Трансформация экосистем
Ecosystem Transformation

ISSN 2619-094X Print
ISSN 2619-0931 Online
www.ecosysttrans.com

Review

Study isssues of invasive species of the genus *Solidago*

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Received: 29.10.2021
Revised: 28.12.2021
Accepted: 10.01.2022
Published online: 12.05.2022

DOI: 10.23859/estr-211029
UDC 581.552/504-2:582.991

Translation by D.M. Martynova

Abstract. The impact of invasive species on the ecosystems belongs to the most important environmental problems. Representatives of the genus *Solidago* actively invade various plant communities. About 2300 literary sources were analyzed in order to determine the main tasks for the researchers of invasive species of this genus and to highlight the most relevant issues. Ambiguous evidence of the inhibitory effect of goldenrod on native flora species has been observed. Some studies report on the invasion of species of the genus *Solidago* and the displacement of species of local flora in various natural and climatic conditions. Opposite opinion states that the main changes relate not to taxonomic, but to the functional diversity. The allelopathic effect may be influenced both by edaphic factors and by the stage of plant development, as well as by the flora diversity in different regions and by the mutual influence of these factors. Most likely, essential oil components (terpenes and terpenoids) have an inhibitory effect on competing plants and soil microorganisms.

Keywords: *Solidago canadensis, Solidago gigantea*, plant invaders, soil biota, competitive interactions of organisms, allelopathy.

To cite this article. Zagurskaya, Yu.V., 2022. Study isssues of invasive species of the genus *Solidago*. *Ecosystem Transformation* **5** (2), 42–54. https://doi.org/10.23859/estr-211029

Introduction

One of the most urgent environmental problems at present is the invasive influence of naturalized alien plants on natural ecosystems, which leads to disruption of the natural development and restoration of biocenoses.

According to some authors, goldenrod invasion affects the functional biodiversity more than the taxonomic diversity, since this species forms thickets in anthropogenically transformed areas and does not spread to stable plant communities (Koldomova and Naumenko, 2020; Wang et al., 2019a, b). At the same time, there is evidence of a direct negative impact of *Solidago canadensis* L. on plant communities, where this species does not only dominate, but also promotes the introduction of other native or adventitious weeds. As a result, there is a significant decrease in floristic diversity and suppression of the development of potential dominants (Chen et al., 2013; Fenesi et al., 2015; Shmelev and Pankrushina, 2019; Wang and al., 2019a; Zubek and al., 2020), as well as a concomitant decline in the faunal diversity and decrease in the abundance of some economically valuable insects (Čerevková et al., 2020; Fenesi et al., 2015).

In the Republic of Belarus, active introduction of *S. canadensis* into various biotopes has been observed when assessing its distribution and growth peculiarities; most of the studied phytocenoses, where alien transforming species dominate, are confined to historically developed anthropogenic landscapes (Gusev, 2019). In addition, Canada goldenrod inhabits open wastelands and light deciduous urban forests, which are not subject to significant anthropogenic pressure (Chumakov and Neverdasova, 2017). In Western Siberia, mass invasion of *S. canadensis* occurs primarily when the fertile soil layer is disturbed as a result of plowing/digging or garbage dumps. This mainly takes place at the areas disturbed relatively recently, without affecting previously reclaimed habitats or ecotopes where active restoration of vegetation has started before the penetration of goldenrod (Ufimtsev, 2018). In the European part of Russia, a significant part of the goldenrod populations is associated with an increase in the area of arable land taken out of agriculture cycle (Savin and Shishkonakova, 2021). In Poland, when studying abandoned agricultural lands, an active colonization of *S. canadensis* on recent deposits (2–4 years) and its almost complete disappearance on a 17-year-old wasteland have been observed (Skrajna et al., 2012).

