

***Helianthus tuberosus* at home and away: stronger ecological impacts in invaded than in native range are not explained by arbuscular mycorrhizal colonization**

Silnější impakt *Helianthus tuberosus* v invadovaném než v původním areálu nesouvisí s mykorrhizní kolonizací

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The impact of invasive plants on vegetation can vary greatly depending on the characteristics of the invaders and community invasibility. As to the factors that influence a plant's ability to invade, recent studies suggest that arbuscular mycorrhizal fungi (AMF) may be important regulators in plant invasions. To better understand the interactions of *Helianthus tuberosus* with co-occurring species in its native North American and invaded European ranges, we carried out plot-based field surveys to determine whether the cover of *H. tuberosus*, its stem number and height, bare ground cover and amount of litter differ between ranges and how they interact with numbers of species in the plant community. To provide information about AMF colonization of *H. tuberosus*, we evaluated AMF colonization in both ranges and tested the difference between continents, the effect of cover of *H. tuberosus* and their interaction with AMF. In the invaded range in Europe, *H. tuberosus* plants grew taller, had a greater stem density and there were fewer species in the invaded plant communities than in its native range in North America. In contrast, the cover of *H. tuberosus* and litter cover did not differ between the two continents. Plants of *H. tuberosus* were colonized by AMF in both ranges, but we found no statistical support for the potential effects of continent, the cover of *H. tuberosus* and their interaction with AMF. Overall, our study revealed that *H. tuberosus* exerts a negative impact on co-occurring species in the invaded European range, but not in North America where the species is native. To our knowledge, this is the first evaluation of AMF colonization of *H. tuberosus* at home and away and the results do not support either the degraded or enhanced mutualism hypotheses.

Keywords: invasive plant, Jerusalem artichoke, mycorrhizal colonization, species number

Introduction

Due to direct and indirect consequences of human activities (Pyšek et al. 2004), many plant species have become naturalized in new geographic ranges, overcoming local abiotic and reproductive barriers and establishing self-sustaining populations. A subset of these species has become invasive, spreading across considerable distances (Richardson et al. 2000), posing potential threats to biodiversity (Early et al. 2016) and ecosystem functioning (Linders et al. 2019).

Studies increasingly provide evidence of strong impacts of invasive plants on plant communities, including species richness and diversity (Callaway et al. 2011, Kaur et al. 2012, Ledger et al. 2015, Pal et al. 2015). However, the impact of invasive plants on the invaded vegetation varies greatly depending on the characteristics of the invaders and community invasibility (Hejda 2013, Fried et al. 2014). Fried et al. (2014) suggest that although, on average, the presence of invasive plants is associated with a significant change in resident community diversity and composition, the magnitude and sometimes the direction of response of a community to invasion can vary dramatically.

The factors that determine the success of invasive plants are poorly understood and the relative importance of different mechanisms depend on the specific invasion (Pringle et al. 2009). There is increasing evidence that arbuscular mycorrhizal fungi (AMF) may be important regulators of plant invasion (Marler et al. 1999, Fumanal et al. 2006, Sun & He 2010). AMF can influence plant productivity and diversity (van der Heijden et al. 2015) as they are known to promote vitality and fitness of hosts by increasing plant mineral nutrition (Marschner 1995), enhancing water supply (Augé 2001) and providing resistance to abiotic or biotic environmental stress (Ruiz-Lozano & Aroca 2010, Birhane et al. 2012). For example, Chen et al. (2019) demonstrated that AMF can promote the growth and pathogenic defence of *Wedelia trilobata* in a nutrient-poor environment, which might contribute to their successful invasion of such habitats.

On the other hand, an increasing number of publications indicate that reduced mycorrhizal associations may also benefit invaders in a competitive environment (Seifert et al. 2009, Waller et al. 2016). The “degraded mutualism hypothesis” suggests that an invasive plant can suppress AMF abundance in its vicinity and consequently reduce the competitiveness of locally abundant mycotrophic native plants (Vogelsang & Bever 2009). When mutualistic relationships between AMF and native plants are disrupted, introduced species are able to invade (Awaydul et al. 2019). Moreover, Pringle et al. (2009) propose that exotic plants without obligate dependence on an AMF symbiont have greater opportunities to become invasive compared to those with strong AMF associations. However, the meta-analysis of Bunn et al. (2015), which involved 70 native and 55 invasive species of plants, provides no support for the degraded or the enhanced mutualism hypotheses.

