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Secondary metabolite accumulation and phytotoxicity of invasive species *Solidago canadensis* L. during the growth period

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ABSTRACT

Solidago canadensis L. (*Asteraceae*) is successful invader specie worldwide. We determined the biochemical parameters of *S. Canadensis*, involved in its invasion success. In its aqueous extracts, the total phenolics content (TPC) ranged between 0.968 mg ml^{-1} to 23.591 mg ml^{-1} depending on the plant ontogenetic stage, plant part and extract concentration (r = -0.7). The extract significantly inhibited the germination of rapeseed (r =-0.8) and ryegrass (r =-0.5) across different levels of TPC. Due to accumulated allelochemicals, the invasive *S. canadensis*, might acquire distribution advantage in new territories outside the native habitat range, through the inhibitory effects on germination of native plant species.

Key words: Allelopathy, *Brassica napus*, germination, *Lolium perenne,* phenolics, phytotoxicity, secondary metabolites, *Solidago canadensis*

INTRODUCTION

The biochemical interactions in ecosystems were reported long ago, but Fraenkel [(1959) (16)] emphasised the ecological significance of secondary metabolites (16). The metabolites are involved in different interactions between the plants, hence, it is necessary to fully understand the plant responses in ecosystem (24,36,44). Currently, the chemo-mediator role of secondary metabolites has been reported as multifunctional regulation of structure and functions of both plants and ecosystem (19,32). The phenomenon of allelopathy is alternative explanation for the establishment and spread of invasive species in undisturbed communities, achieved through release of novel and never experienced before phytochemicals by the invader in the invaded ecosystem. These allelopathic compounds are phytotoxic and reduce the growth of neighbouring plants that are not co-evolved with invader. Studies done in different countries confirm certain peculiarities of allelopathic species (6,17,21,27,32). Nonetheless, allelopathy underlies the novel weapon hypothesis (NWH) (10) thus presenting one of numerous explanations for species invasiveness. Other relevant theories include enemy release hypothesis (ERH) (24), superior competitor (9) and evolution of increased competitive ability (EICA) (11). Furthermore, the disturbed habitats are the factors for success of plant invasion (32).

Numerous studies on the impacts of invasive species on neighbouring plant species suggests that invasion reduces the plant species richness (14,43). However, certain groups of species are peculiar with different trophic levels (e.g. herbivores, pollinators and predators) may suffer or benefit due to the presence of invasive plant species (16,35). Currently, most research is directed to find why alien invasive plant species are more successful than native plants (12). The success of invasive species is the production and release of allelopathic compounds by the invader that are harmful to plant neighbours in the introduced range.

Solidago canadensis L. or Canada goldenrod (*Compositae*, syn. *Asteraceae*) native to North America, is successful invader worldwide (37). It is highly aggressive plant, which reduces the species diversity and out-competes all native plants. It is perennial herb spreading by wind-dispersed seeds forming large colonies that reduces the abundance of native vegetation (19). The *Solidago* L. genus has 100 herbaceous species and > dozen species in South America, Europe and Asia. All species are herbaceous, highly variable, hence, difficult to distinguish. All goldenrods are late bloomers, flowers in late summer into the fall and common along the edges of moist forests, roadsides and meadows. It was introduced into Europe in 17th century (41) and now has become most aggressive invader (26,30) naturalised in Lithuania and has spread in slopes and along international highways. The invasion success of *S. canadensis* in Europe may be partly attributed to the release of allelopathic compounds and their adverse effects on competing flora in the new range (1,25,45). It has colonized the Europe, large parts of Asia, Australia and New Zealand (20,21). This species chemical composition has been determined (2,23,25,34,39) to explain its successful invasion worldwide. It releases the secondary metabolites [flavones, phenolics and saponins] (16) and the phenolics are involved in allelopathic interactions and influences the availability of soil nutrients, seed germination and plant growth (20).

This study aimed to (i). determine the biochemical characteristics which help in its invasion success, (ii). determine the total phenolics contents in various plant parts and their biological activity and variability in phytotoxicity during vegetation stages (iii). and their effects on germination of monocot and dicot species.

