled in Europe (Sheppard, Shaw & Sforza, 2006; Fenesi et al., 2015; Tokarska-Guzik et al., 2015). Furthermore, the habitats invaded by them should be restored (Nagy et al., 2020; Szymura, Świerszcz & Szymura, 2022). A reasonable direction of post-invaded ground restoration is species-rich grasslands (Szymura, Świerszcz & Szymura, 2022). Therefore, the selection of grassland species that are resistant to the allelopathic effects of *Solidago* species seems to be important for effective restoration of *Solidago*-invaded lands.The aim of this study was to evaluate the allelopathic effect of *S. canadensis* and *S. gigantea* plant parts (leaves, stems, inflorescences, roots, and rhizomes) on native grassland species in Central Europe. We hypothesised that (1) the native grassland species differ in terms of seed germination and seedling growth under the allelopathic effects of invasive *Solidago* species, (2) the impacts on germination and growth of native species vary depending on the *Solidago* plant parts used to create water-based extracts, and (3) *S. canadensis* and *S. gigantea* differ in terms of their allelopathic influence on native grassland species. Additionally, we also considered the impact on native species from possible interactions between the three factors (grassland species, extracts of different parts of *Solidago* plants, and *Solidago* species).

Material and methods

Studied species

Solidago canadensis and *S. gigantea*, members of the Asteraceae family, are clonal perennial herbs that can form rhizomes. The inflorescences are fasciculate and thyrsoid, the capitula are small and numerous, and the florets are yellow (McNeil, 1976). Alien *Solidago* species occur in soils with a wide range of fertility and moisture levels, creating single-species stands or co-occurring with each other (Weber, 2001; Weber and Jacobs, 2005). The large-range dispersal is realised by numerous, wind-dispersed seeds, whereas short-range dispersal involves vegetative growth through rhizomes (Weber, 2001). The species are able to create large stands in abandoned fields and meadows, riparian habitats, forest edges, and unmowed road verges (Weber, 2001; Weber and Jacobs, 2005; Fenesi et al., 2015).

Solidago species contain bioactive compounds such as cytotoxic compounds, phenolic compounds, and flavonoids (Wandjou et al., 2020; Shelepova et al., 2020; Kato-Noguchi & Kato, 2022). Twenty-three phenolic compounds of different phenolic origin were identified in the leaves and inflorescences of *Solidago* species, and *S. gigantea* was found to have higher amounts of the compounds than *S. canadensis* (Marksa et al., 2020). Essential oils from *S. canadensis*, composed mainly of mono- and sesquiterpene hydrocarbons, also have phytotoxic potential (Synowiec et al., 2017). The highest concentration of phenolic compounds in *S. canadensis* was found in leaves during the blooming stage and in roots during the early growing stage (Baležentienė, 2015).

Plant material

For each *Solidago* species in the current study, we investigated the impact of different plant parts, using aqueous solutions of dried and ground plant material (Fig. S1). The roots, rhizomes, stems, and leaves were collected in July 2020 and the inflorescences in September

2020 in Wrocław, Poland (51°05′57.3″N, 17°04′39.0″E; 51°09′43.7″N, 17°06′54.0″E; and 51°09′40.9″N, 17°06′40.7″E). Thirteen grassland species native to Europe were used in the study (Table 1). These species are typical and widespread in semi-natural grasslands in Central Europe, are important for pollinators, and grow in similar environmental conditions as *Solidago* species. We used species from different plant families, concentrating on species from *Poaceae* and *Fabaceae* families that are the most common in grasslands. The seeds were obtained from Rieger-Hofmann® GmbH company in a ready-to-use form that did not require additional treatments (e.g., freezing) before sowing.

Allelopathic bioassay

Extracts from the different plant parts of the two *Solidago* species were prepared as 10% aqueous solutions. The concentration was based on previous allelopathic experiments that identified a concentration representative of a high degree of invasion (Butcko & Jensen, 2002; Ravlić, Baličević, & Peharda, 2015; Novak et al., 2018; Sekutowski et al., 2019). To create the solutions, powdered material (10 g) from each part of the plants was mixed with distilled water (100 ml). The mixtures were set aside in the dark for 24 h at room temperature (20-25 °C) and then filtered, using filter paper to remove plant residues from the solutions (Fig. S2).

