UNIVERSITY OF PÉCS

Doctoral School of Biology and Sport Biology

Biogeographic perspectives of Jerusalem artichoke (*Helianthus tuberosus* L. s. l.) invasion

PhD Thesis

Rita Filep

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'It is not the strongest of the species that survives, nor the most intelligent that survives. It is the one that is most adaptable to change.'

Charles Darwin

I dedicate this dissertation to my family, who have taught me

to work hard to achieve my goals.

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1. MOTIVATION

Currently there are around 400,000 plant species in the world, but their number is constantly changing (Christenhusz and Byng 2016). Plants are among the most important factors of life on Earth and a crucial source of human well-being. They are the main sources of food, they regulate the water cycle, they act as sources of medicines, and the oxygen is brought to us by plants (Usman et al. 2014).

Worldwide tens of thousands of vascular plant species, and several hundred non-vascular plants are used currently by humans for a wide diversity of purposes (Krupnick and Kress 2005). Plant diversity is an essential undergirding of most terrestrial ecosystems. Due to plant diversity, we have a significant amount of resources for the future, if we only think of potential food sources or potential natural active compounds.

There are several factors that can threaten plant diversity. Besides habitat loss caused by human activities biological invasions are the next major threat. Approximately four percent of the world's vascular plant flora has become naturalized in a new (non-native) range (van Kleunen et al. 2015). These non-native plant populations cover far larger areas than native dominant species, exerting a negative impact on species diversity and evenness (Hejda et al. 2009; Parker et al. 2013; Pal et al. 2015; Ledger et al. 2015). Moreover, introduced species are hypothesized to benefit from novel biochemical weapons (Callaway and Ridenour 2004), escape natural enemies (Mitchell and Power 2003), hybridize with natives (Ellstrand and Schierenbeck 2000), purge the genetic load (Facon et al. 2011), and intercations can also occur among these factors. Therefore, the investigation of plant invasion could contribute to reducing the negative impact of plant invasion, and thereby protecting plant diversity.

I was intrigued to do research in plant sciences, since plants have always formed an integral part of my life. Studying plant invasions is one of the most novel, and − due to the large number of unanswered questions − one of the most exciting research topics in plant ecology. On the other hand it bridges several disciplines, bringing together research in plant ecology, phytochemistry, plant physiology, and on top of all it has applied perspectives as well.

2. INTRODUCTION

2.1. Plant invasion

2.1.1. Introduction of alien plants

Many species have been able to establish new populations outside of their native range. Their dispersal throughout the world can be aided both by natural ways and by pathways associated with human activities, such as transfer by planes and ships. On the other hand, their spread can be hindered by natural geological obstacles (e.g. rivers and mountain ranges) and environmental factors (e.g. temperature, altitude and diseases) (Bright 1998). Thus, species introductions have increased exponentially in the past century with 'globalization' (Hulme et al. 2008).

A study of Pimentel et al. (2002) suggests that hundreds of thousands of species have been translocated across continents. The number of introduced species has increased by 76% in all kinds of environments in Europe in less than 40 years (Butchart et al. 2010). Due to direct and indirect consequences of human activities (Pyšek et al. 2004), about 6.2 alien species arrive from other continents into Europe every year (Lambdon et al. 2008). The majority of plants have been introduced into Europe as ornamentals (e. g. *Solidago gigantea* Aiton; Weber 1998) or cultivated species (e. g. *Helianthus tuberosus* L.; Balogh 2006, 2008; Kays and Nottingham 2007) (Lambdon et al. 2008). However, some exotic species escaped cultivation and became subspontaneous agricultural weeds or invaders at various native ecosystems causing serious environmental problems (Kovács 2006). Besides, there are invasive species that prefer human settlements and their periphery (Štajerova et al. 2017). Particularly communities characterized by high resource levels and low stress are likely to become infested with one or a few species that are able to produce a high amount of biomass (Walker et al. 1999).

Exotic plant species follow different patterns of geographic distribution, but we know that most alien species of Europe originate from North America and Asia (Weber 1997, Pyšek et al. 2009). They are mainly members of large global plant families; the highest number of species belong to the Asteraceae family listing around 700 alien representatives (Pyšek et al. 2009).

2.1.2. The process of plant invasion

The English botanist, John Henslow was the first who outlined the concept of nativeness in 1835. By the late 1840s, botanists have adapted the terms native and alien from

common law to help them distinguish those plants that composed a 'true' British flora from artifacts (Chew and Hamilton 2011). Dividing taxa into *native* and *alien* populations has become common practice in invasion biology since the late 1980s (Davis 2006).

There are several definitions of invasive plants, which basically agree on the main features of invasive species. For example, according to the most recent definition of Weber (2017):

'*Invasive alien species are non-native species, brought into new regions by human activities, and exhibiting negative impacts on natural habitats and their communities due to their prolific population growth.*'

To become an invasive species is a process, not an event, including various stages. According to the views of different scientists or schools, there are several models for the invasive process, however, the model of Lockwood et al. (2013) is one of the most emphatic. It suggests that the process of invasion consists of three stages before the plants are able to inflict ecological or economic harm (Fig. 2.1).

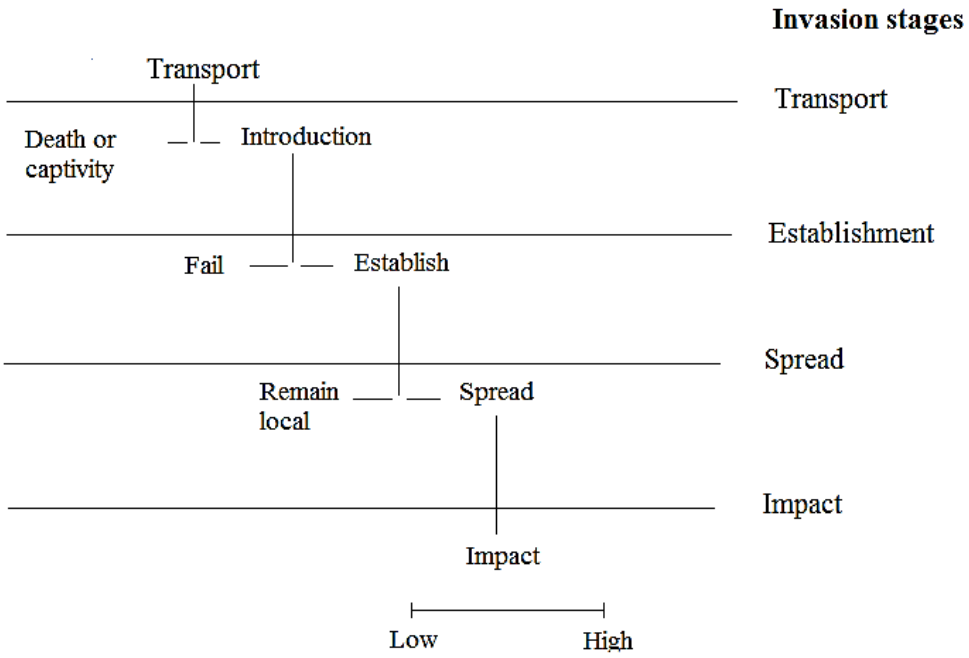


Figure 2.1. Simple invasive process model (Lockwood et al. 2013)

The first stage is the *Transport*, when individuals of the non-native species are picked up in their native range, transported to a new area, and released into the wild. The second stage is *Establishment*, when these individuals establish a self-sustaining population

within their new non-native range, or else the population becomes extinct. In the course of *Spread* an established non-native population starts growing in abundance and expands its geographic range. It is only when the non-native population is widespread and abundant that it will cause some sort of ecological or economic harm, and thus earn the name "invasive".

Not every introduced species become invasive. 'The tens rule' suggests that 1 in 10 of those introduced become established, and that 1 in 10 of those established become a pest (Holdgate 1986; Williamson and Brown 1986; Williamson and Fitter 1996).

2.1.3. The negative impact of plant invasion

The impact of plant invasion falls into broad categories: starting with the environment, through human or animal health, as far as economic. Within the environment category, ecological impacts are the most difficult to quantify (Barney et al. 2013), because they depend on the attributes of recipient ecosystems and the invaders themselves (Levine et al. 2003). Thiele et al. (2010), Vilá et al. (2011), and Barney et al. (2013) summarized the most important ecological impacts of invasive plants at different levels (Table 2.1). This study suggests that invasive plants can exert their effects by different ways, for example, they can influence the fitness, growth or diversity of other organisms.

In the last few decades invasive exotic plants have become the most serious actual causes of species declines and native habitat degradation (Vitousek et al. 1997; Wilcove et al. 1998; Vilà et al 2006; Mollot et al. 2017). Thus, invasive alien plant species have been recognized as one of the potential threats to native plant diversity (Corlett 2016) through reduction of genetic variation via hybridization, facilitation of pathogen spread, parasitism, and predation (Callaway and Maron 2006). A large meta-analysis found that invaders as a group decreased the abundance and diversity of resident native species at small scales (Vilà et al. 2011). Furthermore, the abundance and ecological impacts of some invasive plant species are much greater in their non-native ranges than in their native ranges (Callaway et al. 2011; Inderjit et al. 2011; Kaur et al. 2012; Ledger 2015; Pal at el. 2015).

Table 2.1. Different impacts of invasive plants (Barney et al. 2013)

Level	Impact type	Impact metric
Individual	Fitness	Seed number, seed viability, survival, germination rate, recruitment
	Growth	Plant size, root:shoot ratio
Community	Productivity	Biomass, net primary productivity
	Diversity	Richness, evenness, alpha diversity, seed bank
	Abundance	Number of individuals, density
	Intraspecific	Genetic diversity, intrinsic growth rate
Structure	Physiognomy	Tree, shrub, forb, grass coverage
Biogeochemical	Pools	Nitrogen (N), carbon (C), phosphorus, soil organic matter
	Litter	Litter nutrient content, C:N, decomposition rate
	Fluxes	N, C turnover, pH, salinity
	Moisture	Plant-available water
Ecosystem	Food chain	Trophic connections, trophic-level ratio
	Interactions	Mutualists, herbivore, parasite, pollinator diversity
	Fluxes	Nutrient, sediment
	Disturbance	Fire, flood frequency or intensity
	Geomorphology	Hydrology, sediment gain or loss

A growing body of literature suggests that biological invaders can even threaten human health. In this regard, Mazza et al. (2014) identified four categories: invasive species can (1) cause diseases or infections; (2) expose humans to wounds from bites/stings, biotoxins, allergens or toxicants; (3) facilitate diseases, injuries or death; and (4) inflict other negative effects on human livelihood. For example, pollen from all *Ambrosia* species causes allergies in various European countries, leading to asthma in about 25% of people affected. This, in turn, results in a predicted average annual expenditure of € 24.5 million for treatment of asthma in the region of Eastern Europe, Northern Italy, and the Rhone River Valley (Reinhardt et al. 2003).

Invasive species may cause relevant economic losses (Paini et al. 2016). Depending on methods, regional scale, and number of species included in various studies, the estimated costs vary from less than 1 million USD per year to costs corresponding to 12% of gross domestic product (GDP) for affected countries (Marbuah et al. 2014).

2.1.4. Theoretical background of plant invasion

Various hypotheses try to explain the causes of plant invasion, however, we do not have a single comprehensive hypothesis that can answer every question. The leading invasion hypotheses include the 'enemy release hypothesis' (Keane and Crawley 2002), the 'greater reproductive potential hypothesis', the 'empty niche hypothesis' (Stachowicz and Tilman 2005), and the 'novel weapons hypothesis (NWH)' (Callaway and Aschehoug 2000; Callaway and Ridenour 2004). Besides, increasing attention has been given to the mutualistic interactions between plants and fungi (Richardson et al. 2000a; Reinhart and Callaway 2006; Shah et al 2009; Bunn et al. 2015; Menzel et al. 2017).

2.1.4.1. Allelopathy in plant invasion

The 'novel weapons hypothesis (NWH)' is one of the most accepted hypotheses of plant invasion. A study of Callaway and Ridenour (2004) suggests that some invaders transform their environment, because they possess novel biochemical weapons that function as unusually powerful allelopathic agents, or as mediators of new plant-soil microbial interactions. Allelopathy is a complex phenomenon, because allelochemicals can be influenced by abiotic factors like environmental stress (Catalán et al. 2013) and biotic interactions including soil microorganisms (Inderjit 2005; Reinhart and Callaway 2006). Subsequently, allelopathic effects can also be complex. Many studies suggest that allelopathy may contribute to the ability of an exotic species to become invasive in new plant communities (Ridenour and Callaway 2001; Hierro and Callaway 2003; Callaway et al. 2005; Ledger et al. 2015), and invasive plants are more likely to have potent secondary compounds than native plants (Cappuccino and Arnason 2006). According to the NWH, exotic species may become invasive due to the production and allelopathic effect of biochemicals to which the native species are not adapted (Callaway and Ridenour 2004). The seasonal variation of biotic and abiotic factors such as the presence of herbivores (Karban 2007) and pathogens (Heil and Bostock 2002), as well as temperature (Lur et al. 2009), and precipitation (Gray et al. 2003) can have a pronounced effect on allelochemical synthesis in plants and in turn may cause seasonal changes in phytotoxicity. Although the production of allelochemicals can vary among plant tissues in flowers, leaves (leaf litter), stems, barks, and roots; and even within these tissues over the growing season (Roberts and Anderson 2001; Butcko and Jensen 2002; Ferguson et al. 2003; Khanh et al. 2005; Frizzo et al. 2008; Djurdjević et al. 2012; Helmig et al. 2013;

Anese et al. 2014; Chen et al. 2014; Silva et al. 2014), little attention has been paid to these dynamic changes in allelopathy research.

The most studied group of allelochemicals has been phenolic compounds (Harborne 1980; Kögel 1986; Djurdjević et al. 2005, 2011). Phenolic compounds may accumulate in the rhizosphere mostly due to residue decomposition, thereby influencing the accumulation and availability of soil nutrients and rates of nutrient cycling, which both ultimately affect plant growth (Li et al. 2010). Phenolic allelochemicals can inhibit root elongation, cell division, and change cell ultra-structure, interfering with the normal growth and development of the plant (Cruz-Ortega et al. 1998; Li et al. 2010). High concentrations of phenolic acids were detected in the leaves of *Helianthus tuberosus* (Chen et al. 2014), which were found to be the most allelopathic tissues of the plant (Khanh et al. 2005).

Although a large number of papers have discussed the allelopathic effect of invasive plants in the last decades, the role of allelopathy is far from fully clarified in biological invasions. The majority of studies consider only one time period for testing the allelopathic potential of a plant species, and therefore we have incomplete information about the allelopathic effect of invasive plants throughout the vegetation period.

2.1.4.2. Arbuscular mycorrhizal fungi (AMF) colonization in plant invasion

Around 80% of vascular plant species are associated with a special group of soil fungi known as arbuscular mycorrhizal fungi (AMF) in their natural habitats. These AMF symbioses are essential components in different terrestrial ecosystems (Arora et al. 1991, Turnau and Haselwandter 2002), because they can influence plant productivity and plant diversity (Heijden et al. 2015). Furthermore, AMF are known to promote vitality and fitness of hosts by increased plant mineral nutrition, especially the acquisition of phosphorus (Marschner 1997), enhanced water supply (Augé 2001), and by providing resistance to abiotic or biotic environmental stress (Birhane et al. 2012; Evelin et al. 2009; Füzy et al. 2008; Ruiz-Lozano et al. 2010).

Plant growth responses to mycorrhizal symbiosis can vary widely from highly parasitic to highly mutualistic (Raju et al. 1990; Klironomos 2002, 2003). Some studies report positive impacts of the AMF symbiosis on the growth and development of exotic plant species, which supports the hypothesis that the spread of invasive plant species could be facilitated by AMF (Fumanal et al. 2006, Chmura and Gucwa-Przepiora 2012). For

example, AMF can increase growth and competitiveness of *Centaurea stoebe*, which is one of the most invasive plant species in the intermountain west of the USA (Marler et al. 1999).

In contrast, increasing number of publications suggest that reduced mycorrhizal associations may also benefit invaders in a competitive environment (Seifert et al. 2009; Waller et al. 2016). Moreover, Pringle et al. (2009) proposed that exotic plants without obligate dependence on an AMF symbiont have greater chance to become invasive in the new community compared to those with strong AMF associations.

Responsiveness is the other crucial factor to determine whether invasive plant species are less reliant on the mutualism with AMF (Reinhart et al. 2017). Some suggested that a weak mycorrhizal responsiveness may be a general mechanism of plant invasion (van der Putten et al. 2007; Vogelsang and Bever 2009) because invasions often occur in disturbed habitats (Mooney and Hobbs 2000) that tend to harbor lower AMF abundance (Abbott and Robson 1991). Furthermore, Reinhart et al. (2017) suggested that invasiveness in general is associated with the degree of mycorrhizal responsiveness.

The aforementioned authors highlight that the role of mycorrhizal fungi colonization in plant invasion is controversial, therefore, further studies need to clarify its significance. Furthermore, the biogeographical aspects of mycorrhizal fungi colonization of invaders are among the key factors to understand its role, especially if we consider how little we know about mycorrhiza colonization of the majority of invasive plants in the Carpathian Basin (Mihály and Botta-Dukát 2004; Botta-Dukát and Mihály 2006).