When considering the invasion rate, *Solidago canadensis* and *S. gigantea* Aiton are less aggressive comparing to some other invaders, especially annuals (*Impatiens parviflora* DC., *I. glandulifera* Royle, *Echinocystis lobata* (Michx.) Torr. & A. Gray) and trees (*Robinia pseudoacacia* L., *Reynoutria japonica* Houtt., *Juglans regia* L.) (Bomanowska et al., 2019; Lenda et al., 2019; Zelnik and al., 2020). Moreover, communities with *Solidago* differ from the communities, where other alien species dominate, by the greatest flora doversity (Abramova and Golovanov, 2019). However, most researchers attribute goldenrod not just to invasive species, but to transformers that directly change natural communities (Burlutskiy et al., 2019; Gusev, 2015; Mysliwy et al., 2020; Richardson and al., 2000; Shmelev and Pankrushina, 2019; Stefanowicz and al., 2019; Teixeira and al., 2020; Tokarska-Guzik and al., 2010) and inhibit the restoration of anthropogenically disturbed soils (Gusev, 2019). Active invasion of *Solidago canadensis* and *S. gigantea* is observed mainly in the areas disturbed more than 5 years ago (Brzank et al., 2019); in this case, floristic diversity decreases for a very short time, ~ 2 years (Shelepova et al., 2019). It is assumed that the negative impact on floristic diversity is directly determined by the area of projective cover of *S. canadensis* (Gusev, 2021).

The articles published to date on the species of the genus *Solidago* are mainly devoted to particular issues. Our study aims to identify the main environmental problems and the most relevant aspects of the study for invasive species of the genus *Solidago.*

Materials and methods

The literary sources were searched through several international databases (query 'Solidago', sorting by publication date): ScienceDirect (Elsevier Publishing House), Web of Science (Clarivate Analytics), and Russian bibliographic database RINC (www. https://elibrary.ru/) (Scientific Electronic Library LLC). The relevant papers were analyzed by combining the results and systematizing by areas. In total, about 2300 sources were considered.

Plant taxa names are given in accordance with World Flora Online (2021).

Invasive taxa of *Solidago* genus

Solidago canadensis (s.l.) (Canada goldenrod) and *Solidago gigantea* (giant goldenrod) are herbaceous perennial plants of North American origin, listed in the Black List of Russia (Chernaya Kniga..., 2016; Vinogradova et al., 2010; Vinogradova et al., 2020). Earlier, these species were used in experiments on disturbed land reclamation. There was reported on intensification of hybridization processes in the secondary (invasive) range (Ellstrand and Shierenbeck, 2006) and the active naturalization of new, more resistant taxa (Galkina and Vinogradova, 2019). In particular, these are *S.* × *niederederi* Khek, a hybrid of *S. canadensis* and *S. virgaurea* L., known from Western and Eastern Europe (Karpavičiené and Radušiené, 2016) and noted in the European part of Russia. In 2021, these plants have been found in Tula Oblast in addition to Kaliningrad and Pskov regions, where this species was registered earlier. The hybrid nature of *S.* × *niederederi* individuals from these populations was confirmed by molecular genetic methods (Galkina and Vinogradova, 2019; Galkina and Vinogradova, 2020; Lysenkov and Galkina, 2021). It is assumed that *S.* × *niederederi* populations reproduce as a result of new acts of hybridization of parental species (Lysenkov and Galkina, 2021).

Morphobiological features of invasive *Solidago* species

S. canadensis is the most studied species. Much attention should be paid to its adaptive abilities: the species resists diseases, harsh winters and long summer droughts, it is practically avoided by pests. *S. canadensis* prefers open areas, reducing invasive activity in low-light conditions (Dubovik et al., 2019), being generally shade-tolerant (Balf, 1992; Peshchanskaya, 2009). The reproductive potential of Canada goldenrod also depends on the illumination; the seeds germinate better in the light (up to 96%) than in the dark (21% and less) at 20 °C (Nikolaeva et al., 1985). *Solidago* fruit is a narrow-cylindrical, ribbed achene. One middle-aged plant can simultaneously form about 30 generative shoots; small flowers are arranged in anthodes, forming complex multi-level inflorescences up to 40 cm long; a huge number of small, light seeds develop. Both invasive species of goldenrod are rhizomatous (Semple and Cook, 2006; Werner and al., 1980), they easily propagate vegetatively. As a rule, active reproduction by both types ensures the rapid growth of populations and fast colonizing of territories when introduced into wild communities (Daineko and Timofeev, 2018). Plant achieves the maximum reproductive degree (both by seeds and vegetative) at the 4^{th}–6^{th} year of life (Skrajna et al., 2012).