For the experiment, Petri dishes (78.54 cm^2) with two layers of filter paper were sterilized for 3 h at 120 °C before use. For each grassland species, a sample of 50 seeds was sterilized with 1% NaClO for 15 min, rinsed three times in distilled water, and placed on filter paper to remove excess water. Each sample was then sown onto a Petri dishes and soaked with 8 ml of an extract based on a *Solidago* plant part or with distilled water in the case of the control treatment. Finally, the dishes were closed and placed in a growth chambers (Versatile Environmental Test Chambers SANYO, Model - MLR-352H and FRIOCELL, Model – FC 404 EVO) at 20 °C/10 °C temperature (day/night), with 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetic photon flux density and relative humidity of approximately 70% for 21 days. During the growth period, the Petri dishes were watered with distilled water every 3 days (Fig. S3). Four control treatments for each grassland species and four replications of a particular combination of grassland species (13), *Solidago* species (2), and *Solidago* plant part (5) were prepared (572 Petri dishes in total). For technical reasons, the trials for each species were conducted separately. The experiment was conducted at the Institute of Agroecology and Plant Production, Wrocław University of Environmental and Life Sciences, Poland from October 2020 to September 2021.

Measurements

After 21 days, the experiment was terminated, the number of germinated seeds were calculated. Ten random seedlings were selected for each trial, with fewer seedling selected if germination was poor. The hypocotyl (stem) and root lengths (cm) of the seedlings were measured, using a linear scale and a binocular microscopy. Afterward, the total fresh mass of 10 seedlings from each trial was weighed in grams.

Data analysis

The germination percentage of seeds (GP) was determined for each Petri dish separately by using the following formula (1) (International Seed Testing Association, 1985):

$$\mathrm{GP}\ \% = \frac{\text{Number of seeds germinated}}{\text{Total number of seeds plated}} \times 100$$

The effect of inhibition (EI) on germination, shoot and root length, and seedling weight were calculated in comparison with the control, according to the following formula (2) (Hsu & Chou, 1992):

$$\mathrm{EI} = \frac{\mathrm{C} - \mathrm{T}}{\mathrm{C}} \times 100$$

where C is the measurement associated with the control for a particular species and T is the measurement associated with a particular treatment. Positive values of EI indicated inhibition, values around zero revealed a lack of effect, and negative values showed that treatment had a positive effect on germination or growth.

In statistical analysis, to reduce the pseudo-replication problem (Morrison & Morris, 2000) we considered a Petri dish to be the smallest, independent sample unit; therefore, results of individual measurements were averaged per dish. Additionally, strong germination inhibition in many cases precluded performing measurements other than an assessment of seed germination because of a lack of seedlings. To focus on the main output of the evaluation, we set the values of inhibition in such cases to 100% for statistical analyses. Correlations between measured traits were checked using Spearman's rank correlations coefficient using Past software (Hammer, Harper & Ryan, 2001). Differences in average values between groups were analysed within a generalised linear model framework with glm2 (Marschner, 2011) package in the R environment (R Core Team, 2022), with assumed normal distribution and identity link. The significance of differences between treatments, including the interactions, were tested using analysis of deviance with F test using the stats package (R Core Team, 2022). For the post hoc tests, emmeans (Lenth, 2022) and multcomp (Hothorn, Bretz & Westfall, 2008) packages were used with applied Bonferroni corrections.

To clarify the effect of the experiment on a particular plant species, we also performed additional analyses using the leaves and flowers of both *Solidago* species together. These analyses were prompted by observed significant differences between the leaves and flowers and the remaining plant parts; the differences were the same for both *Solidago* species (see Results). To better visualise the differences between particular species, we applied discriminant analysis, also considering only the effect of flowers and leaves of both *Solidago* species in Past software (Hammer, Harper & Ryan, 2001).