Hierro et al. (2005) state there is a lack of quantitative studies on invasive plant species and stress the need for documenting differences in abundance of exotics in their native and non-native range, as well as for applying a biogeographical perspective to test hypotheses that have been proposed to explain exotic plant success. Sun et al. (2015) argue that biogeographic studies can elucidate how the different ecological interactions between the home and introduced ranges affect biotic resistance during the establishment phase of biological invasions.

In the present study, we focused on *Helianthus tuberosus* (Jerusalem artichoke), an herbaceous perennial plant native to North America (Swanton et al. 1992), which was introduced to Europe in the 17th century as a cultivated species (Kays & Nottingham 2007). Since then, it has spread through central Europe (Balogh 2008, Müller & Sukopp 2016, Filep et al. 2018, Jehlík et al. 2019) where it primarily invades riparian ecosystems (Balogh 2008). It is known that arbuscular mycorrhizal fungal (AMF) colonization of *H. tuberosus* occurs in its non-native ranges (Štajerová et al. 2009, Zubek et al. 2011), but we have no information about AMF colonization of *H. tuberosus* in its native range.

To gain a better understanding of the impact of *H. tuberosus* on its co-occurring species and provide information about AMF colonization in native (North America) and non-native (Europe) ranges, we took a biogeographical approach. We hypothesized that (i) *H. tuberosus* would have a greater impact on co-occurring species in the non-native range compared to its native range and that (ii) AMF colonization of *H. tuberosus* in its native and non-native ranges would differ.

Material and methods

Study area

In its native range, *H. tuberosus* was studied in the Midwestern United States (between 41°17'–44°30'N and 87°11'–95°03'W, at altitudes between 155 to 279 m a.s.l.), which is situated within the western central part of its native range (Swanton et al. 1992, Kays & Nottingham 2007). Field data were collected from five states, namely Illinois, Indiana, Iowa, Minnesota and Wisconsin. In the non-native range, the area studied was the Carpathian Basin (between 45°51'–48°26'N and 16°25'–48°28'E, at altitudes between 95 to 510 m a.s.l.) in central Europe, where *H. tuberosus* primarily occurs in floodplains. Our study area was representative of three European countries, namely Hungary, Romania and Ukraine (Fig. 1).

Field measurements

To acquire field evidence of interactions between *H. tuberosus* and neighbouring species, we conducted plot-based surveys in plant communities associated with *H. tuberosus* in its native and non-native ranges. Plot surveys were conducted along 11 freshwater streams in the native range and along 28 freshwater streams in the non-native range (Electronic Appendix 1).

We sampled 201 2 × 2 m plots in a roughly 350 × 610 km area in the United States in 2013, and 750 2 × 2 m plots in a roughly 270 × 750 km area in Europe between 2012 and 2015. Each plot was sampled once during the study. All plots were surveyed during the flowering period of *H. tuberosus*. At each plot we estimated the cover of all vascular plant species in order to determine how the presence of *H. tuberosus* influenced species richness and composition. The plots were randomly selected along river banks if they had previously been found to contain *H. tuberosus* and had vegetative coverage of *H. tuberosus* that ranged from 0 to 100%. By using a handheld global positioning system (GPSMAP® 60CSx Garmin) we identified the geographical position of the plots. In each plot, we quantified the total number of *H. tuberosus* stems; we measured the height of