2.1.5. Biogeographical aspects of plant invasion

In the past decades thousands of papers have been published about the introduction, spread, impact and management of invasive species (Davis 2011). The fact that invasion ecology has consisted primarily as a series of case studies has generally been viewed as a weakness of the research field in the last century (Williamson 1999). Sun et al. (2015) argue that experiments using native assemblages and an exotic “invader” might not be suitable to assess the diversity-invasibility relationship, since it might vary depending on whether the “invader” attempts to colonize its native or its invaded community. Hierro et al. (2005) call our attention to the lack of quantitative studies regarding the abundance and impact of exotic species both in the recipient and native communities. They highlight the need for documenting differences in abundance of exotics at home and away, as well as for applying a biogeographical perspective to test hypotheses that have been proposed

to explain exotic plant success. Invasive plants must possess some unique features that allow for such a degree of dominance in the introduced range. For example, several studies suggest that invasive species suppress diversity to a larger extent in the invaded range than in the native range (Pal et al. 2015; Ledger et al. 2015; Hejda et al. 2017), and European invaders have more profound impacts in North America than North American invaders in Europe, even though the macro climate of these areas is similar (Seastedt and Pyšek 2011; Hejda et al. 2017).

Overall, comparing the structure and diversity of plant communities at home and away, as well as analyzing environmental conditions that are essential in shaping these plant assemblages, can reveal new factors contributing to the success of invasive alien species (Davis et al. 2011).

2.1.6. Herbaria in the research of invasive plants

Due to the fact that currently there are around 3000 active herbaria in 180 countries worldwide which contain approximately 350 million specimens (Thiers 2017), herbaria collections are rich sources of information for ecologists, because the large plant collections are numerous and usually well preserved, and the majority of herbarium specimens have information-rich labels (Lavoie et al 2007).

Several studies suggest that herbarium specimens are useful tools in reconstructing the introduction and spread of invasive plant species (Pyšek 1991; Pyšek and Prach 1995; Saltonstall 2002; Lavoie et al. 2007), because herbaria contain a vast amount of valuable information to evaluate the plant's distribution (Loiselle et al. 2008; Fuentes et al. 2008, 2013; Csontos et al. 2010; Vishnyakova et al. 2016). Furthermore, they are the main and most remarkable sources of available historical data on alien plants (Fuentes et al. 2008). For example, Lavoie et al. (2007) not only reconstructed the spread of *Ambrosia artemisiifolia* in Québec by the help of herbarium specimens, but they also demonstrated the spatio-temporal dynamics of the habitat preferences of the invaders.

From the 350 million herbarium specimens approximately 5 million specimens have been used for documenting environmental changes or biogeographical patterns (Lavoie 2013), which suggests that in the future herbarium specimens can serve as remarkable sources of information regarding the distribution and spread of invasive plants in their non-native range.

2.2. *Helianthus tuberosus* (L.)

2.2.1. Origin and history

Helianthus tuberosus (Jerusalem artichoke) is an herbaceous perennial plant native to North America (Shoemaker 1972) (Fig. 2.2). The plant originates from the Great Lakes area (Simmonds 1976) or possibly from the Ohio and Mississippi River valleys (Wyse et al. 1986). The study of Gray and Trumbull (1883) suggests that native Americans who cultivated the plant must have obtained it from the valleys of the Ohio and Mississippi rivers and their tributaries, where it is still abundant. While a North American center of origin is well accepted based upon the distribution of *H. tuberosus*, it is not certain that the actual center of origin was today's Canada.

Figure 2.2. *Helianthus tuberosus* L. (Source: www. plants.usda.gov)

Wild populations of Jerusalem artichoke can be found in numerous areas of the United States and central Canada (Swanton et al. 1992), ranging from southeastern Canada and the eastern United States, westward to the Rocky Mountains (Gleason and Cronquist 1991).

H. tuberosus was first introduced to Europe by Lescarbot, a travel companion of Champlain, possibly in 1605 (Shomeaker 1927). It became widespread in Paris by 1617 both as food and fodder. In the meantime it was taken to other countries too, including the Netherlands (1613), Italy (1614), England (1617), and Germany (1627) (Balogh 2008). In those times the tubers of *H. tuberosus* were a significant source of dietary carbohydrate in Europe. However, its importance declined after the introduction of potato (*Solanum tuberosum*) (Kays and Notthingam 2007).

By the end of the 20th century its easy propagation by tubers and stolons transformed the species into an invasive plant and a significant weed (Balogh 2006, 2008). Moreover, after World War II numerous reports were published throughout Central Europe about the mass spread of a plant taxon belonging to *H. tuberosus*, especially along watercourses (Priszter 1960, 1997; Soó 1970). Today it is considered a significant invasive species in

Europe (Török et al. 2003, Negrean and Anastasiu 2004; Balogh 2008; Anastasiu and Negrean 2009; Fehér and Končeková 2009, Filep et al. 2010; Balogh 2012).

The history of *H. tuberosus* has been described in a number of articles (Kays and Notthingam 2007). Besides, the extent of its popularity is indicated by the number of books and monographs published (Parmentier 1790; Delbetz 1867; I'Só 1955; Bauer 1974; Diedrich 1991; Marcenaro 2002; Kays and Notthingam 2007).

2.2.2. Systematics

Helianthus tuberosus is member of the *Helianthus* L. genus, *Heliantheae* tribe, *Asteroideae* subfamily, Asteraceae family (formerly Compositae), and Asterales order (Borhidi 2008; Király 2009; Tutin et al. 2010) (Table 2.2). The Asteraceae family is one of the largest families of flowering plants with over 25 000 species (Bremer 1994), which are distributed throughout the world and occupy a wide range of habitat (Funk et al. 2009). The genus *Helianthus* is native to America, comprising 66 species (Balogh 2006, 2008).

Table 2.2. Taxonomic classification of *H. tuberosus*

Kingdom	Plantae
Subkingdom	Tracheobionta
Superdivision	Spermatophyta
Division	Magnoliophyta
Class	Magnoliopsida
Subclass	Asteridae
Order	Asterales
Family	Asteraceae
Genus	*Helianthus* L.
Species	*Helianthus tuberosus* L.

The taxonomical classification of adventive sunflowers (*Helianthus*) is controversial, regarding the question which species have naturalized in Europe or have spread as weeds, mostly in shoreline plant communities (Soó 1970; Balogh 2006, 2008). This can be attributed to the fact that the majority of herbarium specimens, identification manuals and

flora monographs lack descriptions of distinguishing features of below-ground parts (Balogh 2008).

Moreover, from the 20th century *H. tuberosus* has had two different aspects, being present both as a crop and an invasive species in Europe. The two different aspects of the plant are probably due to its unsettled taxonomy, because *H. tuberosus* and its close relatives (*H. decapetalus, H. strumosus*) are species that are difficult to distinguish, and often seem to grade into each other (Balogh 2006, 2008). *H. tuberosus* is a polyploid with 102 chromosomes, and polyploids are known to develop through the hybridization of two different species, giving rise to a progeny in which chromosome doubling occurs (Kays and Nottingham 2007). In addition, Bock et al. (2014) suggest that *H. tuberosus* crop species originates recursively from perennial sunflowers via hybridization between tetraploid hairy sunflower (*H. hirsutus*) and diploid sawtooth sunflower (*H. grosseserratus*), but we have no information about wild populations.

2.2.3. Morphology

There are various depictions of *H. tuberosus* from the 17th century, which not only demonstrate that the plant was well-kown in Europe by then, but also draw attention to the morphological differences (Fig. 2.3). The first botanist who described the plant was Fabio Colonna (1616), who no doubt contributed to the incorrect impression that the tubers were distributed throughout Europe from the Farnese Gardens in Rome (Kays and Notthingam 2007).

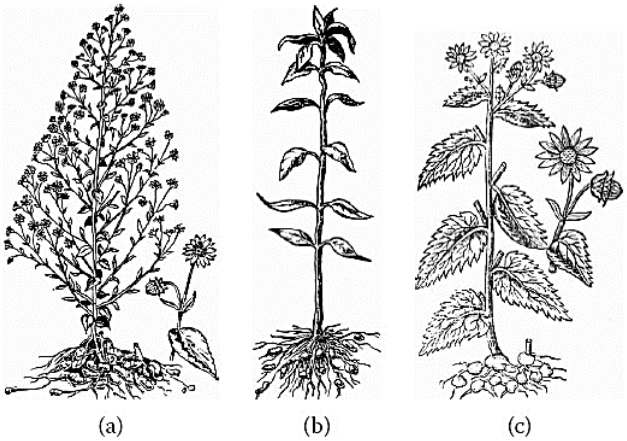


Figure 2.3. Botanical drawings of *H. tuberosus* by (a) Colonna (1616), (b) Lauremberg (1632), and (c) Parkinson (1640) from the early 17th century (Source: Kays and Notthingam 2007)

H. tuberosus is a perennial plant species, with coarse stems reaching around 3 m or taller (Heiser et al. 1969; Rogers et al. 1982; Balogh 2006, 2008; Kays and Notthingam 2007; Szabó 2010). Leaves are numerous, with opposite arrangement in the lower third, alternate above; their shape is broadly lanceolate or broadly ovate, being 10-25 cm long and 4-12 cm broad on better-developed individuals (Balogh 2006, 2008; Szabó 2010). The flower heads are yellow and resemble those of the cultivated sunflower (Swanton et al. 1992), but they are only 3-5 cm diameter with a 1.5-2.3 cm disk (Wyse and Wilfahrt 1982). Flower heads occur alone or in groups at the ends of the stem and axillary branches (Swanton et al. 1992; Kays and Notthingam 2007; Szabó 2010). The fruit is an achene, glabrous or hairy, and generally few are formed (Szabó 2010, Tutin 2010), usually less than 5 seeds are produced per flower head (Alex and Switzer 1976). The species produces slender rhizomes that become enlarged terminally into tubers (Heiser et al. 1969; Rogers et al. 1982; Swanton 1986). Tubers vary in size, shape and colour (Swanton et al. 1992). As a species, *H. tuberosus* is highly competitive, quickly shading the soil surface and creating a zone of captured resources, thereby repressing the growth of most other species (Kays and Nottingham 2007).

To overcome the problems raised by the unclarified taxonomy of the *Helianthus* genus, Balogh (2006, 2008) created the "Identification of sunflower species occurring in Central Europe as cultivated, escaped or naturalized populations". In these works, Balogh (2006, 2008) distinguished the wild and cultivated forms of *H. tuberosus* based on their morphological features, particularly the below-ground parts of the plants (Table 2.3).

Table 2.3. Main morphological differences of wild and cultivated Jerusalem artichoke (Source: Balogh 2008)

Feature	**wild Jerusalem artichoke (*H. tuberosus sensu lato*)**	**cultivated Jerusalem artichoke (*H. tuberosus sensu stricto*)**
Total height	1.5-3.5 m	1.5-3.0 m
Below-ground parts: rhizome length	15-20 cm	8-10 cm
Below-ground parts: modifications of rhizomes and their shape	rhizomes with terminal swellings, and often narrow fusiform, ± elongated tubers	rhizome lateral shoots with large, mostly rounded or thick, fusiform tubers
Number of heads	(5-) 40-100 (-150)	3-7
Head diameter	7-12 cm	4-8 cm
Number of ray florests	10-20	10-15
Degree of naturalization	naturalized, invasive	casual (occasionally escaping)

2.2.4. *Helianthus tuberosus* in its native (North America) and in non-native (Carpathian Basin) range

As we mentioned before, *H. tuberosus* is native to North America (Balogh 2006; Kays and Nottingham 2007). The tuber of *H. tuberosus* was discovered as a food source by Native Americans (Moerman 1998; Kays and Nottingham 2007), who ate the tubers both raw and cooked (Kosaric et al. 1984). The Indian name "skibwan" means "raw thing", suggesting that tubers were eaten raw like a radish (Kosaric et al. 1984). The plant occurs mainly along rivers but also favors humid, open or shady habitats with clayey soils. It can also be abundant on oldfields and fallows. In the eastern parts of North America it is a common roadside plant as a relict from Native Americans' cultivations (Balogh 2008; Kays and Nottingham 2007). Furthermore, it grows better in the northern United States than in the far south (Boswell 1959) and has also been successfully grown in Alaska (Munro 1928).

Based on literature data, the judgment of *H. tuberosus* has been controversial in the Carpathian Basin for the last few centuries. In the genus *Helianthus*, *H. tuberosus* is the

second most significant species after the economically valuable *H. annuus*, due to the acceptable nutritive value accompanied by a high biomass yield and carbohydrate content (Kays and Nottingham 2007; Balogh 2008, 2012). The main storage carbohydrate of the tuber is inulin, which is beneficial in the diet of people suffering from *diabetes mellitus* (Kleessen et al. 2007; Roberfroid 2007; Kays and Nottingham 2007). The first study which refers to the cultivation of the plant in the Carpathian Basin was written as early as 1664 by Lippay, who provided useful information about the cultivation of the species. In addition, a large number of publications referred to the cultivation of *H. tuberosus* in the first part of the 20th century (Bittera 1922; Gyárfás 1925; Villax 1940; I'só 1943; Grábner 1948).

At the same time, an increasing number of references focus on the negative aspect of the plant in the non-native territories. Based on its easy propagation by tuber and stolon, *H. tuberosus* is considered one of the significant invasive plants of Europe (Balogh 2008, 2012, Müller and Sukopp 2016, EPPO 2018; DAISIE 2018). In the Carpathian Basin it occurs in most countries (Török et al. 2003; Negrean and Anastasiu 2004; Kovács 2006; Balogh 2006, 2008, 2012; Anastasiu and Negrean 2009; Fehér and Končeková 2009). Early examples on documenting the plant's occurrence in the Carpathian Basin include a reference to Temes county, where "it is grown or it has escaped" (Borbás 1884), and to Vas county in Western Hungary (Balogh 2008). According to Priszter (1997), the first data on the escaping of the plant known as *H. decapetalus* (having naturalized for quite a while) dates back to 1910 (Balogh 2006, 2008). The most important vectors are rivers and brooks, which can transport the tubers to large distances (Balogh 2008; 2012).

3. OBJECTIVE

In this study, we sought to obtain a better understanding of *Helianthus tuberosus* invasion. We organized our research around the following objectives:

1. We aimed at clarifying the distribution of *H. tuberosus* in the Carpathian Basin from the time of the plant's introduction until 1990, using data obtained from herbarium specimens.

2. We aimed at understanding how allelopathy acts as a complex mechanism for *H. tuberosus* invasion, thus:
   - First, we used bioassays to determine the effect of *H. tuberosus* root and leaf extracts on seed germination and initial plant growth of *Sinapis alba* (L.) and four species commonly co-occurring with *H. tuberosus.*
   - Secondly, we sought to gain insight into the seasonal dynamics of phenolic compounds at monthly intervals throughout the plant's seasonal development by supercritical fluid chromatography.
   - Lastly, we wanted to determine whether *H. tuberosus* had an allelopathic effect on four commonly co-occurring species, via allelopathic root exudates in a pot experiment.

3. In our biogeographic study we aimed at clarifying the main differences of *H. tuberosus* in its native (North America) and non-native (Europe) ranges, thus:
   - First, we acquired field evidence of interactions between *Helianthus* and co-occuring species, we characterized communities with *Helianthus* in its native and non-native ranges.
   - Secondly, we aimed at resolving which factors influence the species composition of *H. tuberosus* stands by analyzing 27 variables.
   - Lastly, we acquired information about arbuscular mycorrhizal fungi (AMF) colonization of *H. tuberosus* at home and away, and thereby got closer to clarifying its role in plant invasion.

4. MATERIALS AND METHODS

4.1. *Helianthus tuberosus* in the Carpathian Basin

4.1.1. Distribution of *Helianthus tuberosus*

4.1.1.1. Study area

The Carpathian Basin is located in East-Central Europe, forming a topographically distinct unit surrounded by the Carpathian Mountains, the Alps, and the Dinarides (Perczel 1996; Dövényi 2012). Due to geographic features, we can consider the study area as a whole, because political boundaries do not correspond to biological and ecological barriers (Richardson et al. 2000b).

The periphery of this area can be characterized mostly by alpine and subalpine vegetation, which turns into broadleaved deciduous forest at lower elevations. The central part of the basin is dominated by submediterranean forest-steppes, although only remnants of salty and sand steppes have survived to date (Dövényi 2012). The native flora of the Carpathian Basin is rich, including about 6000 species in the Carpathian Mountains and lowlands, which counts more than 7500 species with introduced and invasive species (Bajňanský and Fargašová 2007).

4.1.1.2. Data collection in herbaria

To obtain more information about the presence and distribution of *Helianthus tuberosus* in the Carpathian Basin, we examined *H. tuberosus* specimens available in 16 herbaria between 2008-2016 (Table 4.1).

The identity of the specimens examined was confirmed based on their morphology, which was clarified by identification keys (Balogh 2008). All available specimens were collected from the time of the plant's introduction until 1990 which was a crucial year not only in European politics but also in the spread of the species due to the removal of the iron curtain.

In the literature there are different views about the taxonomy of *H. tuberosus*, because the majority of herbarium specimens, identification manuals and flora monographs lack the description of the crucial distinguishing features of below-ground parts (Balogh 2006, 2008, 2012). Therefore, in this study we will discuss features of *H. tuberosus* agg. (species aggregata), which includes wild *H. tuberosus* (*H. tuberosus* sensu lato), and cultivated *H.*

tuberosus (*H. tuberosus* sensu stricto). In addition, we would like to revise *Helianthus decapetalus* specimens, analyzing the studies of some Eastern-European researchers who identified and considered *H. tuberosus* as *H. decapetalus* in the 20th century (Balogh 2006, 2008, 2012).