Results

In general, we observed that extracts had a negative effect on seed germination, which was expressed as positive values of inhibition effect (Fig. 1). There were significant correlations between measured traits, showing that inhibition of germination usually also reduces the biomass and the shoot and root lengths of the studied species (Table 2, Fig. 3).

We observed that all experimental treatments and their interactions significantly affected all germination and growth characteristics. The results of statistical comparisons for the entire experiment are shown in Table 3. The detailed results, with *post hoc* comparisons, are presented in the Appendix (Tables S1-S4). The results consistently show that leaves and flowers cause stronger inhibition compared with roots, rhizomes, and stems (Fig. 1 and Fig. S4-S7), regardless of *Solidago* species. Considering only the effects of leaf and flower extracts, we observed significant differences between examined species in germination (Fig. 2) as well as other measured traits (Fig. 3). The species *Trifolium pratense*, *Daucus carota*, *Lolium perenne*, and *Leucanhemum vulgare* were more resistant to the allelopathic effects of *Solidago*, while *Campanula patula*, *Lychnis flos-cuculi*, *Lotus corniculatus*, *Trifolium repens*, *Festuca* *arundinacea*, *Festuca pratensis*, *Festuca rubra*, *Phleum pratense*, and *Poa pratensis* were more sensitive (Fig. 2 and 3).

In spite of the observed germination inhibition, extracts from root, rhizome, and stem for some tested species slightly enhanced the growth of shoots (*Trifolium repens*, *Lychnis flos-cuculi*, *Phleum pratense*, *Trifolium pratense*, *Lolium perenne*, *Leucanhemum vulgare*, *Daucus carota*, *Festuca arundinacea*, and *Festuca pratensis*) and roots (*Daucus carota*, *Lotus corniculatus*, and *Trifolium pratense*) as well as the biomass (*Phleum pratense*, *Festuca arundinacea*, *Trifolium repens*, and *Trifolium pratense*) (Fig. S4-S7).

Discussion

Numerous previous studies report the effect of water extracts from *S. gigantea* and *S. canadensis* on the germination and growth of other plants. Most of the studies focussed on *S. canadensis* (e.g. Wang, Wu & Jiang, 2019; Wei et al., 2020a; Wei et al., 2020c; Zandi et al., 2020), while a lower number focussed on *S. gigantea* (e.g. Pal et al., 2015; Baličević, Ravlić & Živković, 2015; Sekutowski et al., 2019). The results are inconsistent because target species, extract concentrations, and tissues from which the extracts were produced varied between studies.

Our results revealed that the tested grassland species differ in susceptibility to *Solidago* allelopathy, which confirms our first hypothesis. The most resistant species in our experiment were *Daucus carota*, *Leucanhemum vulgare*, *Lolium perenne*, and *Trifolium pratense*. Chen, Mei and Tang (2005) and Megenhardt (2015) observed that grasses were more sensitive than forbs and legumes to the allelopathic impact of *S. canadensis*. However, in our experiment we did not observe such a pattern, and between *Trifolium repens* and *T. pratense*, legumes belonging to the same genus, *T. pratense* was more resistant than *T. repens*. Species detected here as being more resistant to the allelopathic effects of *Solidago* are considered useful in restoring semi-natural grasslands (da Silva, Overbeck & Soares, 2017; Thiébaut, Tarayre & Rodríguez-Pérez, 2019; Zandi et al., 2020). The obtained results suggest that the above-mentioned species should be prioritised when grasslands are restored on sites invaded by *Solidago*.