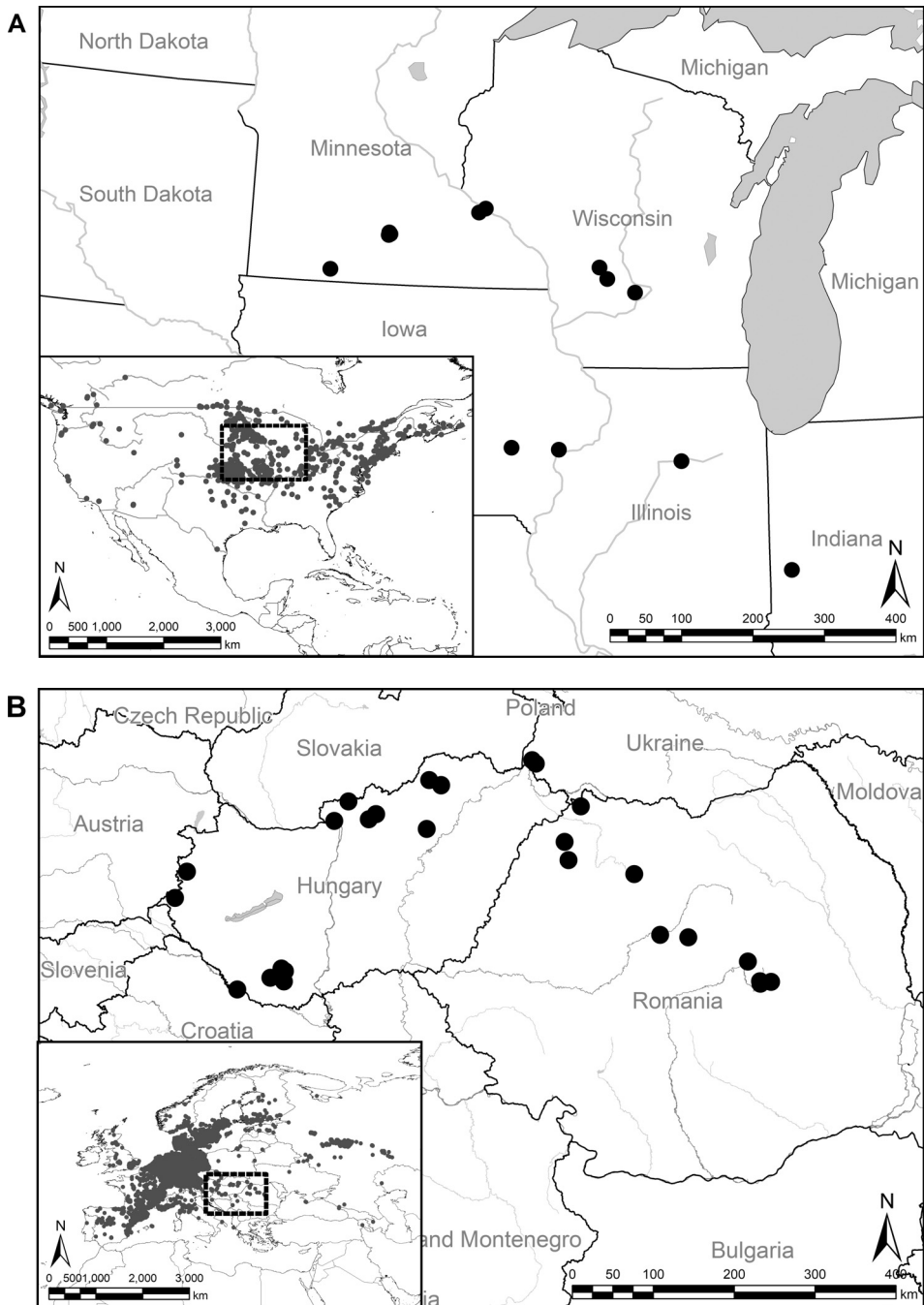


Fig. 1. – Occurrences of *Helianthus tuberosus* based on the Global Biodiversity Information Facility (GBIF) database and distribution of study sites in (A) North America, its native range, and (B) Europe, its non-native range. The scale is too large to separate many individual points that represent more than one stand of *H. tuberosus*.

10 randomly selected individual stems of the target species and recorded the percentage cover of bare ground and litter.

Colonization by arbuscular mycorrhizal fungi (AMF)

To obtain information on the colonization of *H. tuberosus* by arbuscular mycorrhizal fungi (AMF) at home and away, we collected 64 samples of roots from its native range and 56 from its non-native range between 2012–2015 (Electronic Appendix 1).

The roots were prepared according to the modified Phillips and Hayman (1970) method based on Füzy et al. (2008). Root samples were cleared in 15% KOH for 40 minutes and then rinsed in water, stained in 0.01% aniline-blue for 30 minutes and acidified in 40% lactic acid for 30 minutes. Stained root fragments were stored in 40% glycerol until analysed. For each sample, 30 stained root fragments were randomly chosen and mounted on two slides for observation using a light microscope (Motic SFC-28, at a magnification of 100×). The following mycorrhizal parameters were estimated according to the five-class system of Trouvelot et al. (1986): frequency of mycorrhiza in the root system (F%), intensity of the mycorrhizal colonization in the root system (M%), intensity of the mycorrhizal colonization in the root fragments (m%), arbuscular abundance in the root system (A%), and arbuscular abundance in the root fragments (a%). In addition, the number of vesicles was counted.