MATERIALS AND METHOD

Experimental setup

Allelopathic impacts (total phenolics content, total concentration and dynamic, influence on seed germination) of *S. canadensis* were examined during 2012-2013 in my laboratory. The plants were sampled in spring (May, rosette), summer (June, flowering) and autumn (September, seed maturity) for preparing the aqueous extracts. The biochemical (allelopathic) characteristics of *S. canadensis* aqueous extracts were examined at different plant growth stages: rosette (39 BBCH; end of May), flowering (65 BBCH; end of June) and milky stage (76 BBCH; end July). Principal (0-9) and secondary (0-9) growth stages as per universal BBCH (Biologische Bundesanstalt, Bundessortenamt and Chemical industry) scale description and coded using uniform two-digit code of phenologically similar growth stages of all mono- and dicotyledonous plant species (29). The plant samplings were taken when 50% of plants had reached the same developmental

stage. Plants leaves, stems, blossoms, seeds and roots were separated and chopped into 0.5 cm long pieces before extraction. Fifty g of each plant part were immersed in a 15 x 20 x 5 cm plastic tray containing 250 ml distilled water. Containers were closed with glass plates and kept at 5°C in an incubator. After 12 h, the aqueous extracts were filtered through Whatman No 1 filter paper and diluted to 0.02, 0.05, 0.1 and 0.2% (w/v) concentrations and used for germination assays. Leaves, stems, blossoms at flowering stage and seeds at dough stage were used to prepare 0.1 and 0.2% (w/v) extracts.

Germination bioassay

Allelopathic activity of *S. canadensis* was estimated based on seed germination bio-screening and expressed in conventional coumarine units (CCU). Germination responses of biologically different seeds from various taxon groups (Monocot and Dicot) were tested.

The germination was recorded under seed germination >50% (G_{50}) in distilled water (control). Thereafter the G_{50} rate was equated to 100%. This method enables to assess not only inhibitory, but also stimulatory effects of extracts. Fast germinating and high germination energy oil rapeseed (*Brassica napus* L., Dicot) cv. *Kasimir* (NPZ / Saaten-Uninio, Germany) and perennial ryegrass (*Lolium perenne* L., Monocot) cv. *Sodrė* were chosen as receptor plants. One hundred seeds were placed on filter paper in each Petri dish (6-cm dia). Five ml aqueous plant extracts (concentrations 0, 0.02, 0.05, 0.1, and 0.2 % w/v) were put in Petri dish as per treatments. Treatments were replicated four times. Petri dishes were kept at 26°C for 16 h. Seeds sown in distilled water served as control. Germination was considered when 1 cm long radicle emerged from the seed coat. Seed germination rate was used to calculate the allelopathic potential of aqueous extracts in conventional coumarine units (CCU) (4). A universal index of allelochemicals activity was evaluated by a nomogram (4), which depends on the coumarine activity and germination.

Phenolic compounds

Total phenolics content (TPC) was determined in extract samples following Singleton and Rossi's method, which relies on a colorimetric reaction and direct measurement of photo absorption in the ultraviolet. In determining the TPC, the standard curve with chlorogenic acid (Sigma, Aldrich, Germany) was used. One ml of extract was mixed with 45 ml distilled water. One ml of Folin-Ciocalteu reagent (Merck, Darmstadt, Germany) was added and mixed thoroughly. After 3 min 3 ml of Na_2CO_3 was added then the mixture was allowed to stand for 2 h. The absorbance was measured at 760 nm. Samples were analyzed in two replications. Identification and quantification of individual target polyphenolic compounds was carried out by UV-Vis spectrophotometry (Bechman DU-40, Germany). To evaluate the effects of selected chemicals, a standard equivalent of the total phenolics content in *S. canadensis* was estimated via the standard curve of chlorogenic acid. Equivalent value was calculated by multiplying the absorbance of each sample by a single value of equivalent chemical weight per absorbance unit determined under the same condition. In crude extracts of each fraction, TPC of *S. canadensis* was expressed as a fresh weight basis in mg per g chlorogenic acid equivalent (CAE).

Statistical analysis: The confidence intervals of the estimates were based on Student theoretical criterion. Standard deviation (SD) was calculated at $p<0.05$. Correlation

coefficient between TPC and germination was calculated in order to evaluate their interaction. Significant differences among the means were determined using Tukey's honest significant difference test. The results of allelopathic effects were statistically evaluated by using the statistical package STATISTICA of Stat Soft. The results regarding germination, phenols concentration and CCU are presented as mean ± SD of 4 independent analyses at the $p<0.05$ significance level.