Table 4.1. The visited herbaria in the Carpathian Basin between 2008-2016

Herbarium	**Country**	**County/Region**	**Settlement**	***H. tuberosus* specimen**
Herbarium of the *Alexandru Borza* Botanical Garden and Botanical Museum [CL]	Romania	Cluj	Cluj-Napoca	yes
Herbarium of the Comenius University	Slovakia	Bratislava	Bratislava	no
Herbarium of the *Eszterházy Károly* University	Hungary	Heves	Eger	no
Herbarium of the *Haáz Rezső* Museum	Romania	Harghita	Odorheiu Secuiesc	no
Herbarium of the Hungarian Natural History Museum [BP]	Hungary	Pest	Budapest	yes
Herbarium of the Mátra Museum	Hungary	Heves	Gyöngyös	no
Herbarium of the *Móra Ferenc* Museum [SZE]	Hungary	Csongrád	Szeged	yes
Herbarium of the *Munkácsy Mihály* Museum	Hungary	Békés	Békéscsaba	yes
Herbarium of the Pásztó Museum	Hungary	Heves	Pásztó	no
Herbarium of the *Rippl-Rónai* Museum	Hungary	Somogy	Kaposvár	no
Herbarium of the Savaria Museum [SAMU]	Hungary	Vas	Szombathely	yes
Herbarium of the Slovak National Museum in Bratislava	Slovakia	Bratislava	Bratislava	no
Herbarium of the *Tuzson János* Botanical Garden	Hungary	Szabolcs-Szatmár-Bereg	Nyíregyháza	no
Herbarium of the University of Debrecen [DE]	Hungary	Hajdú-Bihar	Debrecen	yes
Herbarium of the University of Nyíregyháza	Hungary	Szabolcs-Szatmár-Bereg	Nyíregyháza	no
Herbarium of the University of Pécs	Hungary	Baranya	Pécs	yes

Abbreviation: square brackets [ ] contain the international abbreviation of institute (Index Herbariorum)

The specimens were documented by photos, and all data of the labels were entered into an Excel spreadsheet. The recorded information included the following: common species name, date and place of collection, collector's name, and other useful information. The distribution map of the species was prepared in ArcMap 10.3.

4.1.2. Allelopathy effect of *Helianthus tuberosus*

4.1.2.1. Bioassays

To determine the inhibitory effect of *H. tuberosus* on the germination and growth of other plant species, we performed bioassays with aqueous extracts from roots and leaves of *H. tuberosus*. The root and leaf samples were collected along a stream in South Hungary (Pécsi-víz, 46°02′ N, 18°12′E). Four specimens of the plant were collected along a one-km-long transect on the first day of each month from June to October 2013. Plant parts were washed with water and dried at room temperature. Roots and leaves were detached from the dried plants, were separated by tissue and ground in a KM13-type grinder (Robert Bosch Hausgeräte GmbH, Stuttgart, Germany). Four replicate extracts were prepared from the leaves and roots samples from four different plants. Five grams of air-dry sample of each replicate was measured into glass vials, and 100 mL of distilled water was added. The vials were kept on a KL-2 type shaker (Edmund Bühler GmbH, Hechingen, Germany) for 24 h at 150 mot1/min. Samples were filtered twice through cotton, then twice through Whatman# 1 filter paper.

The solvent was partially evaporated from the filtrates by RV 0400 SD-type rotary evaporator (Dialab Kft., Hungary). For bioassays, the concentrations of 1 and 10 μg/mL were set on the basis of plant dry matter content, by adding the appropriate amount of distilled water.

Based on our field observations, four species that commonly co-occur with *H. tuberosus* were selected for performing bioassays (*Elymus repens*, *Galium mollugo*, *Solidago gigantea*, and *Tanacetum vulgare*). In the field, similarly to *H. tuberosus*, these test species germinate in spring (Ujvárosi 1973). We also included *Sinapis alba*, a frequently used test species in bioassays (Bogatek et al. 2006; Csiszár et al. 2012; Pannacci et al. 2013).

The seed surfaces of test species were sterilized by soaking in 50 % ethanol for 1.5 min. For each of the four replicates, 15 seeds of a test species were evenly placed on filter papers in sterilized 196 cm^2 Petri dishes. Five mL of the 1 or 10 μg/mL *H. tuberosus* leaf or root extracts was added to each Petri dish per treatment, and distilled water was used as control. During the 5 months, altogether 600 Petri dishes were used. Dishes were incubated in a germination chamber at an average temperature of 20 °C for 6 days. On the 4^{th} day of the experiment, additional 2 mL of the appropriate extract was given to each Petri dish to avoid desiccation. Germination (%) was determined by counting the number

of germinated seeds after 6 days. Radicle and plumule lengths of germinated seeds were measured to the nearest millimeter using a centimeter scale.

4.1.2.2. Identification of allelochemicals

We used supercritical fluid chromatography (SFC) coupled with diode array detector and mass spectrometer (DADMS) to identify and quantify the production of phenolic compounds in *H. tuberosus* leaves and roots throughout the vegetation period. After cleansing and drying, Jerusalem artichoke leaf and root samples were ground in a KM13-type grinder (Robert Bosch Hausgeräte GmbH, Stuttgart, Germany). The fragments were separated by sieves according to Pharmacopoeia Hungarica VII (Végh 1986), the nominal dimensions of apertures being between 0.32-1.20 mm.

An aliquot of 100 mg of dried leaf or root sample was extracted with 1500 μL 100 mM of aqueous ammonia solution in an ultrasonic bath for 10 min and then centrifuged at 20,000 RCF for 10 min. To 500 μL of the supernatant, 5.55 μL trifluoro-acetic acid was added; after vortex homogenization, the extract was centrifuged again at 20,000 RCF for 10 min. To 450 μL of the supernatant, 450 μL tert-butyl alcohol was added; after homogenization, 200 μL tert-butyl-methyl ether was added to the mixture. From the upper layer, 550 μL was frozen at -55 °C. The frozen sample was lyophilized and stored at -20 °C until further analyzed. Freeze-dried extracts of root and leaf samples were redissolved directly before the chemical analysis in 60 μL iso-butyl alcohol:heptane 1:1.

The concentrations of the investigated compounds (salicylic acid, coumarin, 4-OH-benzaldehyde, transcinnamic acid, and 2-OH-cinnamic acid, all standards obtained from Sigma Aldrich Ltd.) were determined in the extracts with an SFC system comprising a Waters UPC2 core system with a photodiode array detector (Acquity UPC2 PDA), a single quadrupole detector (Waters SQD), a makeup pump (Waters 515), and an Acquity UPC2 BEH column (1.7 μm, 3.0 9 100 mm).

The gradient consisted of solvent A (supercritical carbon dioxide medical grade) and solvent B (15 mM ammonium acetate in ethanol, MS grade, and gradient grade) applied at a flow rate of 1.25 mL/min as follows: from 97 % A at 0 min to 70 % A at 4.5 min in a linear gradient; from 70 % A at 4.5 min to 60 % A at 7 min in a linear gradient; from 60 % A at 7 min to 97 % A at 7.5 min in a linear gradient; the makeup pump worked isocratically at a flow rate of 0.20 mL/min with ethanol (gradient grade). The column was

thermostatted at 60 °C and the backpressure regulator was set to 200 bar. From the redissolved extracts, thermostatted in the autosampler at 15 °C, 1 µL sample was injected. The DAD scan range was set from 200 to 600 nm. The mass spectrometer scan range was set from 30 to 300 m/z in negative ion mode. The signal of coumarin was monitored at 267 nm, salicylic acid at 137.1 m/z, 4-OH-benzaldehyde at 121.1 m/z, trans-cinnamic acid at 147.1 m/z, and 2-OH-cinnamic acid at 163.1 m/z. Compounds were identified by comparing their retention times and UV spectra or mass spectra with those of standards and were quantified using external standard calibration curves. The lower limit of detection was 100 ng/mL (0.218 µg/g dried plant) for 4-OH-benzaldehyde; 250 ng/mL (0.545 µg/g dried plant) for salicylic acid and for trans-cinnamic acid; 500 ng/mL (1.092 µg/g dried plant) for 2-OH-cinnamic acid; and 1000 ng/mL (2.183 µg/g dried plant) for coumarin.

4.1.2.3. Competition experiment

To test whether the root exudates of *H. tuberosus* had an allelopathic effect on co-occurring species (see above), we grew *H. tuberosus* and test species together with and without activated carbon in a greenhouse. Each species was planted in 7.5x9x10 cm (588.75 cm^3 volume) containers alone and in all pairwise species/*Helianthus* combinations in 14 replicates. This resulted in a total of 560 pots with 1008 plants (Fig. 4.1).

Figure 4.1. *H. tuberosus* and test species in the greenhouse

The pots were filled with a 50:50 mixture of sterilized soil and sand (mean grain size 0.85 mm). The soil was collected from four different Southern Transdanubian floodplains (Baranya patak, Baranya csatorna, Bükkösdi-víz and Pécsi-víz) where *H. tuberosus* was present.

Finely ground activated carbon (SORBOPOR MV 125) in the concentration of 20 ml L^{-1} was added to the sand and soil mixture in half of the containers with solitary test species and with test species/*Helianthus* combinations. Activated carbon is often used in allelopathy studies, because it efficiently absorbs biochemicals, due to its high surface to volume ratio (Callaway and Aschehoug 2000; Murrell et al. 2011; Del Fabbro et al. 2014;

Del Fabbro and Prati 2015). The soil was sterilized by autoclaving at 121°C for 1 h (Raypa AE28 DRY), partly to avoid the effect of the majority of soil microbes (Inderjit 2005) and partly because activated carbon can disrupt plant symbioses (Wurst et al. 2010). Pots were arranged in a completely randomized design and were rotated weekly to minimize spatial variation.

The tubers of *H. tuberosus* were collected from four natural populations (same as above for soil samples) during the first part of April 2014. The seeds of test species were provided by the Research Centre for Agrobiodiversity, Tápiószele, Hungary, with the exception of *S. gigantea* seeds, which were collected in a natural population in South West Hungary.

The experiment was terminated after 4 months, when the number of shoots was counted, and the height of all plants was measured. Afterward, the plants were harvested, dried at 60°C, and weighed for aboveground, belowground, and total biomass.

4.1.2.4. Data analysis

Statistical analyses were carried out in R software version 3.1.2 (R Development Core Team 2014). Bioassay analyses were accomplished to test the allelopathic effects of different plant organs of *H. tuberosus* at different sampling times on the measured attributes of the five test species. Our dependent variables were the measured attributes (germination; radicle length, and plumule height of germinated specimens), while the independent variables were the plant organs, sampling time, the test species, and concentration. Germination was analyzed using a generalized linear model (function glm; Binomial error distribution; link function: logit), while radicle length and plumule height were analyzed using a linear model (function lm; Gaussian error distribution; link function: linear). Analyses of the concentrations of different chemicals of *H. tuberosus* were performed with a linear model (function lm; Gaussian error distribution; link function: linear), where the dependent variables were the concentration of agents, and the independent variables were the plant tissues and sampling time.

Analyses of the pot experiment of *H. tuberosus* were carried out with mixed models using function lmer and glmer (Bates et al. 2015), where the dependent variables were the measured attributes (survival, stem number, height, root, shoot, and total biomass), and the independent variables were the identity of neighbors and the presence or absence of

carbon to test the allelopathic effects of *H. tuberosus* on co-occurring species. All independent variables were treated as fixed factors and population of *H. tuberosus* was treated as a random factor. Survival was analyzed with generalized linear mixed models (function: glmer; Binomial error distribution; link function: logit), while the other variables were analyzed with linear mixed models (function lmer; Gaussian error distribution; link function: linear). Number of stems was log transformed.

Omnibus statistics in model of germination and survival were carried out with log-likelihood tests, while the other models were carried out with Type III F tests. Transformation and testing residuals were based on graphical evaluation according to Crawley (2014). For pairwise comparisons, Tukey post hoc tests were conducted in both cases with multcomp package (Hothorn et al. 2008).

4.2. *Helianthus tuberosus* at home and away

4.2.1. Study area

Our study "at home" was carried out in the Midwestern United States, which is the native range of *H. tuberosus* (Balogh 2008). As provided by archaeological evidence, *H. tuberosus* was grown in the Mississippi valley as early as 3000 B.C. (Balogh 2006, 2008). Beside the Great Lakes the Mississippi River is another great waterway, because with its tributaries, the Missouri and Ohio rivers are the largest river systems in the region (Wuebbles and Hayhoe 2004). The Midwest is located far from the moderating effects of the oceans, and lacks mountains to the north or south. The climate here can be characterized by large daily temperature fluctuations, and unpredictable precipitation patterns (Kunkel et al. 2013). From the twelve Midwestern states (Faber-Langendoen 2001) Illinois, Indiana, Iowa, Minnesota and Wisconsin were our study area (Fig. 4.2).

In the non-native range, the selected study area is located in the Carpathian Basin, which is part of East-Central Europe. The geographical characteristics of the Carpathian Basin have been detailed above; therefore, we only summarize information relevant to this chapter. Our study area represents three countries in the Carpathian Basin, namely Hungary, Romania, and Ukraine (Fig. 4.2).

Our study sites were located at 41°17'-44°3' latitudinal and 87°11'-95°03' longitudinal gradient in native range; and 45°51'-48°26' latitudinal and 16°25'-48°28' longitudinal gradient in non-native range. The studied area in North America is covered by temperate continental forest (TeDc), characterized by warm summers, cold winters and changeable

weather during the fall. Earlier this entire zone was heavily forested, however, the majority of the forests around the Great Lakes and the northeastern United States have disappeared due to urbanization and agricultural activity. In addition, temperate steppe (TeBSk) zone was also represented, influenced by its location in the heart of the continent. Spear grass (*Heteropogon contortus*), wheat grass (*Agropyron* spp.) and blue grama grass (*Bouteloua* spp.) used to be the dominant species in this grasslands, while sagebrush (*Artemisia tridentata*) is still abundant (FRA 2001).

Our study site in Europe is dominated mostly by the temperate continental forest (TeDc) zone, which is characterized by warm summers and cold winters, and the main vegetation consists of various forest types, their distribution influenced by climatic gradients and nutrient availability. Deciduous broadleaved forests are dominant elements, such as oak-hornbeam and mixed forests in Central Europe (FRA 2001).

Sites in the non-native range were at consistently higher altitudes than in the native range (155 to 279 m in the native range; 95 to 510 m in the non-native range).

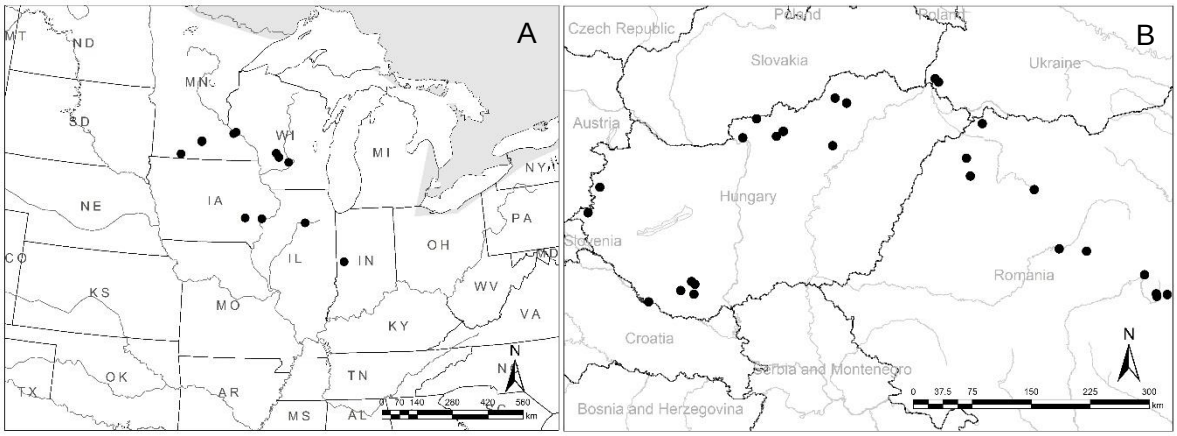


Figure 4.2. Distribution of study sites in (A) North America, the native range, and (B) Europe, the non-native range of *Helianthus tuberosus*. The scale is too large to separate many individual points that represent more than one stand of *H. tuberosus*

4.2.2. Field study – field measurements

To acquire field evidence of interactions between *Helianthus* and neighboring species we described *Helianthus* communities in its native (North America) and non-native (Europe) ranges. Communities were described from plot surveys conducted along 11 freshwater streams in native range and 29 freshwater streams in non-native range. *Helianthus* communities were identified with the help of *H. tuberosus* distribiution maps issued by

the United States Department of Agriculture (USDA) in North America (USDA 2018), while Hungarian distribution maps of the plant aided our field work in Europe (Bartha and Király 2015).

In the fall (September-November) of 2013 we sampled 201 2×2 m plots in a roughly 350×610 km area in the United States; while 750 individual 2×2 m plots were surveyed in a roughly 270×750 km area in Europe in four consecutive years (2012-2015). The size of the plots (4 m^2) was determined based on the study of Dancza (2007), who suggested that the adequate plot size of ruderal plant communities was between 4 and 9 m^2. At each plot we estimated absolute aerial coverage of all vascular plant species in order to see how the presence of *Helianthus* influenced species richness and composition. The plots were randomly selected on river banks that had previously been found to contain *H. tuberosus*, and coverage of *H. tuberosus* ranged from 0 to 100%. By using a handhold global positioning system (GPSMAP® 60CSx Garmin) we identified geographical position of the plots.

In each plot, we counted the total number of *Helianthus* stems; we measured the height of ten randomly chosen individual stems of the studied species, and we recorded percentage of bare ground, and percentage of litter.

4.2.2.1. Data analyses

In total, 951 plots were obtained from the two ranges and they were entered into a TURBOVEG database (Hennekens and Schaminée 2001).

Comparison of the mean height, stem number, and litter of *H. tuberosus;* species richness; and bare ground in the native and non-native range were performed with Mann-Whitney-Wilcoxon test. P-values were estimated asymptotically from 10000 permutations of the raw data.

The diversity of the two studied ranges was analyzed using multiplicity-adjusted p-values (Pallmann et al. 2012) for differences in effective numbers of species of orders 0, 1 and 2 (Jost 2006) and 10000 bootstrap samples.