Most significant interspecies differences between *S. canadensis* and *S. gigantea* are associated with the structure of rhizomes, leading to different growth patterns. *S. canadensis* forms separate fairly dense groups, while thickets of the long-rhizomatous *S. gigantea* are usually monodominant and more extended. Inflorescence density, pappus color, and pubescence of upper stem are also significant as distinguishing features for these two taxa (Ustinova and Lysenkov, 2020; Weber and Jakobs, 2005; Werner et al., 1980).

The morphological diversity of invasive *Solidago* species is highlighted by many researchers. The sizes of aboveground plant organs are especially variable, including at the intra-taxon (population) level; they depend on the climate, soil parameters, and the diversity of phytocenoses populated by these species (Dong and He, 2019; Hejda et al., 2019; Jacobs et al., 2004; Sakaguchi and al., 2019; Weber, 1997; Weber and Jacobs, 2005; Weber and Schmid, 1998). Total adaptive capacity of these plants does not correlate with polyploidy, but with an increase in the mycorrhizal chromosome set; as a result, adaptive capacity is associated with increased metabolism in the rhizosphere (Wan et al., 2020; Wu et al., 2019). No relationship has been found between increased plant size and increased competitiveness (Pal et al., 2020).

Impact of invasive *Solidago* on soils and soil biota

The interaction of invasive plants and soil microorganisms is one of the most studied issues (Reinhart and Callaway, 2006); the invasion of *S. canadensis* has a positive effect on some soil characteristics, such as soil microbial biomass, respiration, and use of carbon sources, etc. (Liao et al., 2011), when the development of both local plants and soil pathogens is inhibited (Zhang et al., 2009b). Root exudates of *S. canadensis* stimulate the germination of *Kummerowia striata* Thumb seeds (Fabaceae family), this phenomenon is explained by the indirect effect of arbuscular mycorrhiza on fungal communities; treatment of mycorrhizal cultures with inoculums increases the biomass and phosphorus concentration in the aboveground parts of *S. canadensis* (Yang et al., 2014). When studying the allelopathic effect, it has been noted that if soil pathogens are absent, tomato seedlings are inhibited by *S. canadensis* plants, although when *Pythium ultimum* Trow is present, tomato seedling suppression is reduced at the plots with *S. canadensis* compared to control (Zhang et al., 2011). However, a statistically significant decrease in the diversity of arbuscular mycorrhiza fungal communities has been reported as a result of *S. canadensis* invasion, regardless of soil parameters (Řezáčová et al., 2021).

According to the data obtained by the method for measuring the N_2 fixation rate *in vitro, S. rigida* L. and *S. canadensis* have the strongest acetylene reduction out of the 7 species of the genus *Solidago* (McKone and Biesboer, 1986). However, the content and rate of nitrogen uptake does not increase (Yang et al., 2014). The development and influence of *Solidago* root exudates depends directly on the composition and abundance of soil microorganisms, especially fungi of arbuscular mycorrhiza (Jin et al., 2004; Sun and He, 2018), which should be taken into account when performing experiments in a sterile medium, such as autoclaving, etc. (Sun and He, 2018). It should be noted that plants do not depend much on the composition and structure of the substrate, but the best and longest development of *Solidago canadensis* is achieved on heavy (rich) soils (Bornkamm and Hennig, 1982).

Along *S. gigantea* is usually noted together with *S. canadensis* as the most successful invaders of new territories, its positive effect on the fungi biomass and the fungi/bacteria ratio has been noted (Stefanowicz et al., 2019). However, no unequivocal conclusions about its ability to stimulate or suppress the development of microorganisms have been proposed (Scharfy et al., 2010; Zhang and al., 2009a).

Researchers suggest that the N:P ratio in the environment is one of the limiting factors in determining the competitiveness of plants, which is due to the different requirements of species for these chemical elements and the redistribution of resources due to invasion process (Wan et al., 2018).