RESULTS AND DISCUSSION

Phenolics content

Phenolics compounds play major role in ecosystems functioning as they are involved in many interactions among plants and their biotic and abiotic environment (10). Moreover, they can play an important role on many processes including seed development and germination and thus protect the plants against different stresses. The content of secondary compounds (38) in plant is subject to ontogenesis (genetically limited), plant part or season-contingent environment (1,17,22,26). Significant variations in phenolic compounds accumulation were observed in *S. canadensis* roots and shoots throughout the vegetation period (Fig. 1). In aqueous extracts of *S. Canadensis,* TPC ranged between 0.968 mg ml^{-1} to 23.591 mg ml^{-1} depending on plant ontogenetic stage, plant part and extract concentration (r=-0.7). The highest phenolics content (23.591 mg ml^{-1}) was observed in leaves at flowering stage. This finding is in agreement with growth–differentiation balance hypothesis (15).

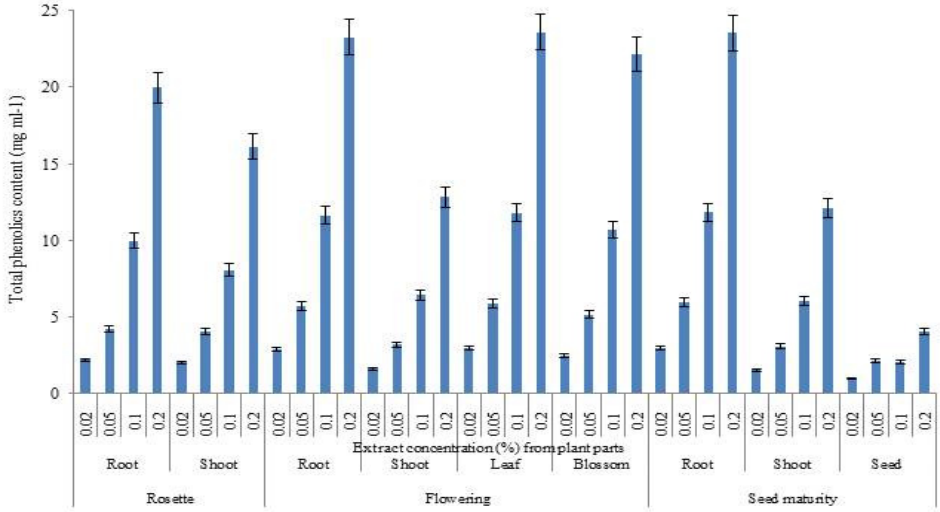

Figure 1. Total phenolics content (TPC) in *Solidago canadensis* extracts in different plant parts at various growth stages (Mean ±SE, $p<0.05$). Aqueous extracts were prepared in 4 concentrations (0.02; 0.05; 0.1 and 0.2%) from different parts of *S. canadensis* at rosette, flowering and maturity stages. Additionally leaf and blossom at flowering and seed extracts at maturity were prepared.

The lowest TPC was observed in *S. canadensis* seed (0.968 mg ml^{-1}) in accordance with plant resource allocation theory (36), which states that some ontogenetic developments are restricted at plant maturity stage. Consequently, deficiency of resources suppressed the TPC accumulation in *S. canadensis* shoots and seeds at maturity stage. Nonetheless, phenolics content remain high in roots at this growth stage, possibly due to most intensive conversion of synthesized materials.

Even so, the mean extract TPC rate (10.33 mg ml^{-1}) was higher in roots than in shoots (6.42 mg ml^{-1}), tending to increase gradually from 9.08 mg ml^{-1} at rosette to 10.86 mg ml^{-1} at flowering and 11.06 mg ml^{-1} at maturity. Meanwhile, the mean TPC rate of shoot extract was lower than the root extracts, showed a decrease from 7.56 mg ml^{-1} at rosette to 6.01 mg ml^{-1} at flowering and 5.68 mg ml^{-1} at maturity. The differences in TPC accumulation in roots and shoots depend on species genetically limited biological peculiarities (1). Moreover, these TPC variations should explain different inhibitory effects of extracts on germination rate of acceptors.

Moreover, the low-temperature stress increases the synthesis of phenolics in plants (33). At winter chilling temperatures, the permeability of cell membranes and the activity of membrane bound enzymes are changed thus leading to accumulation of toxic intermediates in cells. This induces physiological stress in plant cells and considerably increases the level of phenylalanine ammonia lyase (PAL) enzyme (involved in phenolic biosynthesis catalysing the reductive deamination of phenylalanine to form cinnamic acid). Subsequently, high phenolic content was found in *S. canadensis* roots from early growth stage (rosette).