Different parts of *Solidago* were assumed to differ in their allelopathic effect (Marksa et al., 2020; Kato-Noguchi & Kato, 2022; Zhu et al., 2022). Allelopathic studies have most often used aboveground parts such as leaves, stems, and flowers, with leaves being most commonly found to have an effect (Wang, Wu & Jiang, 2019; Wei et al., 2020a; Wei et al., 2020c; Zandi et al., 2020; Kato-Noguchi & Kato, 2022; Zhu et al., 2022). Direct comparisons revealed that aboveground parts of *S. canadensis* had a significant allelopathic effect, but the effect of belowground parts was not significant (Yu et al., 2022). It was also observed that extracts from *S. canadensis* rhizome stimulated the germination of *Raphanus sativus* seeds and lengthened their shoots (Anžlovar & Anžlovar, 2012). In contrast, other studies showed that *S. canadensis* rhizome extract inhibited seed germination and root growth of several native Chinese plant species (Chen, Mei & Tang, 2005) and *Zoysia japonica* (Sun et al., 2022). In the case of *S. gigantea*, water extracts of its rhizomes and roots increases the dry biomass of *Echinochloa crus-galli* and *Amaranthus retroflexus* (Sekutowski et al., 2019), while leaf and stem extracts reduced the growth of *E. crus-galli*. However, Pal et al. (2015) showed that root extracts reduced the shoot growth of plant species native to Europe. The observed differences could be due to different reactions of specific target species as well as different concentrations of the extracts. When the extract was at a low concentration (1%), it could even increase the growth of lettuce (Wang, Wu & Jiang, 2019; Wei et al., 2020b). In addition, Ye et al. showed that a water extract of *S. canadensis* shoots up to a concentration of 12.5% could increase the growth of *Zea mays* (Ye, Meng, & Wu, 2019). However, it should be noted that *Z. mays* seeds are exceptionally large, and the allelopathic effect could weakened due to good isolation of the embryo. In our study, 10% extracts of leaves and flowers consistently showed stronger effects compared with extracts of rhizomes, roots, and stems without leaves, regardless of the *Solidago* species used (Fig. 1). Additional noise in data could be also related to differences in the allelopathic effect of leaves and stems. If stems with leaves are used for preparing solutions (e.g. Baličević, Ravlić & Živković, 2015; Sekutowski et al., 2019; Ye, Meng, & Wu, 2019), then the uncontrolled proportion of leaf versus stem biomass could change the results obtained. There is great variability in the chemical composition of potentially allelopathic substances between particular parts, seasons and geographical locations in the case of *Solidago* species (See Marksa et al., 2020; Kato-Noguchi & Kato, 2022; Zhu et al., 2022). Therefore, it is impossible to attribute the allelopathic effect observed here to particular chemical substances and differences in their concentrations between plant parts.

The results also seem to confirm the general hypothesis that allelopathic effects differ between the examined *Solidago* species (Table 2); however, we also observed strong effects associated with interactions, which impeded making straightforward conclusions. Previous studies reported inhibition of seed germination and seedling growth in numerous plant species caused by allelopathic effects of both *S. canadensis* (Wang, Wu & Jiang, 2019; Wei et al., 2020a; Wei et al., 2020c; Zandi et al., 2020) and *S. gigantea* (Pal et al., 2015; Baličević, Ravlić & Živković, 2015); however, Marksa et al. (2020) found that the leaves of *S. gigantea* contained more active antioxidant compounds than leaves of *S. canadensis*, which suggested that the first species had a stronger allelopathic potential. We assumed that comparing the differences in allelopathic effects of extracts from various parts of *Solidago* and the differences in the susceptibility of target species, the differences between the two invasive species would have minor practical implications. In practice, the results of a pot experiment showed that *S. canadensis* and *S. gigantea* have similar competitive abilities (Szymura & Szymura, 2016).

Conclusions and practical implications

The results of our investigation yield some practical implications. First, to reduce the allelopathic effect of *Solidago* during habitat restoration, the aboveground parts should be removed, including fallen leaves, since the leaves have a strong allelopathic effect. The effects of roots and rhizomes seem to be of secondary importance, and the results of other experiments have shown that restoration is possible without extraction of the belowground parts (Szymura, Świerszcz & Szymura, 2022). Second, given the expected allelopathic effects of *Solidago*, relatively resistant species such as *Daucus carota*, *Leucanhemum vulgare*, *Lolium perenne*, and *Trifolium pratense* should be favoured for site restoration. Third, the difference in allelopathic effects of leaves versus stems suggest that these two plant parts should be considered separately, and not mixed, in allelopathic trials. Our results suggest that hard-to-control differences in fractions of leaves and stem biomass in a plant material used to produce extracts may significantly influence experimental outcomes.