There is evidence that the invasion of *S. canadensis,* compared with the native dominants of pioneer communities, accelerates the cycle of macroelements due to an increase in aboveground productivity and accumulation of nutrients, which has a positive effect on soil processes (Ye et al., 2019). However, in this study, all natives are the species of the Poaceae family, so the differences may be explained by their taxonomic features. In general, the substrate quality decreases as a result of *S. canadensis* invasion, which may lead to a reduce in reproduction of competing species (including the factor of nitrogen availability) and a concomitant increase in the root mass of the invader (Ren et al., 2019; Ren et al., 2020a; Zubek and al., 2020). As the soil temperature and nitrogen concentration increase, the productivity of *S. canadensis* does so, increasing the risk of its successful invasion (Ren et al., 2020b; Zhou et al., 2019). The soil pH increases most strongly after the invasion, this may also explain the change in some microbiological parameters of the soil (Bobuľská et al., 2019) It is hypothesized that some chemical properties of the soil and microbial communities may be used as indicators of the population density of invasive *S. canadensis* (Zhang et al., 2009a).

Competitive plant interactions (allelopathy)

The allelopathic properties that promote invasion are among the most important features of the species potentially dangerous for ecosystems (Bais et al., 2003; Gao et al., 2018; Hierro and Callaway, 2003; Kondratiev and Larikova, 2018; Kondratiev et al., 2017; Rice, 1984; Ridenour and Callaway, 2001; Zhang et al., 2019a). The inhibitory effects of *S. canadensis* on the development of native plants and explanations of these mechanisms are quite different; in addition, ambiguous results are obtained in both laboratory and mesocosm (microcosm) experiments (Bruckner et al., 1995; Del Fabbro and Prati, 2015a, b; Stefanowicz and al., 2019). Chinese scientists note that the negative effect of *S. canadensis* seedlings on plants of local origin (*Agropyron cristatum* (L.) Gaertn., *Cichorium intybus* L., *Elymus dahuricus* Turkish. ex Griseb., *Poa pratensis* L., and *Setaria plicata* (Lam.) T. Cooke) turns out to be much weaker than on the plants originated from North America: *Achillea millefolium* L., *Calamagrostis canadensis* (Michx.) P. Beauv., *Carex vulpinoidea* Michx., *Elymus canadensis* L., and *Poa secunda* J. Presl (Sun and He, 2018).

The influence of root exudates of *S. canadensis* from various populations of Europe and America to European species (*Arrhenatherum elatius* (L.) Presl., *Trifolium pretense* L., *Lythrum salicaria* L., *Stachys officinalis* (L.) Trevis., *Dactylis glomerata* L. and *Achillea millefolium* L.), growing together with *S. canadensis* generally at the edge of the thicket (except *A. millefolium* with the least inhibitory effect), is stronger in plants from European (invasive) populations compared to local plants (Abhilasha et al., 2008), supporting similar results obtained for other invasive plants (Mallik and Pellissier, 2000; Prati and Bossdorf, 2004).

The result of allelopathic action may be influenced not only by edaphic factors, but also by the stages and development of plants, their origin, the composition of native plants in different regions, as well as the mutual influence of these factors (Del Fabbro and Prati, 2015a; Prati and Bossdorf, 2004; Sun and He, 2018).

According to one of the latest hypotheses about the success of alien species invasion (Novel weapons), the organic substances, produced by invader plants into the soil and previously unknown to natural communities (most often, these are essential oils), may have a decisive importance (Callaway and Aschchoug, 2000).

The variability of the chemical composition of the considered goldenrod species is relatively low (Radusiene et al., 2015). The most studied compounds are polyphenols, including polysaccharide-polyphenol conjugates (Kraujalienė et al., 2017), and terpenes, which are associated with the main medicinal properties of *Solidago* plants*:* antioxidant, bronchodilator, hypotensive, antimicrobial, antifungal, and antiproliferative (Apáti et al., 2003; Bonaterra and al., 2019; Deng et al., 2015; Gomes et al., 2018; Liu and al., 2018; Saluk-Juszczak et al., 2010; Šutovska et al., 2013).