Germination bioassay

Phenolics stimulate the phytotoxicity (6,18) and germination inhibition (13). Accordingly, we found a negative strong (r =-0.8), and medium (r =-0.5) correlation between TPC and germination of rapeseed and ryegrass, respectively. Thus extract phenolics should be considered phytotoxic and featuring a significant inhibition in germination *ex situ* of both acceptor species (Figs. 2 and 3). The results suggested that invasive *S. canadensis* may spread in new territories through inhibitory effects on germination due to accumulated allelochemicals. Nonetheless, slighter inhibition of rapeseed germination, if opposed to that of ryegrass, may be due to different seed coat anatomy and thus, its permeability (30). More specifically, seed germination and seedling emergence are the outcomes of a sequence of biological events initiated by water imbibition followed by enzymatic metabolism of storage nutrients. All these events are influenced by the environment and the seed quality (10). The rapidly germinating rapeseed needs shorter period for G_{50}, whereas ryegrass needs a longer time for G_{50}. Hence, complete inhibition of germination was observed in rapeseed in 0.2% shoot at rosette, leaf at flowering and seed extracts, while for ryegrass it occurred only in 0.2% leaf extract at flowering. The structure of seed coat (*testa*) scarification induces germination (30). The thick, lignified seed coats of ryegrass were impermeable to extracts, thereby maintaining their ability to reduce the phenols inflow to embryo. Hence, ryegrass seeds were specific with lower germination than rapeseed in general. Thus, the tested extracts had a lower impact on ryegrass seed germination if opposed to that of rapeseed.

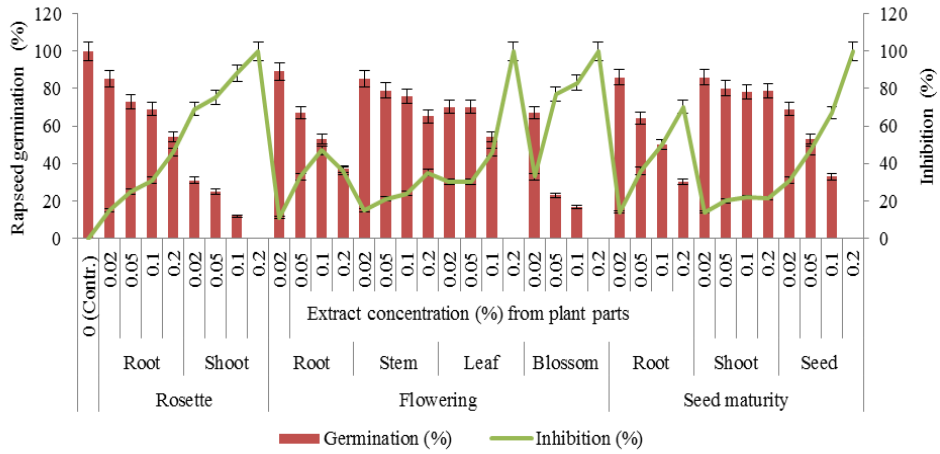

Figure 2. Effects of *Solidago canadensis* extracts from different plant parts and growth stages on germination of rapeseed (Mean ±SE, p <0.05). Aqueous extracts were prepared in 4 concentrations (0.02; 0.05; 0.1 and 0.2%) from different parts of *S. canadensis* at rosette, flowering and maturity stages. Additionally leaf and blossom at flowering and seed extracts at maturity were prepared. Line express calculated inhibition rate (%) over control (0% inhibition)