For each range, we correlated total species number with the *H. tuberosus* cover using Spearman's rank correlation, and trend lines were fitted using LOESS local polynomial regression (Cleveland and Devlin 1988). The relationships between *H. tuberosus* cover (as response variable) and the number of *H. tuberosus* stems (as predictor), as well as between bare ground cover (response) and *H. tuberosus* stems (predictor) were examined

by beta regression (Cribari-Neto and Zeileis 2010) with logit link and cover values expressed on (0; 1) range. First, we built models separately for the two continents to examine specifically the relationships in North-America and Europe. Then, for testing the difference between the two continents, two other models were specified, separately for each response variable. The first model included the response and a single predictor variable, containing all values regardless of the continent. In the second model, besides the number of stems as a predictor, we included also the continent as an interactive term. Then, for these two models (that is, with and without continent as an interactive term) the Bayesian Information Criterion (BIC) was calculated. If the second model obtained lower BIC values, it indicated that inclusion of the continent as a model term improved model fit, thus the continent had a significant effect.

The entire statistical analysis was performed in R environment (version 2.11.1; R Development Core Team) using the vegan (version 1.17-2; Oksanen et al. 2010), the simboot (version 0.2-5; Scherer and Pallmann 2014), the coin (Hothorn et al. 2006) and the betareg (Cribari-Neto and Zeileis 2010) packages.

4.2.3. Factors which could affect the species composition - data collection

Average soil samples (~1000 cm^3 from the upper 20 cm layer) were collected from heavily infested and no *H. tuberosus* infestation territory, conducted in diagonal patterns according to the 90/2008 (VII.18.) Ministry of Agriculture and Regional Development (MARD) Decree, Hungary. The soluble nutrient element content of the soil was tested according to the Hungarian Standard (MSZ 20135:1999) method. The samples were analyzed in the Soil and Plant Testing Laboratory of Újfehértó, Hungary, accredited by NAH (National Accreditation Authority).

For each field investigated 23 environmental variables were compiled, including (a) altitude (1); (b) soil properties, such as (2) soil pH (KCl), (3) soil pH (H_2O), (4) soil texture (coarse sand, sand, sandy loam, loam, clay loam, clay), assessed on the basis of Stefanovits et al. (2005), (5) the content of salt (m/m%), referring to the total amount of salt in the soil that can be dissolved in water, (6) organic matter (m/m%), (7) $CaCO_3$ (m/m%), (8) the content (mg/kg) of N, (9) P_2O_5, (10) K_2O, (11) Na, (12) Mg, (13) NO_3-N+NO_2-N, (14) SO_4, (15) Cu, (16) Mn, (17) Zn; (c) climatic conditions, represented by (18) average annual temperatures and (19) average annual precipitation, (20) average annual temperatures of 1960-1990, (21) average annual precipitation of 1960-1990, (22)

mean annual hours of sunshine, and (23) mean annual hours of sunshine between 1960-1990 obtained from the Hungarian Meteorological Service (HMS 2001), National Administration of Meteorology (Romania), and WorldClim Databases (Hijmans et al. 2005) (Table 4.2).

In addition, from the field measurements, the number of *H. tuberosus* stems, height of *H. tuberosus*, percentage of bare ground, and percentage of litter in the plots were also factors, which could affect species composition.

Table 4.2. Units and ranges of environmental variables used

Variable (unit)	**Native range (North America)**	**Non-native range (Europe)**
Altitude (m)	155-279	95-510
Climatic properties		
Mean annual temperatures (^oC)	5.38-12.33	7.75-12.15
Mean annual temperatures of 1960-1990 (^oC)	5.83-11.38	7.4-11.28
Mean annual precipitation (mm)	58.2-87.31	43.72-71.85
Mean annual precipitation of 1960-1990 (mm)	57.15-78.31	43.36-64.27
Mean annual hours of sunshine	-	167.57-372.5
Mean annual hours of sunshine (1960-1990)	-	75.8-184.1
Soil properties (m/m%)		
$CaCO_3$	0.1-0.1	0.1-3.26
Nitrogen	0.03-0.39	0.03-0.36
Organic matter	0.60-5.19	0.85-5.15
Salt	0.02-0.08	0.02-1.84
Soil properties (mg/kg)		
P_2O_5	64.4-573	17.5-1429
K_2O	59.6-836	107-954
Na	20-63.3	20.1-97.9
Mg	113-974	78.2-755
NO_3^--N+NO_2^--N	1.4-61.1	1.86-207
SO_4^{2-}	50-164	50-425
Cu	1.52-8.31	1.71-12.6
Mn	28-744	38.6-761
Zn	0.93-83.2	0.67-169
Soil pH (H_2O)	6.06-8.02	6.57-8.11
Soil pH (KCl)	5.25-7.62	5.71-7.69
Soil texture (K_A)	25-63	32-69

4.2.3.1. Data analysis

The relationship between environmental factors and plant species composition were analyzed by redundancy analysis (RDA). Before performing the RDA, cover values were subjected to Hellinger transformation (Legendre and Gallagher 2001). According to Legendre and Gallagher (2001), this procedure is able to relate multivariate species data

to explanatory variables more accurately than the commonly applied canonical correspondence analysis (CCA), even if the species response curves are unimodal. As a next step of the multivariate analysis, we assessed gross effects of each explanatory variable according to the methodology of Lososova et al. (2004). The gross effect of a variable was defined as the variation explained by an RDA containing the studied predictor as the only explanatory variable. We also calculated the percentage of the total explained variation and adjusted R^2 of the RDA model, which contained all explanatory variables.

The statistical analyses were performed in R environment (R Development Core Team 2010) by using the vegan package (Oksanen et al. 2010).

4.2.4. Arbuscular mycorrhizal fungi (AMF) colonization

4.2.4.1. Estimation of AMF colonization

To acquire information about arbuscular mycorrhizal fungi (AMF) colonization of *Helianthus tuberosus* at home and away, we collected 64 root samples from the native range, and 56 root samples from the non-native range between 2012-2015. Furthermore, to acquire information about interaction of AM colonization and coverage of *H. tuberosus*, we collected *H. tuberosus* root samples (1) from plots where the coverage of *H. tuberosus* was lower than 50%, and (2) from plots where the coverage of the studied plant was higher than 50%, both in native and non-native range.

Root samples were cleared in 15% KOH for 40 minutes and then rinsed in water, stained in aniline-blue for 30 minutes and fixed in 40% lactic acid for 30 minutes according to the method of Trouvelot et al. (1986). The samples were stored in 40% glycerol until analyzed. Thirty 1-cm-long fragments per replicate were placed on glass slides. Using a light microscope (Motic SFC-28) at magnification 100×, the amount of vesicles and hyphae was assessed in intensity classes of zero to five, and the amount of arbuscules in classes of zero to three as described by Trouvelot et al. (1986). Using the MYCOCALC program (Trouvelot et al. 1986), the following parameters were determined: 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%), arbuscule abundance in the root system (A%), arbuscule abundance in mycorrhizal parts of root fragments (a%).

4.2.4.2. Data analysis

Comparison of the arbuscular mycorrhizal fungi (AMF) colonization of *H. tuberosus* in the native and non-native ranges was performed with asymptotic Mann-Whitney-Wilcoxon test. P-values were corrected by Bonferroni's method.

The statistical analyses were performed in R software environment (R Development Core Team 2010) using the coin package (Hothorn et al. 2006).

5. RESULTS

5.1. *Helianthus tuberosus* in the Carpathian Basin

5.1.1. Distribution of *Helianthus tuberosus*

Altogether, 65 *Helianthus tuberosus* agg. specimens (Fig. 5.1) were examined in the visited 16 herbaria, which were collected from at least 31 different places by 31 authors.

Figure 5.1. *Helianthus tuberosus* agg. specimen from the 19th century (collected by Czetz in 1856)

Nowadays, these data represent four countries in the Carpathian Basin, namely Hungary, Romania, Slovakia, and Ukraine (Fig. 5.2). The majority of *H. tuberosus* agg. specimens were originally identified as *H. tuberosus* (37 specimens), while 28 specimens were identified as other species belonging to the *Helianthus* genus (mostly *H. decapetalus*) (Table 5.1).

According to the number of the deposited specimens, the Herbarium of the *Alexandru Borza* Botanical Garden and Botanical Museum [CL] is the richest from our point of view, possessing 30 *H. tuberosus* agg. specimens, which were collected in Transylvania. The majority of the specimens were originally identified as *H. decapetalus*, and only 9 specimens were named as *H. tuberosus* in this collection. The second richest herbarium is the Herbarium of the Hungarian Natural History Museum [BP] with 22 *H. tuberosus* agg. specimens.

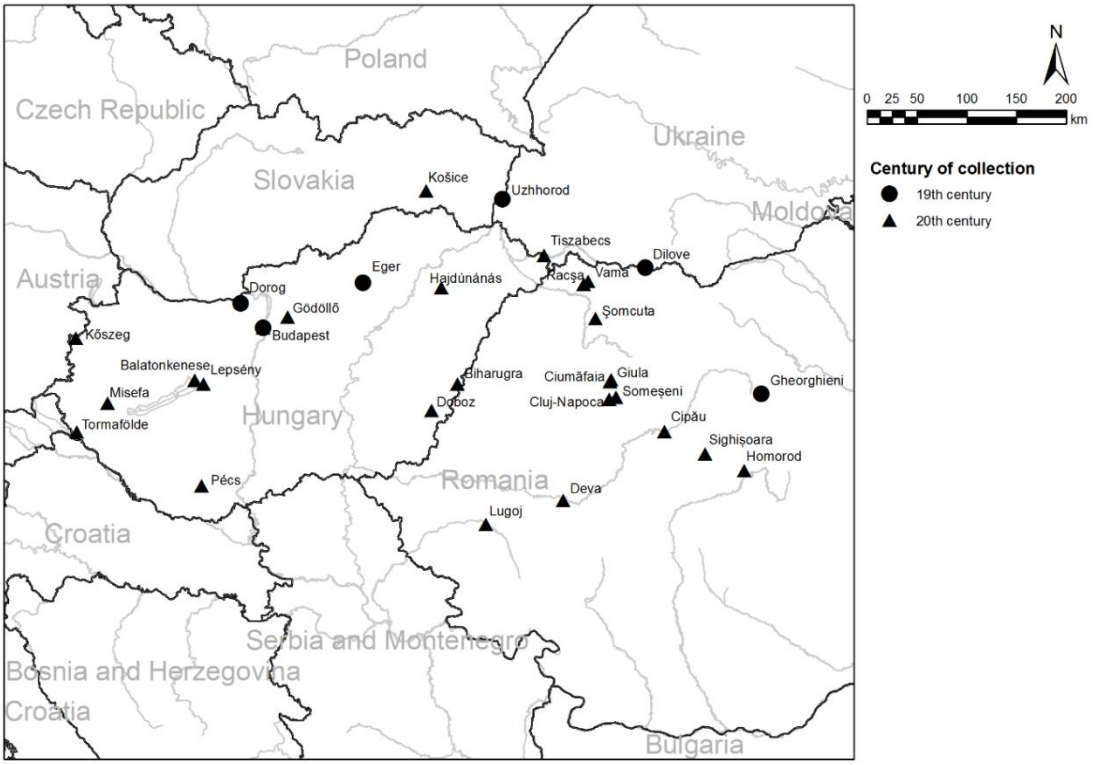


Figure 5.2. Distribution of *Helianthus tuberosus* in the Carpathian Basin based on the 65 herbarium specimens from the time of the plant's introduction until 1990

In temporal aspect, from the documented 65 specimens of the studied collections, the oldest *H. tuberosus* agg. specimens were collected in the 19th century (12 specimens). The exact date of collection is unclarified in the case of five out of twelve specimens from the 19th century. To our knowledge, only one specimen represents the first part of the 19th century (Baumgarten 1826), while the others were collected in the second part of the century. The majority of the specimens were collected in the 20th century (Fig 5.2).

Considering the place of collection, the majority of *H. tuberosus* agg. specimens were collected from cultivation or in floodplains of rivers. Besides the main information of the labels (common species name, date and place of collection, collector's name), other valuable data were documented, which refer to the cultivation or the invasive character of the plant (Table 5.1). For example, it created an invasive stand along the Hernád river (Košice, Slovakia 1941), or it escaped from cultivation in Pest county (Gödöllő, Hungary 1949).

Table 5.1. *Helianthus tuberosus* agg. specimens in herbaria from the Carpathian Basin

Herbaria	Country	County	Settlement	Year of collection	Collector's name	Other data
Herbarium of the *Alexandru Borza* Botanical Garden and Botanical Museum [CL]	Romania	-	-	1826	Baumgarten J.	revised by Filep R. in 2009; originally identified as *H. decapetalus*
	Romania	Cluj	Gheorghieni	1856	Czetz A.	cultivated plant
	Romania	-	-	19thcentury	Pávai-Vajna E.	from Transylvania
	Romania	Cluj	Cluj-Napoca	1903	Richter A.	-
	Romania	Cluj	Giula	1941	NyárádiEGy.	reed plot in meadows along the Samoș River
	Romania	Cluj	Ciumăfaia	1943	Soó R.	-
	Romania	Cluj	Cluj-Napoca	1943	Soó R.	-
	Romania	Mureș	Sighișoara	1948	Țopa E.	floodplain of the Târnava Mare River; revised by Balogh L. in 2017; originally identified as *H. decapetalus*
	Romania	Satu-Mare	Şomcuta	1950	Țopa E.	revised by Balogh L. in 2017; originally identified as *H. decapetalus*
	Romania	Mureș	Sighișoara	1952	Țopa E.	revised by Balogh L. in 2017; originally identified as *H. decapetalus*
	Romania	Mureș	Cipău	1962	Țopa E.	floodplain of the Mureș River; 2 specimens; revised by Balogh L. in 2017; originally identified as *H. decapetalus*
	Romania	Braşov	Homorod	1962	Țopa E.	floodplain of the Homorod River; 4 specimens; revised by Balogh L. in 2017; originally identified as *H. decapetalus*
	Romania	Mureș	Sighișoara	1962	Țopa E.	floodplain of the Târnava Mare River; 4 specimens; revised by Balogh L. in 2017; originally identified as *H. decapetalus*
	Romania	Cluj	Someșeni	1962	Țopa E.	floodplain of the Someșul Mic River; 6 specimens; revised by Balogh L. in 2017; originally identified as *H. decapetalus*
	Romania	Satu-Mare	-	1965	Țopa E.	revised by Balogh L. in 2017; originally identified as *H. decapetalus*
	Romania	Timiș	Lugoj	1969	Vicol E.	runaway; revised by Balogh L. in 2017; originally identified as *H. decapetalus*
	Romania	Satu-Mare	Racșa	1976	Rațiu O., Gergely I.	floodplain of the Talna creek

Table 5.1. Continued

Herbaria	Country	County	Settlement	Year of collection	Collector's name	Other data
Herbarium of the *Alexandru Borza* Botanical Garden and Botanical Museum [CL]	Romania	Satu-Mare	Vama	1977	Rațiu O., Gergely I.	-
Herbarium of the Hungarian Natural History Museum [BP]	Ukraine	Закарпатськаобласть	Ділове	1858	Szénert J.	-
	Hungary	Pest	Budapest	1871	Tauscher J.	-
	Ukraine	Закарпатськаобласть	Ужгород	1878	Mágocsy-Dietz S.	
	Hungary	Pest	Buda	1882	Hermann I.	from a wild population at Hárs hill meadow; 2 specimens
	Hungary	Heves	Eger	19th century	Dejtéri Borbás V.	floodplain
	Hungary	Pest	Budapest	19th century	Gerenday J.	from garden
	Slovakia	Kežmarok	-	19th century	Hazslinszky F.	-
	Hungary	Fejér	between Lepsény and Kemen	1903	Simonkai L.	cultivated plant
	Romania	Hunedoara	Deva	1907	Wagner J.	2 specimens
	Romania	Hunedoara	Deva	1910	Wagner J.	-
	Hungary	Zala	Misefa	1932	Jávorka S.	cultivated plant around the chestnut-grove
	Hungary	Pest	Budapest	1935	-	near the field, forest margin
	Hungary	Pest	Gödöllő	1949	Papp J.	-
	Hungary	Zala	Tormafölde	1950	Károlyi Á.	near the forest; 2 specimens
	Hungary	Fejér	between Lepsény and Kemen	1953	Jávorka S.	-
	Hungary	Pest	Budapest	1958	Csapody V.	cultivated plant; 2 specimens
	Hungary	Szabolcs-Szatmár-Bereg	Tiszabecs	1960	Priszter Sz.	floodplain of the Tisza River; originally identified as *H. decapetalus*
	Hungary	Veszprém	Balatonkenese	20th century	Rapaics R.	
Herbarium of the *Móra Ferenc* Museum [SZE]	Hungary	Komárom-Esztergom	Dorog	19th century	Grundl I.	-
Herbarium of the *Munkácsy Mihály* Museum	Hungary	Békés	Doboz	1984	Kertész É.	2 specimens
	Hungary	Békés	Biharugra	1990	Kertész É.	-

Table 5.1. Continued

Herbaria	Country	County	Settlement	Year of collection	Author	Other data
Herbarium of the Savaria Museum [SAMU]	Hungary	Vas	Kőszeg	1908	Piers V.	3 specimens; revised by Balogh L. in 2016; originally identified as *H. doronicoides*
	Hungary	Vas	Kőszeg	1910	Piers V.	-
	Hungary	Vas	Kőszeg	1919	Piers V.	revised by Balogh L. in 2016; originally identified as *H. cucumerifolius*
Herbarium of the University of Debrecen [DE]	Hungary	Hajdú-Bihar	Hajdúnánás	1929	Igmándy J.	-
	Slovakia	Košice	Košice	1941	Siroki Z.	invasive along the Hernád River
	Hungary	Zala	Tormafölde	1950	Károlyi Á.	forest margin Tormafölde
Herbarium of the University of Pécs [JPU]	Hungary	Baranya	Pécs	1966	Vörös LZs.	revised by Balogh L. in 2016; originally identified as *H. rigidus*

Abbreviation: (-) no data; square brackets [ ] international abbreviation of institute (Index Herbariorum)

5.1.2. Allelopathic effect of *Helianthus tuberosus*

5.1.2.1. Bioassay - effect of concentration, species, tissues and timing

Overall, the 1 μg/mL concentration of the extracts did not influence germination, plumule length, and radicle length of test species compared to the control. However, the 10 μg/mL concentration significantly influenced the germination (df = 2, Dev. res. = 25.5, P < 0.001) and growth (plumule length: df = 2, F = 5.34, P < 0.01; radicle length: df = 2, F = 4.57, P < 0.05) of certain test species. Henceforward, we are going to present the results obtained with 10 μg/mL concentration, discussing the effect of species, tissues, timing, and their interactions on seed germination and growth (Table 5.2).