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Table 1(on next page)

Common grassland species used for the experiment.

Table 1. Common grassland species used for the experiment.

No	Species	Abbreviation	Family
1	*Daucus carota* L.	DC	Apiaceae
2	*Leucanthemum vulgare* Lam.	LV	Asteraceae
3	*Campanula patula* L.	CP	Campanulaceae
4	*Lychnis flos-cuculi* L.	LF	Caryophyllaceae
5	*Lotus corniculatus* L.	LC	Fabaceae
6	*Trifolium pratense* L.	TP	Fabaceae
7	*Trifolium repens* L.	TR	Fabaceae
8	*Festuca arundinacea* L.	FA	Poaceae
9	*Festuca pratensis* Huds.	FP	Poaceae
10	*Festuca rubra* L.	FR	Poaceae
11	*Lolium perenne* L.	LP	Poaceae
12	*Phleum pratense* L.	PhP	Poaceae
13	*Poa pratensis* L.	PoP	Poaceae

Table 2 (on next page)

Results of Spearman's rank correlations (lower part) and associated p values (upper part) among analysed traits.[a]

[a]Germ_inhib = seeds germination inhibition; Shoot_inhib = seedlings shoot length inhibition; Root_inhib = seedlings root length inhibition; Weight_inhib = seedlings weight inhibition.

Table 2. Results of Spearman's rank correlations (lower part) and associated p values (upper part) among analysed traits.[a]

	Germ_inhib	**Weigh_inhib**	**Root_inhib**	**Shoot_inhib**
Germ_inhib		<0.001	<0.001	<0.001
Weigh_inhib	0.77		<0.001	<0.001
Root_inhib	0.75	0.83		<0.001
Shoot_inhib	0.60	0.69	0.56	

[a]Germ_inhib = seeds germination inhibition; Shoot_inhib = seedlings shoot length inhibition; Root_inhib = seedlings root length inhibition; Weight_inhib = seedlings weight inhibition.

Table 3 (on next page)

Results of statistical comparisons (F and p) for seed germination (Germ_inhib), inhibition of seedling shoot (Shoot_inhib), root (Root_inhib), and weight (Weight_inhib), and their interactions ($p < 0.05$).[a]

[a]df = degree of freedom.

Table 3. Results of statistical comparisons (F and p) for seed germination (Germ_inhib), inhibition of seedling shoot (Shoot_inhib), root (Root_inhib), and weight (Weight_inhib), and their interactions ($p < 0.05$).[a]

		Germ_inhib		**Shoot_inhib**		**Root_inhib**		**Weight_inhib**	
	df	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**
Solidago	1	6.3	0.012	13.3	<0.001	4.0	0.045	14.1	<0.001
Part	4	458.9	<0.001	148.8	<0.001	501.7	<0.001	474.4	<0.001
Species	12	149.5	<0.001	67.8	<0.001	98.3	<0.001	63.7	<0.001
Solidago **× Part**	4	12.5	<0.001	6.1	<0.001	15.5	<0.001	10.9	<0.001
Solidago **× Species**	12	4.6	<0.001	13.3	<0.001	3.2	<0.001	2.9	0.001
Part × Species	48	12.2	<0.001	6.8	<0.001	13.9	<0.001	8.4	<0.001
Solidago **× Part × Species**	48	3.4	<0.001	3.9	<0.001	3.7	<0.001	2.6	<0.001

[a]df = degree of freedom.

Figure 1

Inhibition of grassland species germination caused by leaf, flower, root, rhizome, and stem extracts of *Solidago* species, and results of tests (F and p).

The different letters above boxes indicate significant differences detected by post hoc comparisons.