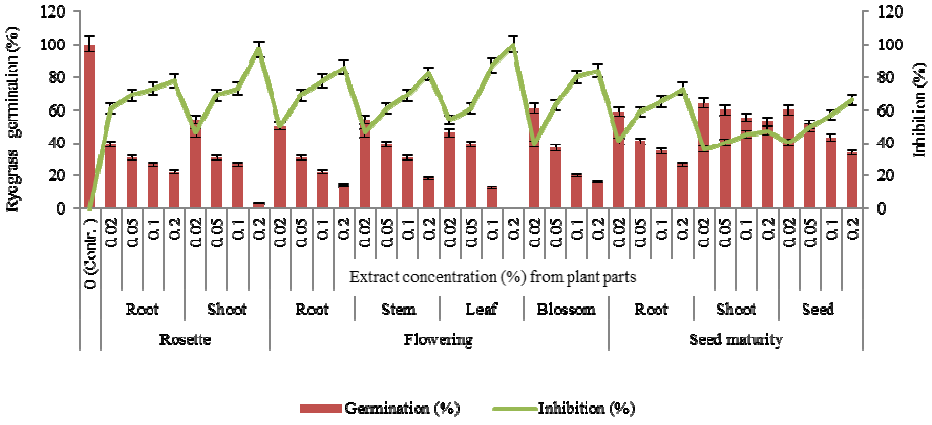

Figure 3. Effects of *Solidago canadensis* extracts concentrations from different plant parts and growth stages on germination of ryegrass (Mean ±SE, p <0.05). Aqueous extracts were prepared in 4 concentrations (0.02; 0.05; 0.1 and 0.2%) from different parts of *S. canadensis* at rosette, flowering and maturity stages. Additionally leaf and blossom at flowering and seed extracts at maturity were prepared. Line express calculated inhibition rate (%) over control (0% inhibition)

Extract phytotoxicity on rapeseed : S. c*anadensis* extract exhibited the phytotxicity due to presence of phenolics compounds, hence, inhibited the rapeseed germination in all treatments. The inhibition increased with extract concentration and TPC gradient with complete inhibition of rapeseed germination at the highest extract concentration (0.02%). The lowest phytotoxicity and the highest germination (86%) were found in root extract at flowering stage (Fig. 2).

The root extracts were less phytotoxic than shoots due to less stressful environment. The stress factors induce production of bioactive compounds including phenolics (32). Moreover, shoots are more sensitive to aerial conditions than underground parts roots, thus higher phytotoxicity of shoot extracts due to higher phenolics content. Consequently, germination was completely inhibited with extracts of aerial plant parts at highest concentration (0.2%), due to the highest TPC.

These differences in phytotoxicity may explain *S. canadensis* invasiveness. The higher phytotoxicity of plant shoots might negatively affect the neighbouring species and thus facilitate the establishment of invasive *S. canadensis* in a new habitat (10). Consequently, this alien species may influence the population of specific native species through allelochemicals. Nonetheless, our experimental design cannot determine, if successful invasion of *S. canadensis* is the direct result of solely allelopathic effects on native flora or it should also be attributed to the escape from parasites and pathogens present in their native ranges etc.

Extract phytotoxicity on ryegrass : The similar trends of ryegrass germination were observed across *S. canadensis* extract concentration gradient (Fig. 3). The lowest ryegrass germination was observed in 0.2% extract and ranged between 0% (leaf extract at flowering stages) and 2% (shoot extract at rosette stage). The lowest extract phytotoxicity and germination inhibition was observed in lowest concentration (0.02%) extract. Germination rate was 3-60% in shoot and 14-64% in root extracts at rosette growth and maturity stages. Germination was reciprocally related to TPC variation (r=-0.5). There is phenomenon of dissimilar effect of plant above- and underground parts on other plants has been reported (4,19,22).

In general, roots featured lower phytotoxicity on ryegrass due to different phenolics or other bioactive material translocation in plant parts.

Coumarine units content

The phenolic compounds play great role in metabolic plasticity enabling the plants to adapt to changing biotic and abiotic environments and thus improve their resistance against different stresses (8). Moreover, phenolics remain important in terms of control of many eco-physiological processes including seed development and germination and thus regulating initial species recruitment or regeneration in plant communities (28). The universal expression of TPC, namely conventional coumarine units (CCU), might be used to compare the biochemical activity of various plant parts or species influenced by different phenolic compounds. The CCU content-a universal index of extract bioactivity varied in accordance with TPC and germination rate in aqueous extracts of *S. canadensis*. CCU content ranged between 16 and 1300 for rapeseed and between 45 and 1300 for ryegrass (Figs. 4, 5).