Statistical analyses

Field data obtained from the 951 plots were entered into a TURBOVEG database (Hennekens & Schaminée 2001). We tested the difference in *H. tuberosus* cover, number of *H. tuberosus* stems, number of species, bare ground cover, litter cover, as well as frequency of mycorrhiza in the root system (F%), intensity of the mycorrhizal colonization in the root system (M%), intensity of the mycorrhizal colonization in the root fragments (m%), arbuscular abundance in the root system (A%), arbuscular abundance in the root fragments (a%) and number of vesicles in the samples from the North American and European ranges. We modelled the above variables as response variables in generalized linear mixed models in which the fixed factors were continent, cover of *H. tuberosus* and their interaction (except for the case when *H. tuberosus* cover was the response variable), random factors were the river and the year of sampling (random factor: 1|river + 1|year). Percentage variables were scaled to (0; 1) and modelled using beta distribution, number of species and number of stems were modelled by a Poisson distribution, while for the height of *H. tuberosus* a Gaussian link function was chosen. Models were evaluated using type II Wald tests. P-values were adjusted for multiple comparisons using Holm's method (Holm 1979).

The statistical analysis was performed in the R environment (version 2.11.1; R Development Core Team) using the *vegan* (Oksanen et al. 2017), *glmmTMB* (Brooks et al. 2017) and *car* (Fox & Weisberg 2019) packages.

Results

Field measurements

The generalized linear mixed models showed significant differences between the native and non-native ranges in the number of species, *H. tuberosus* stem number, *H. tuberosus* height and amount of bare ground. The cover of *H. tuberosus* and litter did not differ between samples from the two continents (Table 1).

We recorded a total of 225 and 249 species in the plots in North America and Europe, respectively. The mean number of species excluding *H. tuberosus* was significantly lower in Europe than in North America ($df = 1$, $\chi^2 = 105.391$, $P < 0.001$). The number of species decreased with increase in *H. tuberosus* cover; however, this decrease was steeper in Europe, where the numbers of species were generally lower (Fig. 2).

There were more stems on average in the European plots (96 ± 4 stems/4 m²) than in the North American plots (48 ± 3 stems/4 m²) ($df = 1$, $\chi^2 = 13.936$, $P < 0.001$); however, this was coupled with a more steeply increasing number of stems in Europe (Fig. 3A).

Helianthus tuberosus stems were significantly taller in Europe (155.4 ± 0.8 cm) than in North America (137.2 ± 1.2 cm) ($df = 1$, $\chi^2 = 36.725$, $P < 0.001$) and on both continents mean height increased with *H. tuberosus* cover similarly (Fig. 3B).

The amount of bare ground in European plots was significantly higher than in North American plots ($df = 1$, $\chi^2 = 7.658$, $P < 0.001$). In Europe, the percentage cover of bare ground increased steeply with increase in cover of *H. tuberosus*, while North American plots showed a neutral relationship (Fig. 4). Litter cover increased with *H. tuberosus* cover and continent had no effect on this (Table 1).

Table 1. – Results of generalized linear mixed models testing the effect of continent, cover of *Helianthus tuberosus* and their interaction on the number of species, number of stems and height of *H. tuberosus*, percentage of bare ground and litter cover. Random factors were the river and the year of sampling.

Investigated variables	Wald χ^2	df	P-value	Adjusted P-value (Holm)
Number of species				
Continent	105.39	1	<0.001***	<0.001***
<i>H. tuberosus</i> cover	114.86	1	<0.001***	<0.001***
<i>H. tuberosus</i> cover \times continent	23.66	1	<0.001***	<0.001***
<i>H. tuberosus</i> stem number				
Continent	13.94	1	<0.001***	<0.010***
<i>H. tuberosus</i> cover	25245.34	1	<0.001***	<0.001***
<i>H. tuberosus</i> cover \times continent	72.30	1	<0.001***	<0.001***
<i>H. tuberosus</i> height				
Continent	36.73	1	<0.001***	<0.001***
<i>H. tuberosus</i> cover	179.01	1	<0.001***	<0.001***
<i>H. tuberosus</i> cover \times continent	3.70	1	0.054	0.217
Percentage bare ground				
Continent	7.66	1	<0.010**	<0.050*
<i>H. tuberosus</i> cover	203.82	1	<0.001***	<0.001***
<i>H. tuberosus</i> cover \times continent	35.72	1	<0.001***	<0.001***
Litter cover				
Continent	0.16	1	0.684	0.684
<i>H. tuberosus</i> cover	58.99	1	<0.001***	<0.001***
<i>H. tuberosus</i> cover \times continent	1.05	1	0.304	0.609