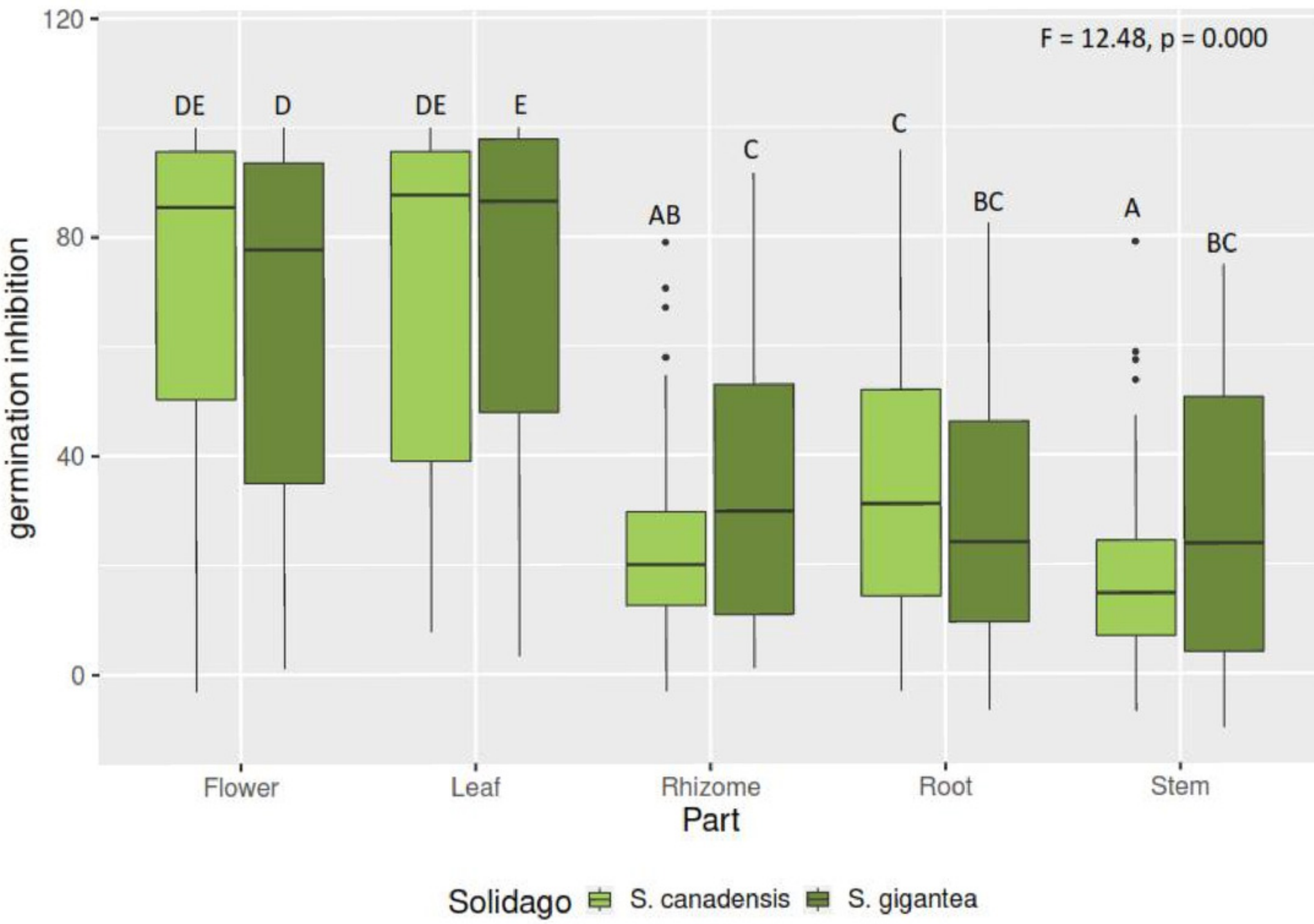

Figure 2

Inhibition of grassland species germination caused by *Solidago* allelopathy, and results of tests (F and p).

Inhibition of grassland species germination caused by *Solidago* allelopathy, and results of tests (F and p). The different letters above boxes indicate significant differences detected by post hoc comparisons. Species name abbreviations are presented in Table 1. The graph shows the results for combined leaf and flower extracts only.