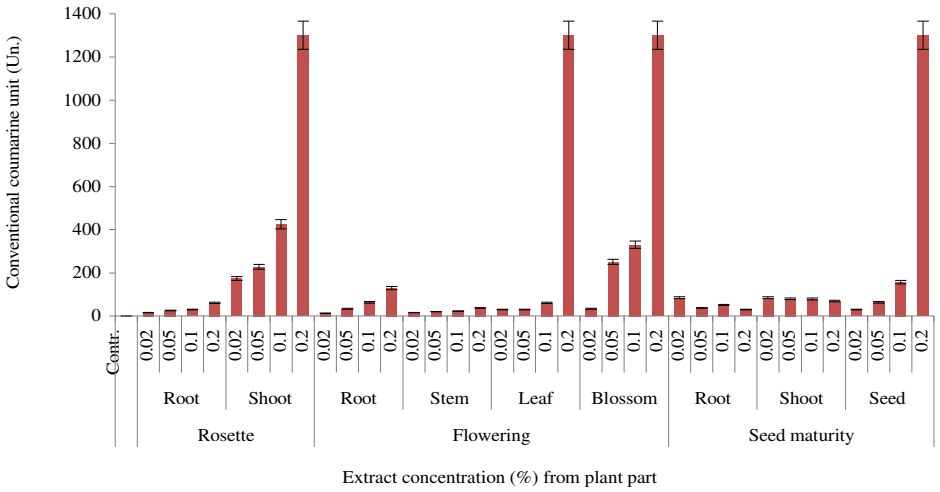

Figure 4. CCU content in *Solidago canadensis* extract for acceptor- rapeseed in different plant part and growth stage (mean ±SE, $p<0.05$). Conventional coumarine unit (CCU) assessed in aqueous extracts of 4 concentrations (0.02; 0.05; 0.1 and 0.2%) produced from different part of *S. canadensis* at rosette, flowering and maturity stages. Additionally leaf and blossom at flowering and seed extracts at maturity were produced.

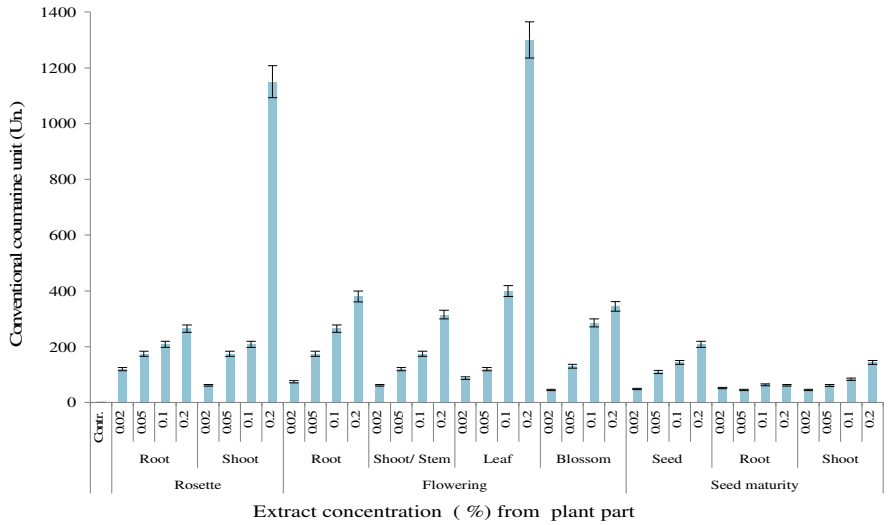

Figure 5. CCU content in *Solidago canadensis* extract for acceptor- ryegrass (mean ±SE, $p<0.05$). Conventional coumarine unit (CCU) assessed in aqueous extracts of 4 concentrations (0.02; 0.05; 0.1 and 0.2%) produced from different part of *S. canadensis* at rosette, flowering and maturity stages. Additionally leaf and blossom at flowering and seed extracts at maturity were produced.

The estimated correlation coefficient, r, confirmed a medium-strong correlation between extract CCU and TPC level (r=0.4 for rapeseed and r=0.6 for ryegrass). The tested acceptors had different germination periods and, therefore, indicated different sensitivity to TPC exposition and germination rate. Accordingly, a strong negative correlation between CCU and germination rate (r = -0.8 for rapeseed and r = -0.7 for ryegrass) was observed (Fig. 4, 5).

Our results confirmed that *S. canandensis* contains phenolics that are phytotoxic to seeds germination of different systematical groups, [Monocots (ryegrass) and Dicots (rapeseed)]. Phytotxicity of *S. canandensis* might impact the germination and consequently regeneration of neighbouring species. Thus, *S. canandensis* might considerably reduce the species diversity or locally out-compete the native plants in habitats. The revealed allelochemical phytotoxicity of *S. canandensis* should be considered as a partial explanation of high aggressiveness of species.