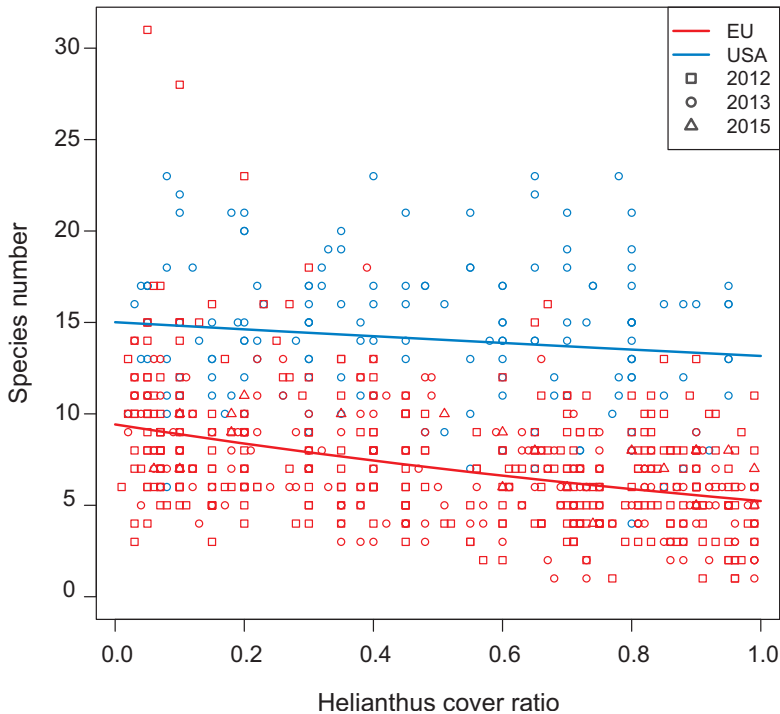


Fig. 2. – Relationship between the cover of *Helianthus tuberosus* and number of species based on generalized linear mixed effect models. EU – Europe, invaded range; USA – North America, native range. Year of sampling is indicated.

Colonization by arbuscular mycorrhizal fungi (AMF)

The microscopic examination of the colonization by arbuscular mycorrhizal fungi (AMF) of *H. tuberosus* indicated that all of the root systems of *H. tuberosus* sampled were colonized by AMF both in the native and non-native ranges, which was indicated by the presence of hyphae, vesicles and arbuscules (Fig. 5). Based on the generalized linear mixed models there was no statistical support for a difference in AMF colonization of the roots of *H. tuberosus* in North America and Europe. AMF colonization was not affected by continent, the cover of *H. tuberosus* or their interaction (Table 2).

Discussion

The key results of this study are that (i) the impact of *H. tuberosus* is stronger on co-occurring species in the invaded European range than in its native North America, (ii) *H. tuberosus* specimens were colonized by arbuscular mycorrhizal fungi (AMF) both in its native and non-native ranges and there were no significant differences in colonization detected between North America and Europe.

Based on this field study, we found that the number of species was significantly lower in Europe than in North America and also declined with increasing cover of *H. tuberosus* in European plots, but not in North America. These results are consistent with the literature