Attempts to explain the effects of *S. canadensis* on tomato seedlings by the presence of saponins and phenolic compounds through an allelopathic effect on the soil root rot pathogen *Pythium ultimum* (Zhang et al., 2011) are not sufficiently substantiated. Plant phenolic compounds (chlorogenic acid, rutin, hyperoside, isoquercitrin, quercitrin, etc.) are adaptive substances that are not significant for invasive spread (Radusiene et al., 2015). In addition, the presence of these compounds in the soil is more likely a consequence of the partial decomposition of soil organic compounds (humic substances) and/or leaching of plant roots from microscopic remains, but not the result of their excretion by the roots of living *S. canadensis* plants.

When studying the allelopathy of invasive species, the mechanisms of action of allelochemicals are important. This may refer to immediate effect, or "Novel weapon" (Callaway and Aschchoug, 2000; Callaway and Ridenour, 2004)), or to that delayed in time (allelopathic heritage), where "hereditary" effects may persist after the death or removal of invaders, affecting communities in the long term (Inderjit et al., 2011) directly or indirectly through the regulation of soil microflora (Del Fabbro and Prati, 2015b). The most likely allelopathic agents of *Solidago* are terpenes and terpenoids (Abhilasha et al., 2008), as well as volatile aromatic compounds. About 80 components belonging to these groups, mainly belonging to the classes of di-, tri-, and sesquiterpenes have been found in *S. canadensis* and other species of this genus *(*Amtmann, 2010; Chaturvedula et al., 2004; Kalemba and Thiem, 2004; Kasali and al., 2002). An indirect effect on soil microflora may also be provided by terpene derivatives, such as cyclocolorenone, which is found in large quantities in the essential oil of *S. gigantea* (Chaturvedula et al., 2004; Stefanowicz et al., 2019).

Therefore, the study of the allelopathic effects of invasive species does not always support the theory of the suppression of the growth of native plants due to the release of chemical compounds into the soil and the stimulation of the development of pathogenic soil biota (Del Fabbro and Prati, 2015a) or via their effect on soil nitrogen-fixing bacteria (Wang et al., 2018).

Changes in the phytocenose structure caused by imbalance in faunal complexes during *Solidago* invasion

As a rule, the degree of the impact of a particular change on the ecosystem is assessed by the degree of disruption in the functioning of adjacent structures and by the consequences for environmental well-being and human economic activity.

When studying invasive plant communities, changes in the composition and structure of ecosystems are noted as a result of the formation of new mechanisms of interaction with local biota (Aerts et al., 2017; Wolfe and Klironomos, 2005; Zhang et al., 2019b). However, all the results obtained and the hypotheses expressed so far are scattered and united only by the variability of the observed effects on the growth, behavior, diversity, and productivity of organisms and communities, even in similar or parallel experiments (Vilà et al., 2011).

When studying thickets of invasive goldenrod species in ruderal urban areas in Germany (Karlsruhe), an increase in the number of crab spiders (Thomisidae) has been noted, but these floristic changes did not affect the total abundance and taxonomic composition of Araneae (Bauer et al., 2021).

In some cases, invasion of *S. canadensis* may negatively affect the abundance of ground beetles and bees, including honeybees, and other groups of pollinators (Fenesi et al., 2015; Groot and al., 2007; Moron et al., 2009). The main mechanism of the impact of invasive *Solidago* species on native plant communities is the invader ability to compete with native species for pollinating insects (Sun et al., 2013). Presumably, this is due to the greater height of the plants, the size of the inflorescences, and the duration of flowering. Interestingly, pollinating insects prefer *S. gigantea plants* over *S. canadensis* with equal opportunities for choice, this may be due to different distribution patterns of these species (Ustinova and Lysenkov, 2020).

Conclusions about the modifying effect of goldenrod on the soil fauna of natural biogeocenoses are not always confirmed by modern studies. In particular, a comparison of communities of soil arthropods under the thickets of *S. gigantea* and of native plants evidences on a high taxonomic similarity for these communities (Ustinova et al., 2021). The influence of *S. gigantea* on the characteristics of the soil nematode community has been reported; however, the changes in various ecosystems are quite ambiguous (Čerevková et al., 2020).