REFERENCES

1. Abhilasha, D., Quintana, N., Vivanco J., and Joshi J. (2008). Do allelopathic compounds in invasive *Solidago canadensis* s.l. restrain the native European flora? *Journal of Ecology* **96:** 993-1001.
2. Azimova, S.S.,Glushenkova, A.I. and Vinogradova V.I. (Eds.) (2012). *Lipids, lipophilic components and essential oils from Solidago canadensis* L. 992 pp. Springer, New York.
3. Bakker, J. and Wilson, S. (2001). Competitive abilities of introduced and native grasses. *Plant Ecology* **157**: 117-125.
4. Baležentienė, L. and Bartkevičius, E. (2013). Invasion of *Heracleum sosnowskyi* (*Apiaceae*) at habitat scale in Lithuania. *Journal of Food, Agronomy and Ecology* **11**: 1370-1375.
5. Baležentienė, L. and Sėžienė, V. (2010). Biochemical impact of dominants' extracts of Scots pinewood cuttings on germination. *Polish Journal of Environment Studies* **19**: 35-42.
6. Bhowmik, P.C. and Inderjit (2003). Challenges and opportunities in implementing allelopathy for natural weed management. *Crop Protection* **22**: 661-671
7. Blumenthal, D. (2005). Ecology-interrelated causes of plant invasion. *Science* **310:** 243-244.
8. Boudet, A.M. (2007). Evaluation and current status of research in phenolic compounds. *Phytochemistry* **68:** 2722-2735.
9. Callaway, R.M. (2002). The detection of neighbours by plants. *Trends in Ecology and Evolution* **17**: 104-105
10. Callaway, R.M. and Aschehoug E.T. (2000). Invasive plants versus their new and old neighbours: a mechanism for exotic invasion. *Science* **290:** 521-523.
11. Callaway, R.M. and Ridenour, W.M. (2004). Novel weapons: a biochemically based hypothesis for invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and Environment* **2:** 436-433.
12. de Groot, M., Kleijn, D. and Jogan, N. (2007). Species groups occupying different trophic levels respond differently to the invasion of semi-natural vegetation by *Solidago canadensis*. *Biological Conservation* **136**: 612-61.
13. Hanley, M. and Whiting, M. (2005). Insecticides and arable weeds: Effects on germination and seedling growth. *Ecotoxicity* **14**: 483-490.
14. Hejda, M. and Pyšek, P. (2006). What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? *Biological Conservation* **132:** 143-152.
15. Herms, D.A. and Mattson, W.J. (1992). The dilemma of plants: to grow or defend. *Quarterly Review of Biology* **67:** 283-335.
16. Iason, G.R., Dicke, M. and Hartley, S.E. (2012). *The Ecology of Plant Secondary Metabolities. From Genes to Global Process*. University press, Cambridge, United Kingdom. 335 pp.
17. Immel, F., Jenny, Renaut and Jean-François Masfaraud (2012). Physiological response and differential leaf proteome pattern in the European invasive Asteraceae *Solidago canadensis* colonizing a former cokery soil. *Journal of Proteomics* **75:**1129-1143.
18. Inderjit (1996). Plant phenolics in allelopathy. *Botanical Review* **62**: 186-202.