Table 5.2. Results of the model analyses testing the interaction effect of species, tissues and time in our bioassay experiment in case of effective (10 μg/mL) concentration

	Germination			**Plumule length**			**Radicle length**		
	df	Dev. resid	P value	df	F	P value	df	F	P value
S	4	427.75	<0.001	4	176.29	<0.001	4	132.76	<0.001
Ts	1	2.77	0.52	1	41.89	<0.001	1	0.02	0.88
Tm	4	132.30	<0.001	4	20.44	<0.001	4	8.64	<0.001
S:Ts	4	25.23	<0.001	4	7.56	<0.001	4	0.30	0.87
S: Tm	16	213.66	<0.001	16	12.78	<0.001	16	12.10	<0.001
Ts:Tm	4	55.16	<0.001	4	10.74	<0.001	4	3.73	<0.001
S:Ts:Tm	16	42.23	<0.001	16	6.73	<0.001	16	5.15	<0.001

Abbreviation: S: species; Ts: Tissues; Tm: Time

Germination rates, plumule, and radicle length were significantly influenced by the test species. *Elymus repens* and *Tanacetum vulgare* were the most sensitive to *H. tuberosus* extracts, which had inhibitory effect on germination and growth (plumule length: t = -4.31, P < 0.01; radicle length: t = -3.602, P < 0.05) of *E. repens*, and exerted an inhibitory effect on plumule length of *T. vulgare*. In contrast, *H. tuberosus* extracts had facilitative effects on all measurements of *S. alba* (plumule length: t = 4.144, P < 0.01; radicle length: t = 4.308, P < 0.01) compared to the control. In the other two test species, *H. tuberosus* extracts did not exert negative effects on germination and growth.

Throughout the study period (from June to October), germination and growth of test species were affected in a different rate depending on the tissue of *H. tuberosus* from which the extract was prepared. The leaf extract significantly reduced the germination rate of *G. mollugo* compared to root extract; however, the germination rates of *E. repens*, *S. alba, S. gigantea*, and *T. vulgare* were not influenced by either the root or leaf extracts

of *H. tuberosus*. The growth of germinated seeds was also influenced in various ways by different tissues. Plumule growth was significantly inhibited by the root extracts in *E. repens*, and it was stimulated by leaf extract in *S. alba* compared to the root extract. *H. tuberosus* extracts did not cause significant changes in plumule growth of *G. mollugo, S. gigantea*, and *T. vulgare*. Radicle length was significantly inhibited by leaf extracts in *G. mollugo* compared to root extracts, in contrast to *E. repens, S. alba, S. gigantea*, and *T. vulgare*, where no relevant differences were detected between the effect of leaf and root extracts.

The last crucial factor for the allelopathic potential of *H. tuberosus* was the harvest time of plant parts. Monthly analysis showed that the negative impact of *H. tuberosus* extracts on the number of germinated seeds was larger in the first and the last month of the study. In June and October, the leaf extracts decreased germination rates of four out of the five studied species (except *S. alba* and *G. mollugo*, respectively), while in the other months in some species, stimulating effect was observed, too. Similarly, *H. tuberosus* extracts had the highest effect on radicle and plumule growth in the first and the last months of the study (Table 5.3).

Table 5.3. Effects of *Helianthus tuberosus* leaf and root extracts on germination (%) and growth (cm) of studied species during the vegetation period compared to the control (which was considered 100% in each measurement)

Species		June		July		August		September		October	
		Leaf	Root	Leaf	Root	Leaf	Root	Leaf	Root	Leaf	Root
E. repens	**Germination**	**33.33**$^{***}\downarrow$	**145.45**$^{***}\uparrow$	**54.54**$^{***}\downarrow$	**20.00**$^{***}\downarrow$	**54.54**$^{***}\downarrow$	**38.46**$^{***}\downarrow$	**58.82**$^{**}\downarrow$	**76.47**$^{**}\downarrow$	**83.33**$^{**}\downarrow$	100.00
	Plumule	2.01±0.40	**2.29±0.51**$^{*}\downarrow$	1.51±0.43	1.75±0.65	0.58±0.08	2.30±0.95	1.88±0.50	0.29±0.07	**2.52±0.24**$^{***}\downarrow$	0.64±0.09
	Radicle	3.24±0.52	**3.11±0.57**$^{*}\downarrow$	3.36±0.75	3.10±0.60	1.18±0.28$^{*}\uparrow$	3.90±1.50	3.04±0.56	1.46±0.23	**1.31±0.13**$^{***}\downarrow$	**1.05±0.15**$^{**}\downarrow$
G. mollugo	**Germination**	**33.33**$^{***}\downarrow$	**25.00**$^{***}\downarrow$	**125.00**$^{**}\uparrow$	**43.75**$^{***}\downarrow$	**50.00**$^{***}\downarrow$	**156.25**$^{**}\uparrow$	**150.00**$^{***}\uparrow$	**84.61**$^{**}\downarrow$	90.90	**110.00** $^{*}\uparrow$
	Plumule	0.20±0.05	0.56±0.24	0.44±0.15	0.62±0.30	0.43±0.33	0.83±0.11	0.65±0.12	0.29±0.09	**0.40±0.04**$^{**}\downarrow$	0.26±0.03
	Radicle	0.76±0.21	0.76±0.18	0.26±0.08	0.52±0.19	0.46±0.23	0.80±0.07	0.23±0.02	**0.61±0.12**$^{*}\uparrow$	**0.18±0.02**$^{**}\downarrow$	0.66±0.05
S. alba	**Germination**	95.00	**81.81**$^{*}\downarrow$	**134.48**$^{**}\uparrow$	**107.40**$^{*}\uparrow$	**133.33**$^{**}\uparrow$	**205.55**$^{***}\uparrow$	**150.00**$^{***}\uparrow$	**155.55**$^{***}\uparrow$	**83.33**$^{**}\downarrow$	**137.50**$^{**}\uparrow$
	Plumule	3.45±0.29	**2.99±0.31**$^{**}\uparrow$	**2.72±0.23**$^{*}\uparrow$	**2.19±0.36**$^{**}\uparrow$	**2.94±0.37**$^{**}\uparrow$	**2.92±0.34**$^{**}\uparrow$	2.86±0.26	2.86±0.24	4.70±0.32	4.20±0.30
	Radicle	2.20±0.40	**2.48±0.43**$^{**}\uparrow$	1.66±0.30	1.55±0.43	2.23±0.56	1.51±0.35	3.68±0.81	5.15±0.98	2.90±0.25	5.38±0.37
S. gigantea	**Germination**	**50.00**$^{**}\downarrow$	**86.66**$^{*}\downarrow$	**67.74**$^{**}\downarrow$	**193.33**$^{***}\uparrow$	**166.66**$^{***}\uparrow$	**144.44**$^{**}\uparrow$	**200.00**$^{***}\uparrow$	**300.00**$^{***}\uparrow$	**83.33**$^{**}\downarrow$	**122.22**$^{**}\uparrow$
	Plumule	1.03±0.10	1.01±0.15	0.96±0.08	1.23±0.06	**0.66±0.10**$^{*}\uparrow$	0.99±0.08	1.00±0.17	**0.71±0.13**$^{*}\uparrow$	**0.31±0.03**$^{*}\downarrow$	**0.65±0.08**$^{*}\uparrow$
	Radicle	0.31±0.03	0.20±0.04	0.27±0.02	0.30±0.03	0.18±0.03	0.17±0.02	0.14±0.03	**0.21±0.05**$^{*}\uparrow$	0.20±0.02	0.37±0.06
T. vulgare	**Germination**	**58.33**$^{**}\downarrow$	100.00	**77.77**$^{**}\downarrow$	**71.42**$^{**}\downarrow$	**40.00**$^{***}\downarrow$	**116.66**$^{*}\uparrow$	**75.00**$^{**}\downarrow$	**116.66**$^{*}\uparrow$	**50.00**$^{***}\downarrow$	**200.00**$^{***}\uparrow$
	Plumule	1.48±0.18	1.40±0.07	1.22±0.16	**0.52±0.06**$^{*}\downarrow$	1.10±0.22	1.14±0.17	1.03±0.13	0.60±0.08	0.69±0.07	**0.52±0.04**$^{***}\downarrow$
	Radicle	0.22±0.04	**0.23±0.03**$^{*}\downarrow$	0.11±0.02	0.10±0.001	0.12±0.02	0.17±0.03	0.46±0.17	0.22±0.04	0.23±0.03	**0.25±0.02**$^{**}\downarrow$

5.1.2.2. Identification of allelochemicals

Our analysis of the phenolic fractions by SFC-DADMS resulted in separation and identification of 2-OH-cinnamic acid, 4-OH-benzaldehyde, coumarin, salicylic acid, and trans-cinnamic acid. Concentrations of the phenolic fractions were influenced by plant tissues and harvest time. The interaction of tissues and time did not result in significant differences (Table 5.4).

Table 5.4. Results of the linear model analysis testing the interaction effect of tissues and time during vegetation period

	Concentration		
	df	F	P-value
Tissues	1	19.40	<0.001
Time	4	3.62	<0.01
Tissues:Time	4	1.18	>0.05

The quantity of 2-OH-cinnamic acid was found to be the most prevalent in all fractions during the vegetation period, followed by salicylic acid, 4-OH-benzaldehyde, and trans-cinnamic acid, while coumarin was measured only in traces. The concentration of 2-OH-cinnamic acid, salicylic acid, and 4-OH-benzaldehyde was significantly higher in the leaves than in the roots, whereas no significant difference was found between the trans-cinnamic acid content of the leaves and the roots.

The level of phenolic compounds was different not only in various plant organs, but also at different sampling occasions, exhibiting characteristic distribution patterns throughout the vegetation period. The 2-OH-cinnamic acid, salicylic acid, and 4-OH-benzaldehyde content in the leaves and 2-OH-cinnamic acid content in the roots were the highest in June, their concentration gradually decreased from July to September, and an increase was observed in October (Fig. 5.3).

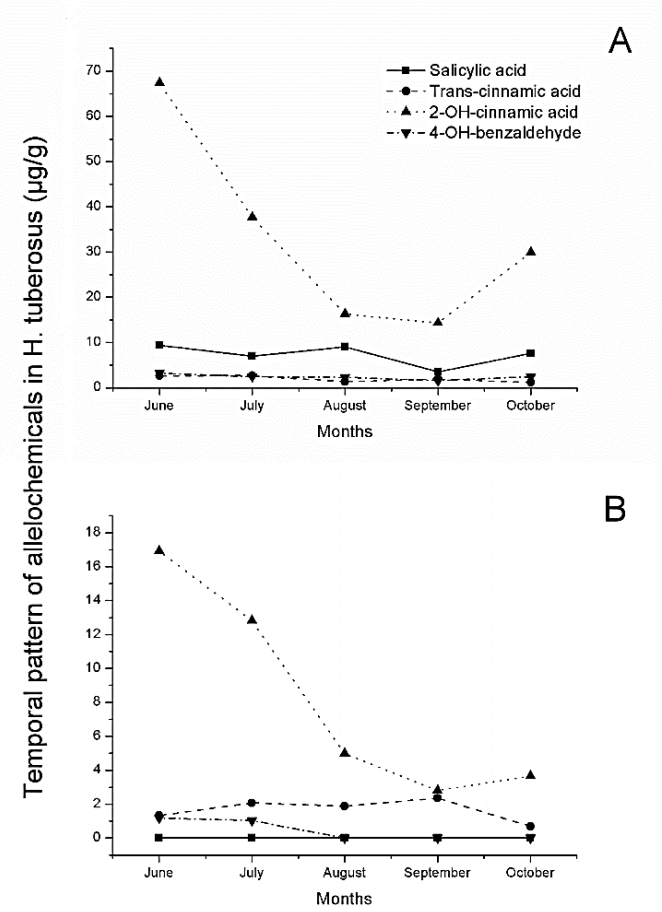


Figure 5.3. Temporal pattern of allelochemicals in leaf (A) and root (B) of *H. tuberosus*

The trans-cinnamic acid content in the leaves, 4-OH-benzaldehyde, salicylic acid, and trans-cinnamic acid levels in the roots did not fit into the pattern above, but exhibited some unique features. The highest concentration of trans-cinnamic acid in the leaves was measured in June, followed by a gradual decrease. In root extracts, 4-OH-benzaldehyde content remained constantly low in September and October compared to June (June-September: $t = -5.309$, $P < 0.001$; June-October: $t = -5.005$, $P < 0.001$) and July (July-September: $t = -4.621$, $P < 0.01$; July-October: $t = -4.357$, $P < 0.01$). In the roots, the salicylic acid content remained very low, constantly 0.0004 mg/kg dried plant material during the 5 months of the study. In the roots, the trans-cinnamic acid concentration was the highest in September and the lowest at the beginning and at the end of the vegetation period (June and October).

5.1.2.3. Competition experiment

Our pot experiment, testing the allelopathic effects of *H. tuberosus* root exudates on four commonly occurring neighboring species indicated that neighbor and species were the most important factors. Number of stems was not significantly affected by two-way interactions (Table 5.5).

Table 5.5. Results of the mixed-effect model analyses testing the interaction effect of neighbor species and carbon treatment in our pot experiment

	Survival			**Height**			**Number of stems**			**Total biomass**		
	df	Dev. resid	P value	df	F	P-value	df	F	P value	df	F	P value
N	5	518.80	<0.001	5	250.07	<0.001	5	134.55	<0.001	5	179.86	<0.001
C	1	0.40	0.50	1	34.33	<0.001	1	0	1.00	1	20.61	<0.001
S	5	194.10	<0.001	5	74.27	<0.001	5	69.61	<0.001	5	13.89	<0.001
N:C	4	0	1.00	4	9.75	<0.001	4	0.13	0.71	4	5.21	<0.05
N:S	3	12670.20	<0.001	3	4.37	<0.001	3	1.34	0.78	3	0.24	0.81
C:S	3	12.30	<0.01	3	0.96	<0.01	3	0	1.00	3	0.04	0.99

Abbreviation: N: neighbor; C: carbon; S: species; Three way interactions were never significant, so they were not visualized

The presence of *H. tuberosus* exerted a strong negative effect on all test species, independent of the treatment (with or without activated carbon). *H. tuberosus* significantly reduced the number of surviving plants, the shoot length, the aboveground, belowground, and total biomass of the test species compared to the plants grown without *H. tuberosus* (Table 5.6).

Fewer individuals of *S. gigantea* and *T. vulgare* survived in competition with *H. tuberosus*, compared to plants growing without *H. tuberosus*; but no significant difference was observed in the number of surviving plants between the carbon-treated and untreated condition. However, in the non-carbon-treated soils, allelochemicals of *H. tuberosus* decreased the number of surviving plants of *G. mollugo* and *E. repens* compared to the carbon-treated plants (Fig. 5.4).

In our pot experiment, the activated carbon treatment did not have any significant effect on the shoot length, aboveground, belowground, and total biomass of three out of four studied species (*G. mollugo, S. gigantea*, and *T. vulgare*) when they grew in competition with *H. tuberosus*. However, *H. tuberosus* reduced the shoot height of *E. repens* compared to the carbon-treated soil (Fig. 5.4).