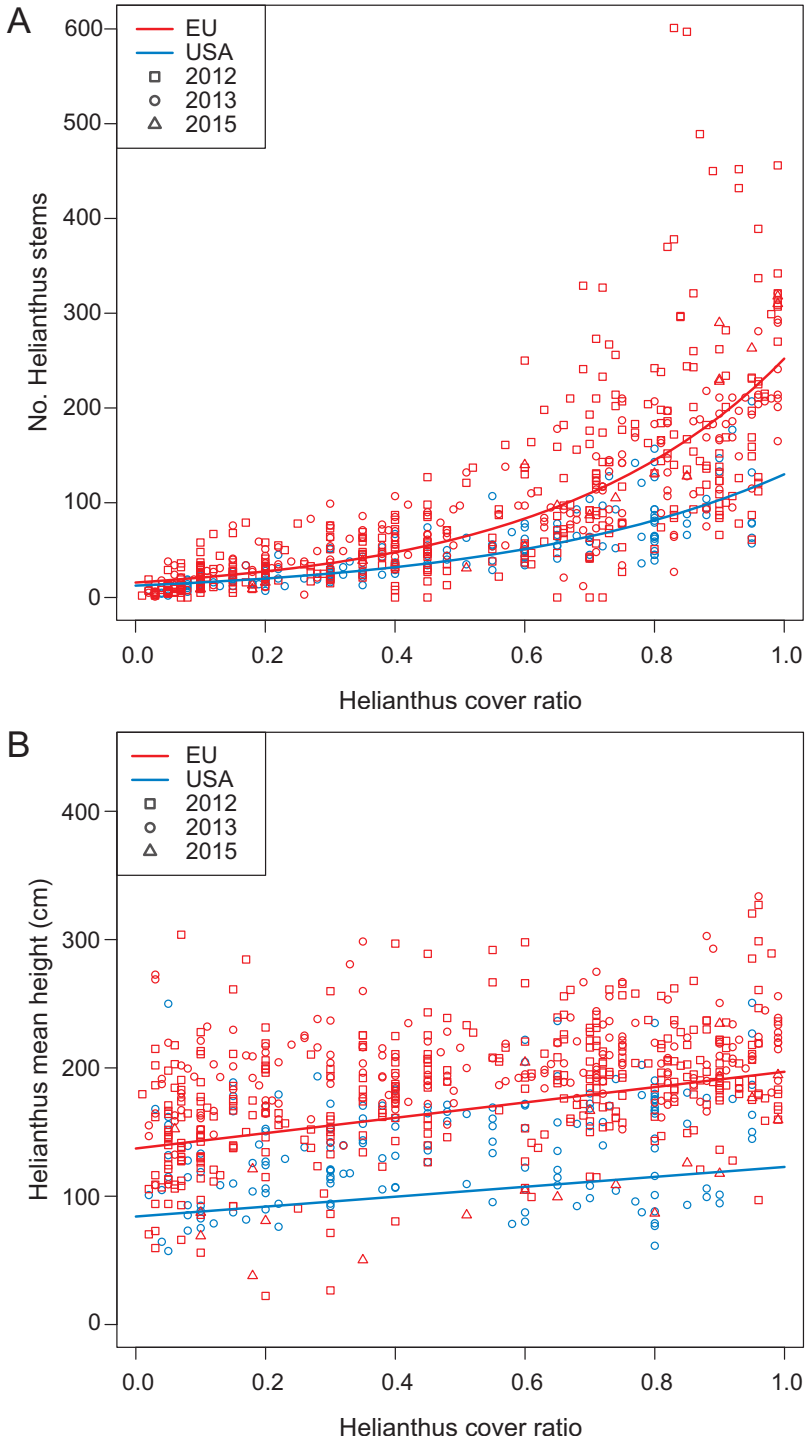


Fig. 3. – Relationships between cover of *Helianthus tuberosus* and (A) number of its stems, and (B) its mean height based on generalized linear mixed effect models. EU – Europe, invaded range; USA – North America, native range. Year of sampling is indicated.

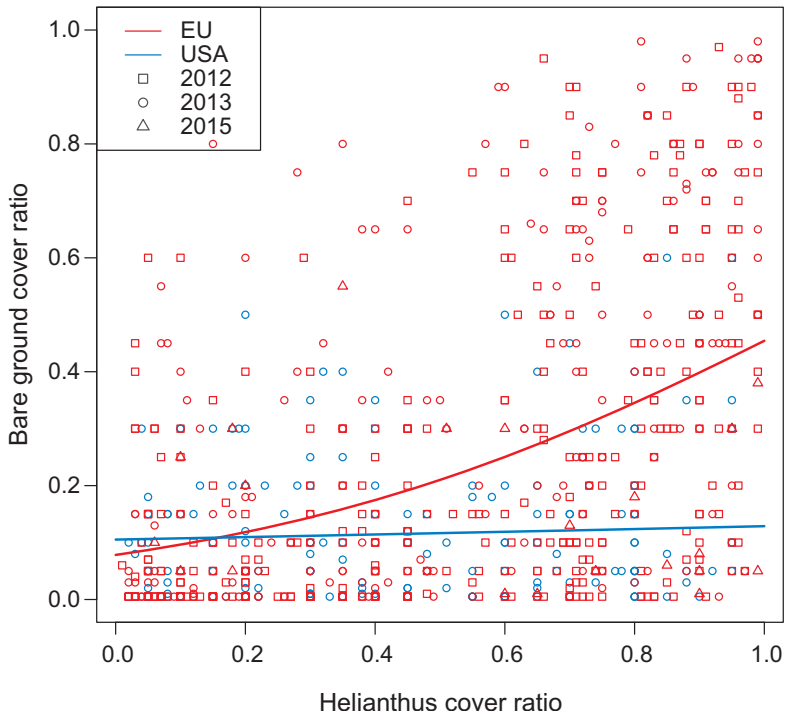


Fig. 4. – Relationship between cover of *Helianthus tuberosus* and percentage of bare ground based on generalized linear mixed effect models. EU – Europe, invaded range; USA – North America, native range. Year of sampling is indicated.