19. Inderjit and Bhowmik, P.C. (2002). Allelochemicals phytotoxicity in explaining weed invasiveness and their function as herbicide analogues. *Chemical Ecology of Plants: Allelopathy in Aquatic and Terrestrial Ecosystems* (Eds., Inderjit and A.U. Mallik). pp 187-197. Birkhauser, Basel, Switzerland. 261 pp.
20. Inderjit, Callaway, R.M. and Vivanco, J.M. (2006). Can plant biochemistry contribute to understanding of invasion ecology? *Trends in Plant Science* **11:** 574-580.
21. Kabouw, P., Nab, M. and van Dam, N.M. (2010). Activated carbon addition affects substrate pH and germination of six plant species. *Soil Biology and Biochemistry* **42:** 1165-1167.
22. Kasali, A.A, Ekundayo, O., Paul, C. and König, W.A. (2002). Epi-Cubebanes from *Solidago canadensis*. *Phytochemistry* **59:** 805-810
23. Keane, R.M. and Crawley, M.J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution* **17**: 164-170.
24. Kowarik, I., (2003). *Biologische Invasionen - Neophyten und Neozoen in Mitteleuropa*. Verlag Eugen Ulmer GmbH & Co., Stuttgart, Germany. 215 pp.
25. Kowarik, I. and Starfinger, U. (2002). *Biologische Invasionen*. Verlag Eugen Ulmer GmbH & Co., Stuttgart, Germany. 198 pp.
26. Liao, M., Xie, X., Peng, Y. and Ma, A. (2011). Changes of Soil Microbiological Characteristics After *Solidago canadensis* L. Invasion. *Agricultural Sciences in China* **10**: 1064-1071
27. Mallik, A.U. (2003). Conifer regeneration problems in boreal and temperate forest with ericaceous understory: role of disturbance, seedbed limitation, and keystone change. *Critical Review of Plant Sci*ence **22**: 341-366.
28. Meier, U. (Ed.). (2001). *Growth Stages of Mono and Dicotyledonous Plants. BBCH* Monograph. IGZ, Erfurt, Germany. 103 pp.
29. Moise, J.A., Han, S., Gudynaite-Savitch, L., Johnson, D.A. and Miki, B.L.A. (2005). Seed coats: Structure, development, composition and biotechnology. *In- Vitro* cellular deviation biology. *Planta* **41**: 620-644.
30. Moroń, D., Lenda, M., Skórka, P., Szentgyörgyi, H., Settele, J. and Woyciechowski, M. (2009). Wild pollinator communities are negatively affected by invasion of alien goldenrods in grassland landscapes. *Biological Conservation* **142**: 1322-1332.
31. Müller-Schärer, H., Schaffner, U. and Steinger, T. (2004). Evolution in invasive plants: implications for biological control. *Trends of Ecology Evolution* **19:** 417-422.
32. Padda, M.S. and Picha, D.H. (2008). Effect of low temperature storage on phenolic composition and antioxidant activity of sweetpotatoes. *Postharvest Biology and Technology* **47**: 176-180.
33. Pawlaczyk, I., Czerchawski, L., Pilecki, W., Lamer-Zarawska, E. and Gancarz, R. (2009). Polyphenolic-polysaccharide compounds from selected medicinal plants of *Asteraceae* and *Rosaceae* families: chemical characterization and blood anticoagulant activity. *Carbohydrate Polymers* **77:** 568-575.
34. Reznicek, G., Jurenitsch, J., Plasun, M., Korhammer, S., Haslinger, E., Hiller, K., and Kubelka W. Four major saponins from *Solidago canadensis*. *Phytochemistry* **30:** 1629-1633
35. Rice, E.L. (1984). *Allelopathy*. Academic Press, New York, USA. 422 pp.
36. Semple, J.C. and Cook, R.E. (2006). *Flora of North America. Magnoliophyta: Asteridae, Part 7: Asteraceae*, Part 2. Oxford University Press, New York.
37. Steliopoulos, P., Wüst, M., Adam, K.-P. and Mosandl, A. (2002). Biosynthesis of the sesquiterpene germacrene D in *Solidago canadensis*: ^{13}C and ^{2}H labeling studies. *Phytochemistry* **60**: 13-22. .
38. Šutovská, M., Capek, P., Kocmálová, M., Fraňová, S., Pawlaczyk, I. and Gancarz R. (2013). Characterization and biological activity of *Solidago canadensis* complex. *International Journal of Biological Macromolecules* **52**: 192-197.
39. Weber, E. (1998). The dynamics of plant invasions: A case study of three exotic goldenrod species (*Solidago* L.) in Europe. *Journal of Biogeography* **25:** 147-154.
40. Weber, E. (2003). *Invasive Plant Species of the World. A Reference Guide to Environmental Weeds*. CABI Publishing, Oxon, UK. 548 pp.
41. Weiner, J. (2004). Allocation, plasticity and allometry in plants. Perspect. Plant Ecol. Evol. Syst. 6, 207-215
42. Whittaker, R.H. and Feeny P.P. (1970). Allelochemics: Chemical interactions between plants. *Science* **171**: 757-770.
43. Willis, R.J. (2007). *The History of Allelopathy*. Springer, Berlin, Germany. 330 pp.
44. Yang, R., Yu G., Tang, J. and Chen, X. (2008). Effects of metal lead on growth and mycorrhizae of an invasive plant species (*Solidago canadensis* L.). *Journal of Environmental Sciences* **20**: 739-744.
45. Zhang, S., Zhu, W., Wang, B., Tang, J. and Chen, X. (2011). Secondary metabolites from the invasive *Solidago canadensis* L. accumulation in soil and contribution to inhibition of soil pathogen *Pythium ultimu*m. *Applied Soil Ecology* **48**: 280-286.