Table 5.6. The effect of *H. tuberosus* on height and biomass of test species with or without active carbon compared to the control or each other

	Species	Height (cm)				Shoot biomass (g)				Root biomass (g)				Total biomass (g)			
		Est.	**Std. e.**	**t value**	**P**	**Est.**	**Std. e.**	**t value**	**P**	**Est.**	**Std. e.**	**t value**	**P**	**Est.**	**Std. e.**	**t value**	**P**
E. repens	*H*-C vs. control	-37.427	1.986	-18.845	<0.001	-0.361	0.024	-14.878	<0.001	-0.070	0.007	-9.679	<0.001	-0.434	0.028	-15.470	<0.001
	H+C vs. control	-43.038	1.918	-22.438	<0.001	-0.388	0.024	-16.016	<0.001	-0.076	0.007	-10.868	<0.001	-0.476	0.027	-17.569	<0.001
	H+C vs. *H*-C	-5.611	1.817	-3.088	<0.01	-0.027	0.021	-1.257	>0.05	-0.005	0.006	-0.894	>0.05	-0.042	0.025	-1.638	>0.05
G. mollugo	*H*-C vs. control	-41.254	3.842	-10.737	<0.001	-0.740	0.074	-9.947	<0.001	-0.139	0.040	-3.429	<0.01	-0.930	0.176	-5.277	<0.001
	H+C vs. control	-36.094	2.649	-13.627	<0.001	-0.730	0.067	-10.793	<0.001	-0.126	0.027	-4.556	<0.001	-0.901	0.120	-7.506	<0.001
	H+C vs. *H*-C	5.160	4.057	1.272	>0.05	0.009	0.072	0.133	>0.05	0.013	0.042	0.310	>0.05	0.029	0.185	0.157	>0.05
S. gigantea	*H*-C vs. control	-17.956	1.711	-10.495	<0.001	-0.463	0.025	-18.144	<0.001	-0.189	0.036	-5.215	<0.001	-0.662	0.097	-6.798	<0.001
	H+C vs. control	-18.068	2.216	-8.152	<0.001	-0.463	0.025	-18.227	<0.001	-0.192	0.046	-4.093	<0.001	-0.661	0.126	-5.246	<0.001
	H+C vs. *H*-C	-0.111	2.635	-0.042	>0.05	0.0003	0.025	0.013	>0.05	-0.003	0.055	-0.056	>0.05	0.0003	0.150	0.002	>0.05
T. vulgare	*H*-C vs. control	-22.062	3.150	-7.003	<0.001	-0.686	0.030	-22.679	<0.001	-0.159	0.062	-2.561	<0.05	-0.831	0.181	-4.573	<0.001
	H+C vs. control	-21.887	6.112	-3.581	<0.01	-0.687	0.030	-22.250	<0.001	-0.160	0.120	-1.332	>0.05	-0.838	0.352	-2.378	<0.05
	H+C vs. *H*-C	0.175	6.762	0.026	>0.05	-0.001	0.030	-0.035	>0.05	-0.001	0.133	-0.011	>0.05	-0.007	0.390	-0.019	>0.05

Abbreviation: H-C: *H. tuberosus* without carbon; H+C: *H. tuberosus* with carbon; Est: Estimate; Std. e.: Standard error; *H.*: *Helianthus tuberosus*; C: carbon

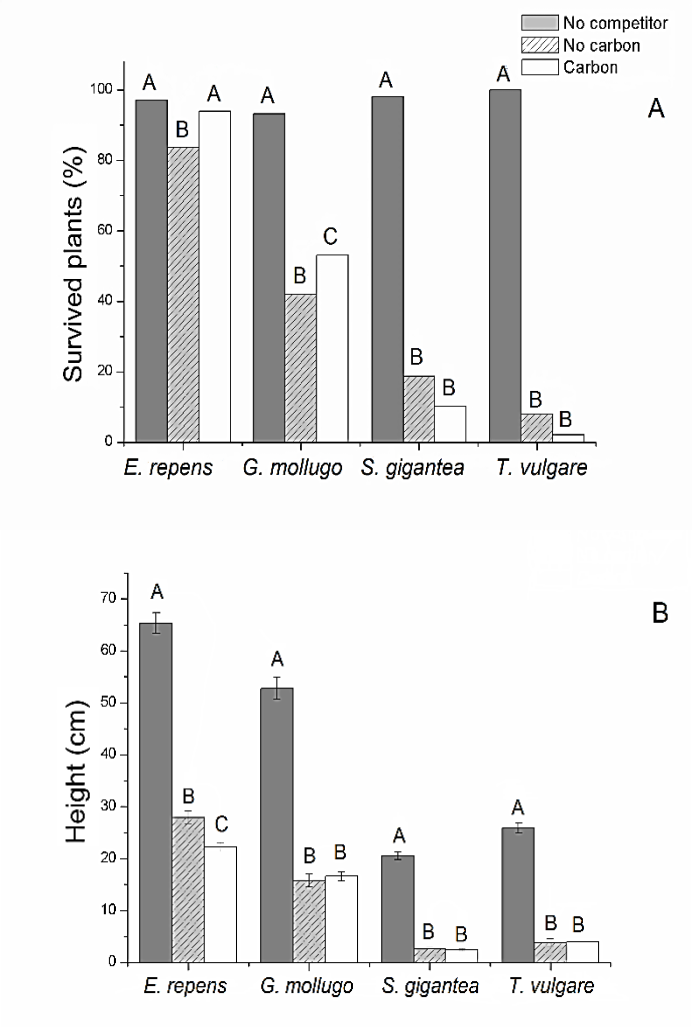


Figure 5.4. Percentage of surviving plants (A) and shoot height (B) of test species grown alone, or with the invasive *H. tuberosus*, either with or without activated carbon in the soil. Capital letters represent the results of Tukey post hoc tests.

5.2. *Helianthus tuberosus* at home and away

5.2.1. Field measurements

We recorded 225 and 249 species summed across all plots in North America and Europe, respectively. However, the mean species richness excluding *H. tuberosus* was significantly lower in Europe, than in North America ($Z = -15.9354$, $p < 2.2e\text{-}16$).

Both native and exotic species richness were higher in North America compared to Europe (native: Z = -10.7835, p < 2.2e-16; exotic: Z = -17.294, p < 2.2e-16). Furthermore, when analyzing the relative[1] native and relative exotic species richness, we found that both were higher in North America than in Europe (native: Z = -16.244, p < 2.2e-16; exotic: Z = -8.9067, p < 2.2e-16) (Fig. 5.5).

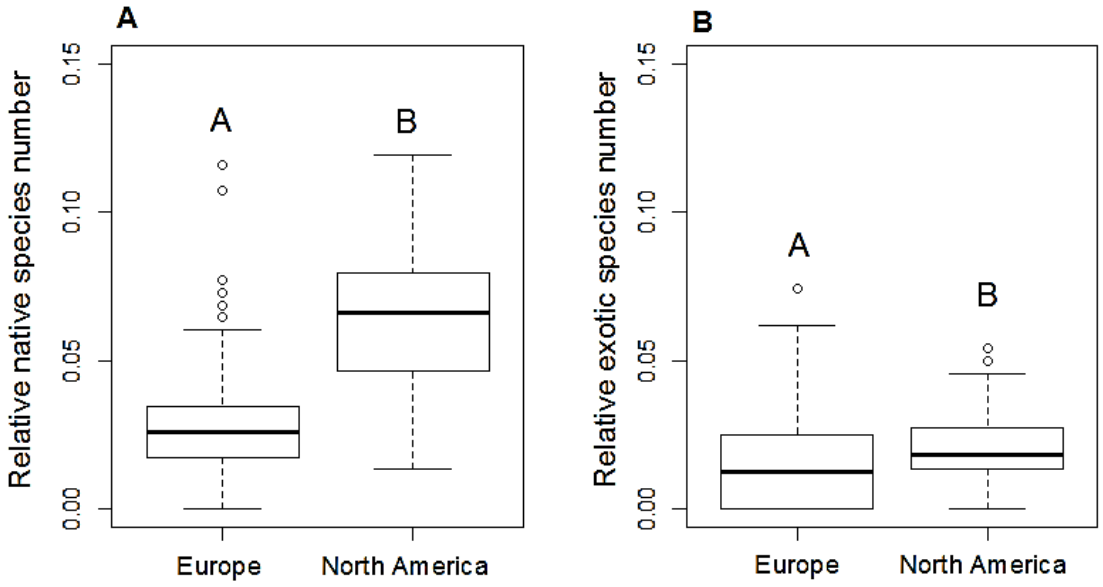


Figure 5.5. Relative native (**A**) and relative exotic (**B**) species number in the native (North-America) and non-native (Europe) ranges (different letters mean significant differences)

Each of the methods used for calculating plant diversity indicated that in European plots plant diversity was significantly lower than in North American plots (p < 0.001) (Fig. 5.6).

[1] relative species richness = species number of the plot / total species number of all plots from the continent

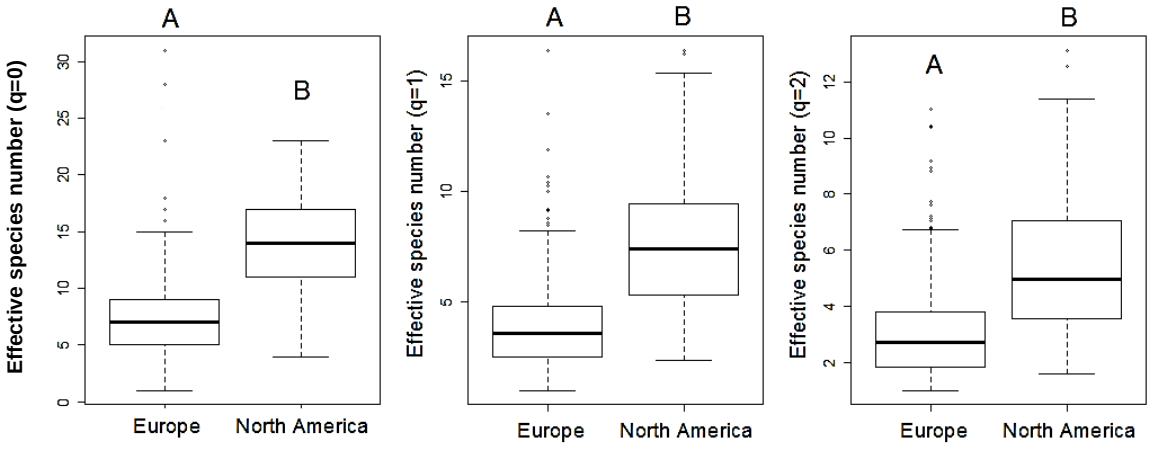
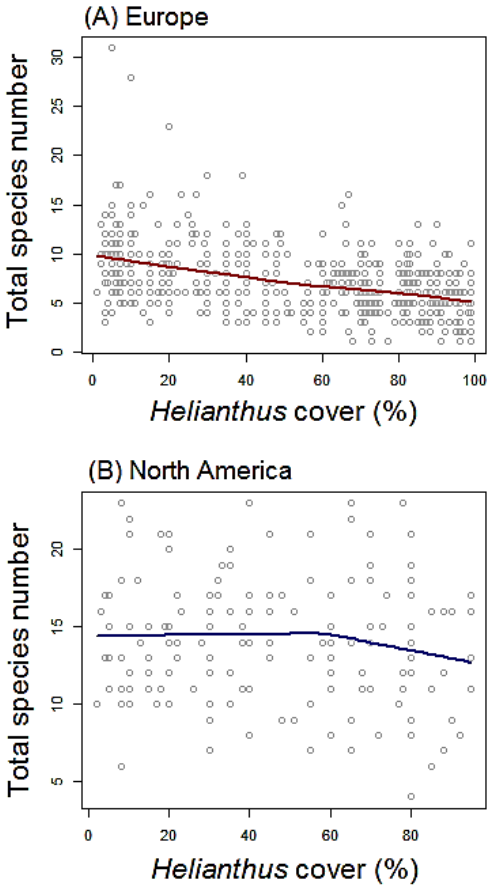


Figure 5.6. Plant diversity in the native and non-native ranges. Calculated for: effective species number (q=0); exponential of Shannon entropy (q=1); inverse Simpson index (q=2)



In European plots, the number of species declined with increasing *H. tuberosus* cover ($r_{spearman}$= -0.438, p < 2.2e-16). In contrast, in North America there was no significant relationship between *H. tuberosus* cover and total species number ($r_{spearman}$= -0.086, p = 0.279) (Fig. 5.7).

Figure 5.7. The relationship between *H. tuberosus* cover and total species richness in the non-native (**A**) and native (**B**) ranges. Trend lines were fitted by LOESS polynomial regression method.

The average total *H. tuberosus* stem density in European plots was 96±4 stems/4 m^2 versus 48±3 stems/ 4 m^2 in North America (Z= 5.26, p < 2.2e-16). The bare ground cover in European plots was significantly higher than in North American plots (Z= 3.2061, p < 0.01), but we did not detect any relevant difference in the litter of *H. tuberosus* in Europe versus North America (Z = -1.6804, p > 0.05). Furthermore, the mean plant height of *H. tuberosus* in North America (137.22±1.24 cm) was significantly lower than in Europe (155.38 ±0.75 cm) (Z = 10.5221, p < 2.2e-16) (Fig. 5.8).

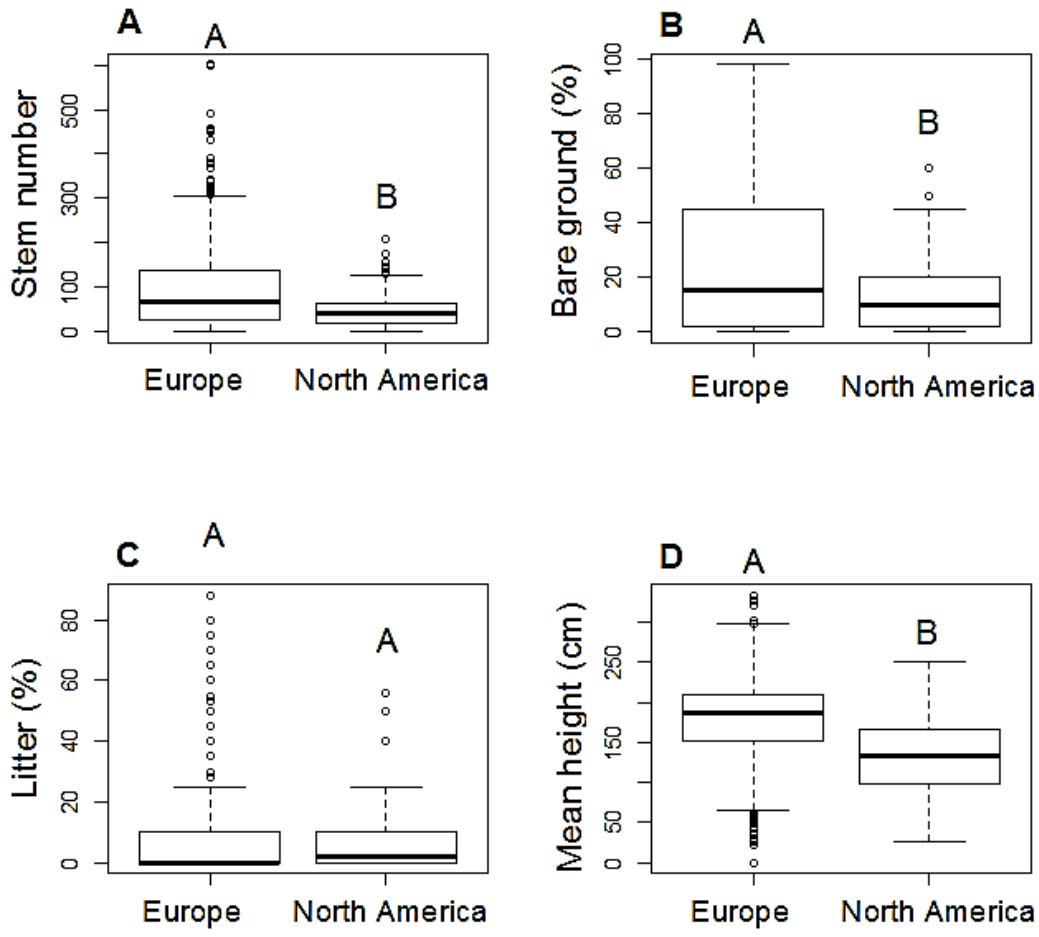


Figure 5.8. Field measurements in the native and non-native ranges: (**A**) stem number of *H. tuberosus*; (**B**) bare ground of the plots; (**C**) litter of *H. tuberosus*; (**D**) mean height of *H. tuberosus*

The relationship between the number of *H. tuberosus* stems and *H. tuberosus* cover was significant both in Europe (slope = 0.014, pseudo-R^2= 0.559, p < 2.2e-16) and in North America (slope = 0.033, pseudo-R^2= 0.624, p < 2.2e-16) (Fig. 5.9). However, in the common models containing data from both continents, the inclusion of the continent as

an interactive term considerably improved models (without continent: BIC = -585.734; with continent: BIC = -651.904), which suggests that a single *H. tuberosus* stem covered a smaller area in Europe versus North America.

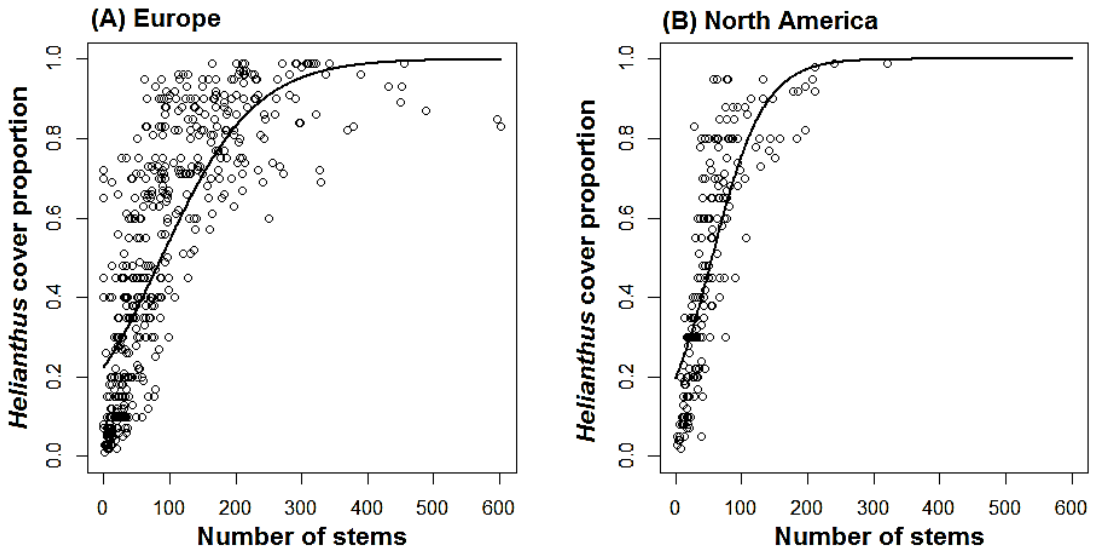


Figure 5.9. The relationship between *H. tuberosus* cover and number of *H. tuberosus* stems in the non-native (A) and native (B) ranges

In plots in Europe, the proportion of bare ground cover rose with increasing *H. tuberosus* cover (slope = 2.095, pseudo-R^2= 0.422, p < 2e-16). In contrast, in North America there was no significant relationship between *H. tuberosus* cover and bare ground cover (slope = 0.283, pseudo-R^2= 0.010, p= 0.175) (Fig. 5.10). The inclusion of continent as an interactive term considerably improved the model (without continent: BIC = -1963.376; with continent: BIC = -2013.433).