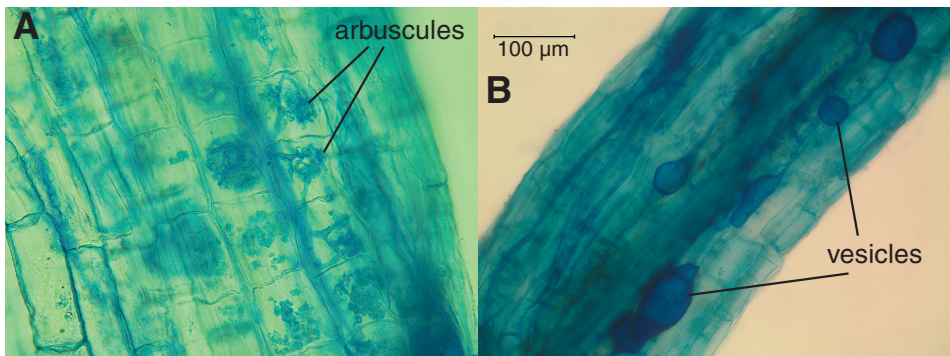


Fig. 5. – Arbuscular mycorrhizal fungi (AMF) colonization of *H. tuberosus* in (A) native and (B) non-native ranges.

in showing that richness of native species responded more negatively to the dominant species in its invaded rather than its native range (Ledger et al. 2015, Pal et al. 2015, Hejda et al. 2017). Hejda et al. (2017) suggest that long-term coexistence and species filtering can be responsible for the lower impacts of dominant species in the native range. But we should mention that invasive species can also suppress some native species more than others (Hejda et al. 2019).

Table 2. – Results of generalized linear mixed models testing the effect of continent, cover of *Helianthus tuberosus* and their interaction on frequency of mycorrhiza in its root system, intensity of mycorrhizal colonization of its root system, intensity of the mycorrhizal colonization of root fragments, arbuscule abundance in the root system, arbuscule abundance in mycorrhizal parts of root fragments and number of vesicles. Random factors were the river and the year of sampling.

Investigated variables	Wald χ^2	df	P-value	Adjusted P-value (Holm)
Frequency of mycorrhiza in the root system (F%)				
Continent	3.17	1	0.074	1.000
<i>H. tuberosus</i> cover	0.15	1	0.702	1.000
<i>H. tuberosus</i> cover \times continent	0.10	1	0.754	1.000
Intensity of the mycorrhizal colonization of root system (M%)				
Continent	4.35	1	<0.05*	1.000
<i>H. tuberosus</i> cover	1.50	1	0.220	1.000
<i>H. tuberosus</i> cover \times continent	0.0001	1	0.990	1.000
Intensity of the mycorrhizal colonization in root fragments (m%)				
Continent	3.64	1	0.056	1.000
<i>H. tuberosus</i> cover	1.29	1	0.255	1.000
<i>H. tuberosus</i> cover \times continent	0.02	1	0.895	1.000
Arbuscule abundance in the root system (A%)				
Continent	5.48	1	<0.05*	0.978
<i>H. tuberosus</i> cover	1.06	1	0.302	1.000
<i>H. tuberosus</i> cover \times continent	0.05	1	0.830	1.000
Arbuscule abundance in root fragments (a%)				
Continent	8.93	1	<0.01**	0.151
<i>H. tuberosus</i> cover	2.12	1	0.145	1.000
<i>H. tuberosus</i> cover \times continent	0.47	1	0.493	1.000
Number of vesicles				
Continent	2.94	1	0.086	1.000
<i>H. tuberosus</i> cover	1.17	1	0.280	1.000
<i>H. tuberosus</i> cover \times continent	0.97	1	0.325	1.000

In addition to density, the height of an invader could also play an important role in shaping plant communities. In a study examining 13 invasive species, Hejda et al. (2009) found that tall invasive species capable of forming populations with a cover markedly greater than that of native dominant species exert the most severe impacts on species diversity and evenness. This is in accordance with our findings of shorter North American and taller European *H. tuberosus* populations, which could be responsible for the reduction in the number of species in the non-native range. Our study confirmed that in Europe the percentage of bare ground increased steeply with increase in cover of *H. tuberosus*, while in North America it did not change. This can be explained by the fact that *H. tuberosus* is a highly competitive species in its non-native range, quickly shading the soil surface and creating a zone of captured resources, which results in the reduced growth of other species (Kays & Nottingham 2007, Balogh 2012).