Issues of biodiversity conservation and restoration

Regardless of the penetration mechanisms and the ways of influencing the host ecosystems, invasive transforming species should become a priority for ecological control activities (Khorun, 2014). Due to the active distribution of invaders, the use of ever-increasing raw material reserves of phytomass of invasive *Solidago* species may attract attention. Essential oils from *S. gigantea* and *S. canadensis* may be used as a material for the production of soil pesticides, because they have an insecticidal effect, but they are not toxic to earthworms *Eisenia fetida* (Savigny, 1826) (Benelli et al., 2019).

There are no natural mechanisms for regulating the distribution of goldenrod species. In particular, there has been reported on insignificant grazing of *S. canadensis* and *S. gigantea* by snails and slugs and the inability of the latter to suppress the expansion of invasive plants species in natural populations (Ustinova, 2019). Despite a wide range of conditions for the distribution of invasive goldenrod species, their introduction is limited in highland areas. The last has been explained by low-temperature climatic conditions (Perera et al., 2021); however, the data on the types and structure of soils for the places, where *S. canadensis* and *S. gigantea* are present/absent, are not sufficiently detailed in this article. The dispersal of *S. canadensis* is closely associated with the human factor, in contrast to *S. gigantea.*

The measures to limit the introduction and spread of invasive plants are needed for normal agricultural circulation (Kozak and Pudełko, 2021) or for alternative use of fallow land, especially former arable lands. The establishment and maintenance of integrated coastal protected areas of sufficient width along rivers is recommended (Zelnik et al., 2020). In a long-term experiment, the invertebrate herbivores have a significant effect on the population dynamics of *S. canadensis,* however, it took six years or even more to track it undoubtedly (Korell et al., 2019). The combined effect of two different invaders (by example of *Juglans regia* and *Solidago canadensis)* may be less detrimental to succession process than the impact of each species separately (Lenda et al., 2019).

These plants may be used as indicators of hydrocarbon pollution (Chapman et al., 2013; Ficco et al., 2010). Currently, the whole plants and the aboveground part of the *Solidago canadensis* are considered as organic fertilizer (Izydorczyk et al., 2020; Tang et al., 2020), bioaccumulator for phytoremediation of soils contaminated with polychlorinated biphenyls (PCBs) and sorbent for the removal of Cd (II) from wastewater (Zhang et al., 2018), biofuel (Ciesielczuk et al., 2014; Zihare and al., 2018), as well as a source for the production of herbal medicines and dietary supplements (Amtmann, 2010; Chaturvedula et al., 2004; Kalemba and Thiem, 2004; Kasali and al., 2002).

Conclusions

Three taxa of the genus *Solidago* are invasive: North American species *S. canadensis* and *S. gigantea,* as well as *S.* × *niederederi,* which is of hybrid origin (*S. canadensis* × *S. virgaurea)*. They occupy mainly anthropogenically disturbed communities; their ability to penetrate into natural biocenoses, as well as to affect restorative succession and the development of agrocoenoses, depends significantly on climatic and edaphic factors, as well as the flora richness at a particular territory.

An analysis of sources from international scientific reference databases on the chemistry, biology, and ecology of *Solidago* species makes it possible to state that the influence of limiting soil factors and the composition of the soil microbiota on the competitive interactions of plants are the most actively studied issues nowadays. It is difficult to draw unambiguous conclusions about the effect of the root exudates of these plants on the soil microflora, since the results of these studies depend also on the initial soil biota, and the medium sterilization leads to disruption of plant development.

The mechanisms of action and the allelopathic potential of invasive plant species differ significantly depending on the objects of influence and the stage of plant development. Most likely, essential oil components (terpenes and terpenoids) are allelopathic agents of *Solidago* species. The hypothesis about the inhibitory effect of phenolic compounds on plant objects is unfounded.

Acknowledgments

The author expresses sincere gratitude to Dr. Elena Yu. Babaeva (All-Russian Scientific Research Institute of Medicinal and Aromatic Plants) and anonymous reviewers for valuable comments. Thanks to Olga V. Ryzhkova (Paleontological Institute RAS, Moscow) for highly professional editing of the article.

Funding

The study was carried out within the State Task no. 0286-2021-0010 (EGISU NIOKTR no. AAAA-A21-121011590010-5).

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