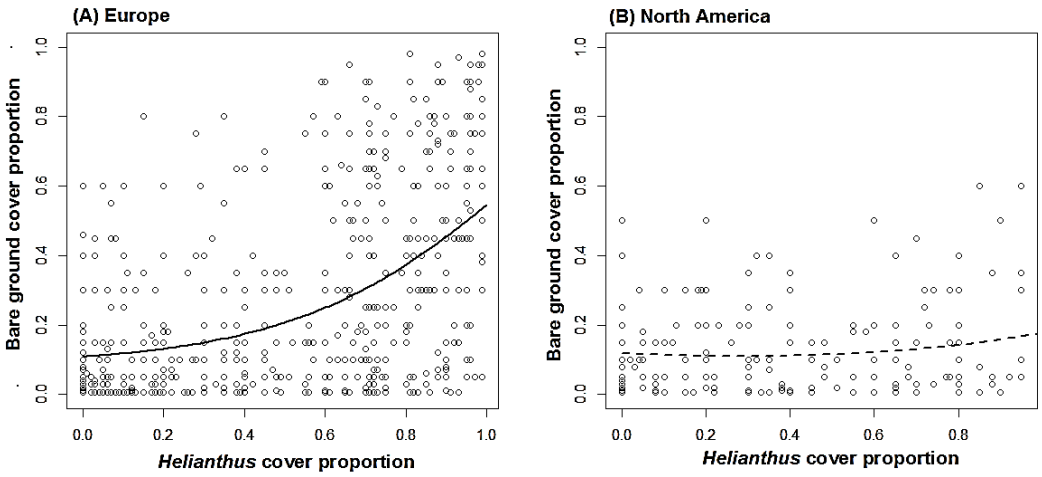


Figure 5.10. The relationship between bare ground and *H. tuberosus* cover in the non-native (**A**) and native (**B**) range

5.2.2. Factors which could affect species composition

Our RDA model containing 27 explanatory variables explained 44.4% of the total variance in North America, and 31.1 % of the total variance in Europe (Table 5.7). Adjusted R^2 were 0.269 and 0.219, respectively. In North America 22 out of 27 variables had significant gross effects, while in Europe 26 out of 27 variables had significant gross effects. According to the RDA models, the most important predictor of species composition was the mean height of *H. tuberosus* in North America, and mean annual precipitation of 30 years (1960-1990) in Europe.

In North America, altitude was a stronger predictor of species composition than in Europe. Furthermore, in North America, the most remarkable climatic predictor was mean annual precipitation; while the most important soil predictor was Mg; and from the field measurements, the mean height of *H. tuberosus* was the most important. In contrast, in Europe the most significant climatic predictor was mean annual precipitation of 30 years (1960-1990); the most important soil predictor was P_2O_5; and bare ground cover from the field measurements.

Table 5.7. Gross effect of the explanatory variables on the species composition, identified using redundancy analyses with single explanatory variables. Within each group, variables are presented in decreasing order of their effect size (F value). Total variation explained by the 27 variables together is 44.4% (adjusted $R^2 = 0.269$) and 31.1% (adjusted $R^2 = 0.219$) for North America and Europe, respectively. Explained variation proportions by separate variables do not add up because of correlations between them.

North America				Europe			
Variables	**Var**	**F**	**P**	**Variables**	**Var**	**F**	**P**
Altitude	0.044	3.229	0.001	Altitude	0.010	2.530	0.007
Climatic properties				***Climatic properties***			
Mean annual precipitation	0.056	4.213	0.001	Mean annual precipitation (1960-1990)	0.021	5.119	0.001
Mean annual temperatures	0.052	3.886	0.001	Mean annual hours of sunshine	0.021	4.968	0.001
Mean annual precipitation (1960-1990)	0.048	3.574	0.001	Mean annual hours of sunshine (1960-1990)	0.020	4.921	0.001
Mean annual temperatures (1960-1990)	0.016	1.175	0.238	Mean annual temperatures	0.016	3.910	0.001
Mean annual hours of sunshine	0	0	-	Mean annual precipitation	0.015	3.653	0.001
Mean annual hours of sunshine (1960-1990)	0	0	-	Mean annual temperatures (1960-1990)	0.013	3.191	0.003
Soil properties				***Soil properties***			
Mg	0.052	3.911	0.002	P_2O_5	0.018	4.381	0.001
Organic matter	0.046	3.409	0.001	Organic matter	0.018	4.311	0.001
Nitrogen	0.046	3.388	0.001	Mn	0.017	4.094	0.001
Soil texture (K_A)	0.040	2.946	0.001	Na	0.017	4.008	0.001
NO_3^--N+NO_2^--N	0.039	2.881	0.001	Cu	0.016	3.810	0.001
Zn	0.038	2.823	0.001	Nitrogen	0.016	3.762	0.001
Mn	0.036	2.647	0.002	K_2O	0.013	3.195	0.001
Salt	0.035	2.587	0.001	$CaCO_3$	0.013	3.051	0.003
pH (KCl)	0.032	2.349	0.003	Salt	0.012	2.828	0.002
pH (H_2O)	0.031	2.265	0.002	NO_3^--N+NO_2^--N	0.012	2.811	0.002
Na	0.030	2.182	0.003	Mg	0.011	2.742	0.003
K_2O	0.028	2.034	0.005	Soil texture (K_A)	0.011	2.640	0.004
Cu	0.026	1.926	0.01	SO_4	0.011	2.578	0.007
P_2O_5	0.026	1.876	0.013	pH (H_2O)	0.008	1.935	0.032
SO_4	0.022	1.594	0.03	pH (KCl)	0.007	1.805	0.031
$CaCO_3$	0	0	-	Zn	0.007	1.735	0.042

Table 5.7. Continued

North America				Europe			
Variables	**Var**	**F**	**P**	**Variables**	**Var**	**F**	**P**
Measured properties				***Measured properties***			
Mean height of *H. tuberosus*	0.059	4.424	0.001	Bare ground	0.020	4.885	0.001
Stem number of *H. tuberosus*	0.027	1.993	0.005	Mean height of *H. tuberosus*	0.010	2.533	0.004
Bare ground	0.024	1.736	0.018	Litter of *H. tuberosus*	0.009	2.184	0.013
Litter of *H. tuberosus*	0.018	1.284	0.141	Stem number of *H. tuberosus*	0.006	1.395	0.147

5.2.3. Arbuscular mycorrhizal fungi (AMF) colonization

Our test for arbuscular mycorrhizal fungi (AMF) colonization of *H. tuberosus* indicated that AMF colonized all collected roots of *H. tuberosus* both at native and non-native ranges, which was represented by hyphae, vesicles and arbuscules (Fig. 5.11).

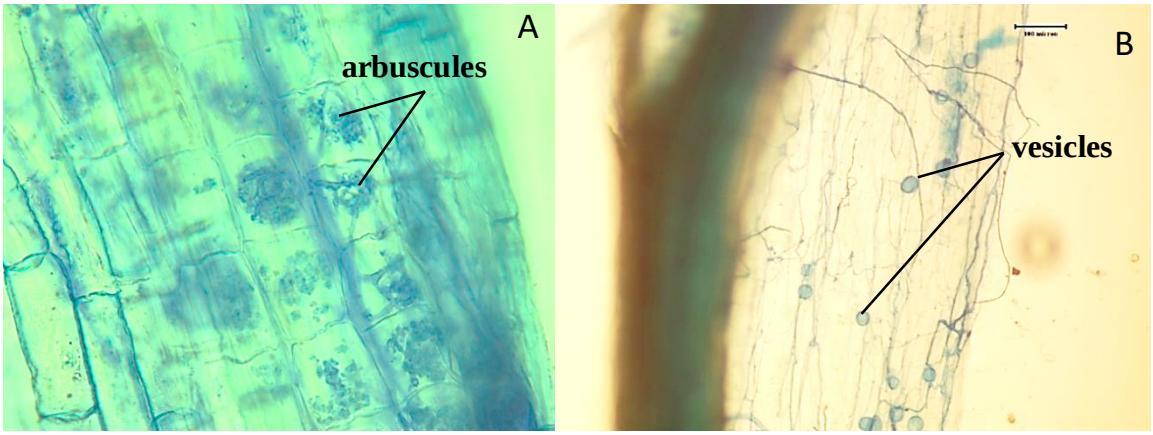


Figure 5.11. Arbuscular mycorrhizal fungi (AMF) colonization of *H. tuberosus* (A) in native and (B) non-native ranges

The AMF colonization of *H. tuberosus* was different in the native versus the non-native range, because intensity of the mycorrhizal colonization in the root system (M%) ($Z = -4.84$, $p < 0.001$), intensity of the mycorrhizal colonization in the root fragments (m%) ($Z = -4.59$, $p < 0.001$), arbuscule abundance in the root system (A%) ($Z = -5.07$, $p < 0.001$), and arbuscule abundance in mycorrhizal parts of root fragments (a%) ($Z = -5.77$, $p < 0.001$) were significantly higher in the United States than in Europe. However, we did not detect any relevant differences between the two continents in the frequency of mycorrhiza in the root system (F%) ($Z = 0.63$, $p > 0.05$) (Fig. 5.12; Table 5.8).

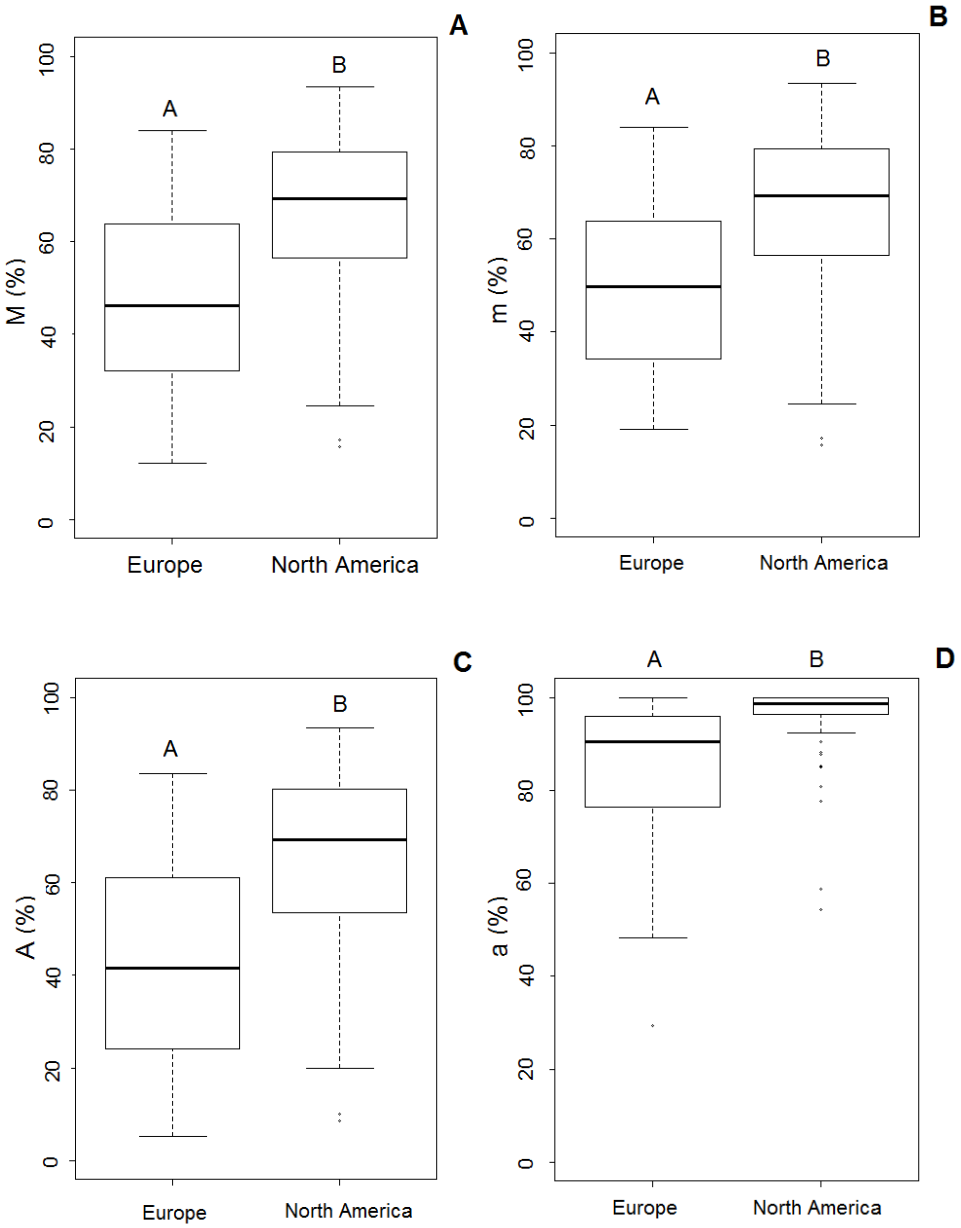


Figure 5.12. Arbuscular mycorrhizal fungi (AMF) colonization of *H. tuberosus* in native vs. non-native ranges. **M:** intensity of the mycorrhizal colonization in the root system; **m:** intensity of the mycorrhizal colonization in the root fragments; **A:** arbuscule abundance in the root system; **a:** arbuscule abundance in mycorrhizal parts of root fragments

Table 5.8. Arbuscular mycorrhizal fungi (AMF) colonization of *H. tuberosus* in native vs. non-native ranges. All data are expressed as mean ± standard error

	F %	**M%**	**m %**	**A %**	**a %**
Native (<50%)	100	69.92±3.19	69.92±3.19	68.17±3.53	95.06±1.65
Native (>50%)	100	62.85±2.87	62.85±2.87	61.65±3.31	96.48±0.98
Non-native (<50%)	96.15±1.49	48.48±3.73	49.77±3.53	43.35±4.26	84.89±2.50
Non-native (>50%)	94.41±1.91	48.32±3.68	50.07±3.53	42.60±4.12	82.96±3.25
Native (total)	100	**67.23±2.28** [a]	**67.23±2.28** [a]	**65.69±2.54** [a]	**95.60±1.08** [a]
Non-native (total)	95.31±1.19	**48.40±2.59** [b]	**49.91±2.47** [b]	**42.99±2.94** [b]	**84.02±2.05** [b]

(<50%): *H. tuberosus* coverage less than 50%; **(>50%)**: *H. tuberosus* coverage more than 50%; **F**: frequency of mycorrhiza in the root system; **M**: intensity of mycorrhizal colonization in the root system; **m**: intensity of mycorrhizal colonization in the root fragments; **A**: arbuscule abundance in the root system; **a**: arbuscule abundance in mycorrhizal parts of root fragments. Bold letters indicate significant differences.

In addition to the comparison of AMF colonization of *H. tuberosus* at home and away, we tested the AMF colonization of *H. tuberosus* when its coverage was lower than 50% compared to coverage higher than 50%, on both continents. Our results suggest that the coverage of *H. tuberosus* did not affect the AMF colonization of the plant (Table 5.8).

6. DISCUSSION

6.1. *Helianthus tuberosus* in the Carpathian Basin

6.1.1. Distribution of *Helianthus tuberosus*

Our extensive study of herbaria specimens verified that (1) *Helianthus tuberosus* agg. has been present in the Carpathian Basin since the first part of the 19th century, and (2) the taxonomy of the plant is unsettled, requiring the revision of earlier plant identifications.

Altogether, 65 *Helianthus tuberosus* agg. specimens were examined in the visited herbaria, which represent an adequate sampling from the Carpathian Basin considering all difficulties of herbaria preparation from the species (around 3 m height, crass stem, tuber etc.).

The fact that the Herbarium of the *Alexandru Borza* Botanical Garden and Botanical Museum (Romania) and the Herbarium of the Hungarian Natural History Museum (Hungary) contained the most specimens of *H. tuberosus* agg. was not unexpected, because they are the most remarkable herbaria in Transylvania (Romania) (Micle 2005) and Hungary (Fekete and Kováts 1974).

From the studied 65 *H. tuberosus* agg. specimens 28 specimens, collected mostly in Transylvania, were originally identified as other species from the *Helianthus* genus (23 specimens as *H. decapetalus)*. Our results are consonant with the studies of Balogh (2006, 2008), who called attention to the large number of reports that were published after World War II about the mass spread of a species related to *H. tuberosus* agg. throughout Central Europe. The majority of Eastern-European researchers identified and considered this species as *H. decapetalus*. Moreover, the oldest specimen which was identified as *H. decapetalus* was the oldest *H. tuberosus* agg. specimen at the same time (Baumgarten 1826). Thus, our results suggest that the identification of *H. tuberosus* agg. as *H. decapetalus* started as early as the first part of the 19th century, which led to the questionable taxonomy of *Helianthus* species nowadays. Moreover, the morphological identification of *H. tuberosus* and its close relatives (*H. decapetalus, H. strumosus*) involves several difficulties, and these species are often mistakenly classified as representatives of another taxa (Balogh 2006, 2008). In addition, Bock et al. (2014) suggest that cultivated *H. tuberosus* originates recursively from perennial sunflowers via hybridization between tetraploid hairy sunflower (*H. hirsutus*) and diploid sawtooth sunflower (*H. grosseserratus*), but we have no information about wild populations.