In contrast, litter cover increased with *H. tuberosus* cover but the continental location had no effect on this, despite the fact that the average density of stems of *H. tuberosus* was

around twice as high in Europe. Invasive alien plants are highly competitive species characterized by fast growth and resource acquisition (van Kleunen et al. 2010), which in turn are associated with leaf traits that are known to result in more decomposable litter (Kazakou et al. 2006, Helsen et al. 2018). Furthermore, Pritekel et al. (2006) report that in non-invasive and invasive sites there are no differences in the decomposition rates of either different types of litter or the overall decomposition of litter. In addition, AMF has also been shown to stimulate the decomposition of plant material (Cheng et al. 2012).

AMF are important mediators of competitive interactions between non-native and native plants (Reinhart & Callaway 2006). Several studies suggest that AMF colonization of exotic plant species may be involved in plant invasions. Menzel et al. (2017) assessment of 13 functional traits of 266 invasive species in Germany, indicates that the persistence of a non-native species of plant in a new habitat depends largely on its mycorrhizal status, with facultative mycorrhizal species being more competitive than obligate and non-mycorrhizal species. Pringle et al. (2009) suggest that exotic plants without an obligate dependence on an AMF symbiont have a greater chance of becoming invasive in the new community compared to those with strong AMF associations.

Roots of all the *H. tuberosus* analysed were colonized by arbuscular mycorrhizal fungi. This is in accordance with findings of Štajerová et al. (2009) who suggest that about 70% of the invasive species (including *H. tuberosus*) are colonized in the field in the Czech Republic and the majority of them belong to the *Asteraceae*. To our knowledge, this is the first study that provides information on the AMF colonization of *H. tuberosus* in its native range and compares it with that in its non-native range.

Contrary to expectation, AMF colonization of *H. tuberosus* did not differ in the two ranges. These results correspond with the meta-analysis of Bunn et al. (2015), in which neither the degraded nor the enhanced mutualism hypotheses were supported. They suggest that AM fungi are most likely to influence invasion trajectories when native and invasive plants belong to different functional groups.

It is important to note that our study was carried out in riparian ecosystems, which are among the most biologically diverse and productive ecosystems worldwide (Tockner & Stanford 2002) and link fluvial and terrestrial ecosystems (Riis et al. 2020). Riparian areas are composed of a mosaic of habitats that differ in soil characteristics, moisture availability, plant community composition and microbial diversity (Whited et al. 2007, Harner et al. 2011). For instance, Deepika and Kothamasi (2015) who evaluated the effects of drought, flooding and optimal soil moisture on AMF community composition and structure in *Sorghum vulgare* roots report that the lower diversity in the flooded treatment was associated with fewer, more dominant AMF associations.

Overall, this study revealed that *H. tuberosus* exerts a negative impact on co-occurring species in its non-native European range, but not in North America. Thus, our results support a growing body of quantitative results that demonstrate a strong biogeographic context to exotic invasions. We provide evidence of arbuscular mycorrhizal fungal (AMF) colonization of *H. tuberosus*, both in its native and non-native ranges, but neither the degraded nor the enhanced mutualism hypotheses were supported, most likely due to the complexity of riparian ecosystems. Further research in these fields is necessary to elucidate the role of AMF in riparian ecosystems.

See www.preslia.cz for Electronic Appendix 1

Acknowledgments

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Souhrn

Dopad invazních rostlin na vegetaci se může velmi lišit v závislosti na vlastnostech invazního druhu a náchylnosti společenstva k invazi. Nedávné studie naznačují, že arbuskulární mykorhizní houby mohou být důležitým faktorem regulujícím rostlinné invaze. Abychom lépe porozuměli interakcím *Helianthus tuberosus* s druhy původních severoamerických a invadovaných evropských společenstev, zjišťovali jsme prostřednictvím terénní studie, zda se pokryvnost *H. tuberosus*, počet stonků a jejich výška, podíl obnažené půdy a množství opadu v obou areálech liší a jak ovlivňují počet druhů ve společenstvu. Vyhodnotili jsme také kolonizaci arbuskulárními mykorhizními houbami na obou kontinentech. V Evropě, kde je druh invazní, byly rostliny vyšší, hustota stonků byla větší a společenstva obsahovala méně druhů, než v oblasti původního výskytu v Severní Americe. Rostliny *H. tuberosus* byly kolonizovány arbuskulární mykorhizou v obou areálech, rozsah kolonizace se ale nelišil. Naše výsledky ukazují, že *H. tuberosus* má negativní dopad na druhovou bohatost pouze v invadovaném evropském areálu, nikoli v Severní Americe, kde je druh původní. Nepodařilo se nám však nalézt podporu pro hypotézy předpokládající významnou roli mutualismu v této invazi.

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