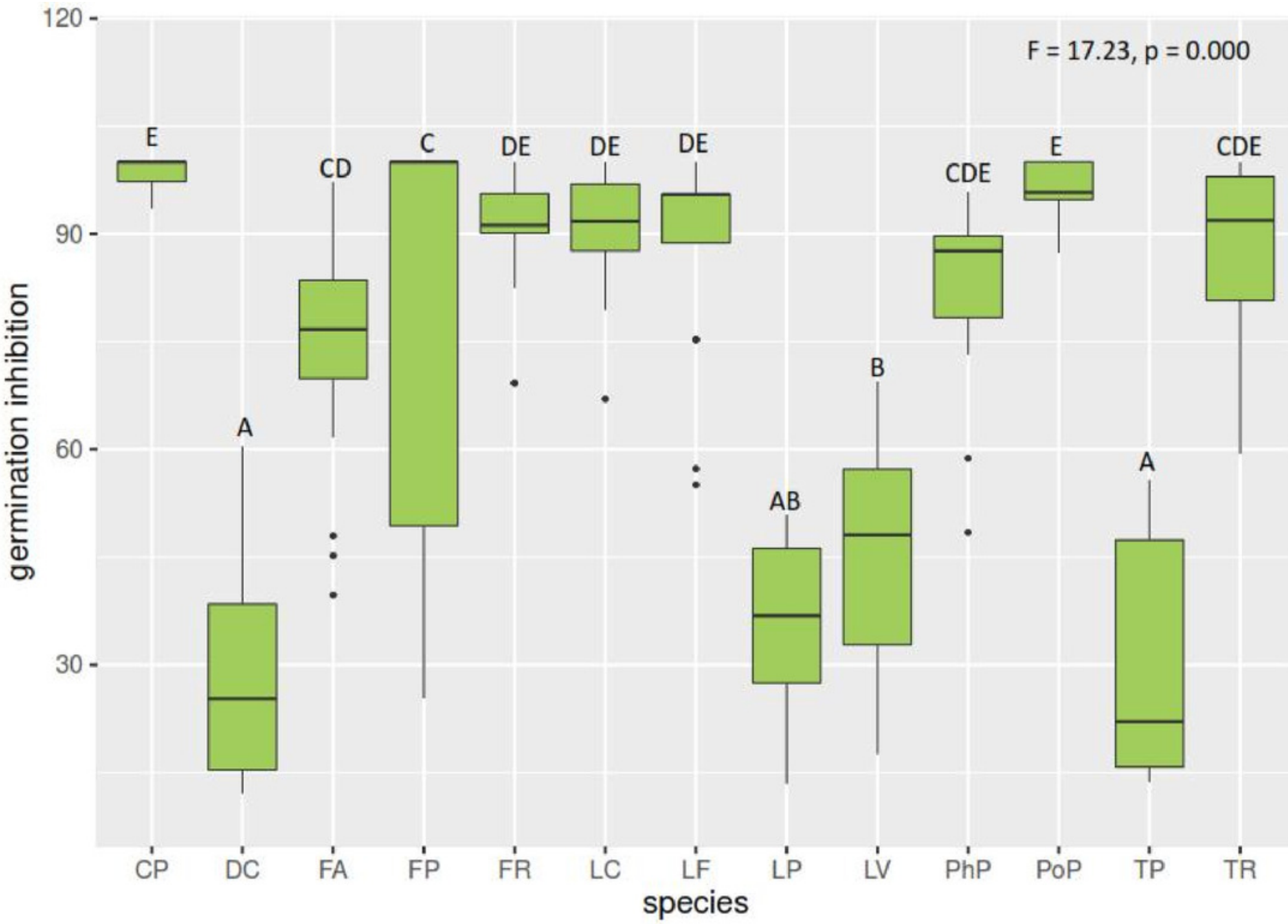

Figure 3

Discriminant analysis for *Solidago* allelopathy inhibition of seed germination, seedling root length, and shoot length and weight of tested grassland species.

Species name abbreviations are presented in Table 1. The graph shows the results for merged leaf and flower extracts only.