The oldest twelve *H. tuberosus* agg. specimens were collected in the 19th century. The exact date of collection of five out of twelve specimens is unknown, but we assume that they were collected in the 19th century, because the collectors lived and were active researchers in this century: Dejtéri Borbás (1844-1905) (Simonkai 1886), Gerenday (1814-1862) (Lukácsy 2011), Grundl (1813-1878) (Kenyeres 1967), Hazslinszky (1818-1896) (Simonkai 1886), and Pávai (1820-1874) (Simonkai 1886). In addition, the exact locations of three out of twelve specimens are unknown, however, we strongly assume that they were collected in the Carpathian Basin, because Baumgarten was one of the most famous botanists of Transylvania (Simonkai 1886), while Pávai and Hazslinszky worked as naturalists in the Kingdom of Hungary (Simonkai 1886). Our results showed that *H. tuberosus* agg. was a well-known taxon in the Carpathian Basin in the 19th century, which is also supported by literature data discussing its cultivation (Pethe 1805, Hazslinszky 1872, Simonkai 1886).

The majority of the herbarium specimens were collected in the 20th century, which is in accordance with earlier data published about the mass spread of a species belonging to *H. tuberosus* agg. throughout Central Europe after World War II (Balogh 2006, 2008).

Our study suggests that in the 19th century *H. tuberosus* agg. could be found both in floodplains as wild habitats and in cultivation. Floodplains remained the most typical habitat of the plant in the 20th century, which refers to the invasive character of the plant: invasive species are known to be very abundant along rivers, where water flow and flooding act as dispersal vectors of plants (Tickner et al. 2001). Moreover, several studies suggest that Central European *H. tuberosus* agg. populations tend to spread with vegetative propagules which can be transported by watercourses (Balogh 2006, 2008).

According to our investigation performed in 16 herbaria, some collectors of *H. tuberosus* agg. specimens referred to the invasive features of the species beginning from the first part of the 20th century. However, the first study which suggested the invasive character of the plant was written by Borbás as early as 1884, who recorded that "it is grown or it has escaped" in Timiş county (Romania). Nevertheless, currently a growing body of the literature suggests that *H. tuberosus* agg. is an invasive species in the Carpathian Basin, causing serious environmental problems in all countries, mostly in Austria (Patzner 1999; Walter et al. 2005), Croatia (Hulina 1998; Lukač 1998; Lukač and Vujčić-Karlo 2000; Boršic et al. 2008), Hungary (Malatinszky and Penksza 2002; Török et al. 2003; Balogh 2003, 2006, 2008, 2012; Filep et al. 2016), Romania (Kovács 2006; Sîrbu and Oprea

2008; Filep et al. 2010; Szatmari 2012; Arsene et al. 2015), Serbia (Vrbničanin et al. 2009), Slovakia (Fehér 2007; Galgóci and Štrba 2008; Týr and Vereš 2012; Žgančíková et al 2012; Gális and Straňák 2013; Pauková 2013), Slovenia (Zelnik 2012), and Ukraine (Protopopova and Shevera 1998; Protopopova et al. 2006; Omelchuk and Prots 2014).

Our results suggest that *H. tuberosus* agg. has been constantly present in the Carpathian Basin since the 17th century (the period when the species was introduced to Europe) (Lippay 1664). However, our results reveal also that from the 19th century *H. tuberosus* agg. has had two different aspects, being present both as crop and invasive species in the Carpathian Basin. To our knowledge, this is the first study documenting the invasive features of the plant already from the first part of the 19th century, relying on herbarium data.

6.1.2. Allelopathic effect of *Helianthus tuberosus*

The results of our allelopathy experiments indicated that (1) concentration, associated species, tissues, and timing play an important role in the allelopathic effect of *H. tuberosus*, (2) the allelochemicals of *H. tuberosus* showed seasonal dynamics, and (3) *H. tuberosus* could inhibit the growth of certain commonly occurring neighboring species via allelopathic root exudates.

Our strongest finding was that the allelopathic potential of the plant showed seasonal dynamics. Our bioassays clearly demonstrated that the overall inhibition of seed germination by *H. tuberosus* allelochemicals was the most intensive in the early summer months, when the plant itself is at an early stage of development. Since late spring is when our five test species germinate in the field (Ujvárosi 1973), inhibition by *H. tuberosus* allelochemicals could likely in natural settings. Plumule and radicle length was inhibited to the greatest degree in June and October, when the concentrations of most allelochemicals were significantly higher than the other three months. Our results showed that allelopathic effects were strongest early in the summer when other species develop and late fall, when the allelochemicals can accumulate in the rhizosphere. Strong seasonal dynamics of phenolic production has also been shown in *Conyza canadensis* by Djurdjević et al. (2012), with their level being the highest during the flowering and fruiting time.

H. tuberosus extracts exerted the most negative effects on germination rate and seedling growth of *E. repens*. These results corresponded with other studies of the allelopathic

activity of *H. tuberosus* (Vidotto et al. 2008; Tesio et al. 2011), in which the development of monocot weeds was inhibited. Although our study was conducted only in non-native range, our results are in accordance with the 'Novel weapons' hypothesis, according to which exotic species release allelochemicals that are relatively ineffective against their neighboring plants in the native range, but highly inhibiting against the native plants in the new habitat (Callaway and Aschehoug 2000). In the field, *E. repens* spreads rapidly by its rhizomes (Palmer and Sagar 1963; Ujvárosi 1973; Werner and Rioux 1977), while its seed production may be naturally limited by late flowering and low seed viability (Williams and Attwood 1971). Thus, it is likely that allelochemicals of *H. tuberosus* can inhibit seed germination and seedling growth of *E. repens* in the field, although allelochemicals are less likely to be effective if root systems do not commingle in the soil. However, active compounds can be transformed in the soil; they may become diluted by soil water, bound by soil particles, or their allelopathic potential may change due to inorganic soil components and microorganisms (Brückner and Szabó 2001). These factors may account for differences observed in laboratory and field studies.

Other studies suggested that some *Helianthus* species can inhibit the germination and growth of *S. alba* (Bogatek et al. 2006; Csiszár et al. 2012). In contrast, our results showed that growth of *S. alba* seedlings was stimulated by *H. tuberosus* extracts in the first half of the vegetation period. This discrepancy can be explained by differences in tissue collection time. The previous bioassays collected donor plant tissues later, during the flowering stage of *Helianthus*, whereas we found a facilitating effect early in growth, prior to the flowering stage. The facilitating effect of *H. tuberosus* on *S. alba* can be explained by the phenomenon that *S. alba* might be able to utilize plant extracts as sources of nutrients. Similar results were detected by Kazinczi et al. (2008, 2013), when they studied the allelopathic effects of different species on germination, seedling growth, and biomass of *Ambrosia artemisiifolia*. This phenomenon, known as hormesis, has been observed both with herbicides and allelopathic extracts in dose-response studies (Duke et al. 2006; Pannacci et al. 2006, 2013; Nikneshan et al. 2011).

In our study, *S. gigantea* was the only test species that has a common evolutionary history with *H. tuberosus*. Both are native to North America and invasive in Europe. Seedling development of *S. gigantea* was not inhibited in most cases by *H. tuberosus* extracts throughout the vegetation period, and in the last 2 months of the study, it was even facilitated. Our results provide more evidence to studies that found allelopathic impact of

co-evolved species less significant to one another, compared to those species that evolved in different biogeographical areas (Rabotnov 1974; Callaway and Aschehoug 2000; Callaway et al. 2008).

In our bioassay study, the growth of germinated seeds was influenced in various ways by different tissues. The variation of allelopathic effects of leaf versus root is not unusual, because different tissues of a donor plant may have different allelopathic potential (Roberts and Anderson 2001). Butcko and Jensen (2002) reported that *S. canadensis* leaf leachates significantly inhibited seed germination of test species, whereas root leachates had no significant effect on germination.

In addition to testing the allelopathic effects of *H. tuberosus* in bioassays, we identified and quantified phenolic compounds of the leaves and roots, reporting for the first time the seasonal dynamics of allelochemicals in *H. tuberosus* throughout the entire growing season. We demonstrated that the concentrations of three of the five allelochemicals were significantly higher in the leaves than in the roots. Chen et al. (2014) reported similarly high or higher concentrations (ranging from 1 to 7750 mg/kg) of phenolic acids in the leaves of *H. tuberosus*, while Khanh et al. (2005) found that leaves are the most allelopathic plant tissues (compared to roots and stems) of *H. tuberosus*.

Tesio et al. (2011) suggest that salicylic acid is the most significant fraction of phenolic acids (2.57-22.46 mg/kg) in *H. tuberosus* leaf samples. In contrast, our analysis found 2-OH-cinnamic acid to be the most prevalent in each leaf sample during the vegetation period, followed by salicylic acid (1.45-8.52 mg/kg). Although the concentrations of salicylic acid are of the same order of magnitude in the two studies, the somewhat lower concentrations measured in our study can be explained by different growth conditions (greenhouse vs. field). Several environmental factors such as pedoclimatic and agronomic factors affect active substance (e.g. phenolics) concentration in plants (Dávid 2004; Manach et al. 2004). Salicylic acid has been widely reported as an inhibitor of weed germination and growth (Shettel and Balke 1983; Inderjit 1996; Jung et al. 2004), which suggests that this substance may be one of the most important allelochemicals produced by *H. tuberosus*. In accordance with the results of Tesio et al. (2011), coumarin was measured only in traces both in the leaves and in the roots of *H. tuberosus* throughout the vegetation period.

The seasonal dynamics of allelochemicals in different tissues suggest that there are two main stages during the vegetation period when the concentration of allelochemicals is significant. The level of 2-OH-cinnamic acid in leaves and roots, as well as salicylic acid and 4-OH-benzaldehyde in leaves, suggests that the concentrations of allelochemicals were higher in the beginning and in the end of the vegetation period, when they can be more effective: during the spring, when other species germinate and during the fall when *H. tuberosus* litter covers the soil. Our findings are consistent with the results of Ben-Hammouda et al. (1995), who evaluated the chemical basis for the allelopathic potential of *Sorghum* hybrids and reported that the total concentration of phenolic acids was positively correlated with the allelopathic potential.

In our pot experiment, the allelopathic effect of *H. tuberosus* was observed on *E. repens* and *G. mollugo*. These species were inhibited not only by the presence of *H. tuberosus*, but our results also suggest that allelochemicals have a significant effect on the number of surviving plants and their growth. These findings support our bioassay results, where the germination and the growth of *E. repens* were influenced by allelochemicals of *H. tuberosus*. It has to be noted, however, that an activated carbon treatment can only detect direct impacts of allelochemicals and extrapolation to field conditions may produce different results. Activated carbon can influence plant growth (Lau et al. 2008), disrupt plant symbioses (Wurst et al. 2010; Yuan et al. 2014), and mediate plant-microbe interactions (Nolan et al. 2014).

In conclusion, our results show that *H. tuberosus* can interfere with other species through allelochemical interactions. Moreover, seasonal dynamics of allelochemicals could be more important than suspected in plant competition and is likely to play an important role in the spread of the invasive *H. tuberosus* into new areas.

6.2. *Helianthus tuberosus* at home and away

6.2.1. Field measurements

Our results indicate strong biogeographical differences in the impact of *Helianthus tuberosus* in the field. The total species number was higher in Europe than in North America, however, the mean species richness, and both native and exotic species richness were significantly lower in Europe, than in North America. These results support a growing body of literature demonstrating stronger effects of invasive plant species on other species in their non-native ranges than in their native ranges (Hierro et al. 2005;

Callaway et al. 2011; Ledger et al. 2015; Pal et al. 2015). Furthermore, the number of species declined with increasing *H. tuberosus* cover in European plots, but not in North America where *H. tuberosus* is native. Our findings are consistent with the results of Pal et al. (2015), who investigated the impact of *Solidago gigantea* in the native and non-native ranges and reported that the number of species declined sharply with increasing *Solidago* stem density in the non-native range.

Similarly, plant diversity demonstrated a much stronger effect of *H. tuberosus* in the non-native range compared to the native range, thus, in European plots plant diversity was significantly lower than in North American plots. These results are consistent with the study of Corlett (2016), which suggests that invasive alien species pose a potential threat to native plant diversity. It has been demonstrated that invasive plant species can have significant local impacts by reducing native plant diversity (Pyšek et al. 2012), but information regarding their longer-term effects on regional and global plant diversity is still scarce (Corlett 2016).

Three out of four properties measured in the field (plant height, stem density, bare ground cover, percentage of litter) exerted a significant impact on species composition both in native and non-native range.

Mean plant height of *H. tuberosus* was significantly higher in Europe compared to North America. This result corresponded with "the evolution of increased competitive ability" hypothesis, which predicts that exotics should no longer invest into high-cost defensive traits, once they are free from their native enemies. By allocating less resources to traits of resistance, exotics could evolve to use more resources for traits that provide greater competitive advantage, such as size (Blossey and Nötzold 1995).

The bare ground cover in our European plots was significantly higher than in North American plots, which 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 a reduced growth of other species (Kays and Nottingham 2007; Balogh 2012). The importance of the shading role of *H. tuberosus* was confirmed in our study, because in European plots the proportion of bare ground cover rose with increasing *H. tuberosus* cover. Thus, bare ground was the most important factor which influenced the species composition in Europe. In contrast, in North America there was no relationship between *H. tuberosus* and bare ground cover.

Contrary to expectation, we detected no significant difference in the percentage of litter of *H. tuberosus* in Europe versus North America, despite the fact that the average total *H. tuberosus* stem density was around twice as high in our European versus in our North American plots. We have to bear in mind that some of the most invasive plant species are known to decompose more quickly than native species in the ecosystem (Rothstein et al. 2004; Arthur et al. 2012). Moreover, a meta-analysis of litter decay rates revealed that invasive plants decompose, on average, 117% faster than co-occurring native species (Liao et al. 2008). Species composition was significantly influenced by the litter of *H. tuberosus* in Europe, but not in North America. This suggests that the litter of invasive species can influence species composition to a greater extent, supposedly due to the released allelochemicals which the native species are not adapted to (Callaway and Ridenour 2004).

The relationship between the number of *H. tuberosus* stems and *H. tuberosus* cover was considerable both in Europe and in North America, however, the common models which were used in the statistical analysis suggested that a single *H. tuberosus* stem covered a smaller area in Europe versus in North America. In our opinion, this result does not correspond with what we can experience in the field, and may be due to the fact that the average total *H. tuberosus* stem density was around twice as high in our plots in Europe versus in North America, thus *H. tuberosus* stems probably shaded each other in the non-native range.

6.2.2. Species composition and environmental factors

The present analysis aimed to identify the main environmental factors affecting species composition of *H. tuberosus* populations in order to rank the relative importance of environmental factors as explanatory variables in the native and non-native ranges. The importance of environmental factors in the case of invaders was discussed by Thuiller et al. (2006), who demonstrated that, although biological invasion is species specific, the distribution and spread of major plant invaders can be explained partially by environmental factors.

In our study the total variation explained by the 27 variables together was 44.4% and 31.1% for North America and Europe, respectively. Similarly to earlier studies (Pinke et al. 2012, 2016), climatic variables are discussed together with altitude, since the latter directly influences the climatic conditions of the site. In our study altitude was found to

be less important in Europe than in North America. The experienced lower influence of altitude is consistent with the results of Lenoir et al. (2008), who claim that climate warning led to a significant increase in the optimum elevation of species, in average 29 meters per decade.

Four out of seven climatic variables in North America, and all studied climatic variables in Europe exerted significant influence on species composition in the present study. Besides altitude, mean annual precipitation, mean annual precipitation of 30 years, and mean annual temperatures were significant variables in both ranges. *H. tuberosus* thrives under a wide climatic range (Kays and Notthingam 2007), tolerating annual precipitation in the range of 31 to 282 cm (Duke 1983), and temperatures in the range of a few degrees above 0ºC to a maximum of 20 to 35ºC (Kays and Notthingam 2007), which could be an advantage for the plant, because rapid adaptation to climate facilitates expansion of invasive plants (Colautti and Barrett 2013).

The effect of climatic variables on species composition was stronger in the native range of the plant compared to the invaded range. Flanagan et al. (2015) also found that climate-driven variables have a stronger effect on native species compared to invasive species in riparian ecosystems. Furthermore, Lososová and Cimalová (2009) suggest that the relative importance of climatic variables decrease with decreasing lengths of their gradients. This can be also illustrated in our own study area, which can be characterized by a relatively short altitudinal gradient (ranging from 95 to 510 m) and a fairly wide horizontal extent in Europe.

In our study soil attributes were also important factors affecting species composition of *H. tuberosus* populations both in the native and non-native ranges. However, their effect was more important in North America. The study of Flanagan et al. (2015) concluded that in riparian ecosystems soil nutrient availability has a stronger influence on the abundance of invasive species than climatic variables. Soil Mg content was the most important soil property in North America and it was also a significant variable in Europe. Some recent studies (Andreasen and Skovgaard 2009; Pinke et al. 2011) also showed that soil Mg content influenced the occurrence of certain species. Moreover, Pinke et al. (2011) suggest that Mg levels can be affected by complex interactions of soil chemistry with plant functions, or even might be correlated with other soil properties.

Our results suggest that species composition was associated with P_2O_5 content in Europe. These results corresponded with the study of Pal et al. (2013), in which P_2O_5 content was

found to affect species composition of cereal fields in Italy. Tarmi et al. (2009) found that species diversity was negatively related to the amount of phosphorus.

Organic matter content was the second most important soil property that defined species composition in both ranges. As we know, riparian zones are unique and dynamic systems (Mikkelsen and Vesho 2000), where water table approaches the surface and soils become more anaerobic, accompanied by an increase of soil organic matter and denitrifier populations (Groffman et al. 1992).

Soil texture was a significant factor in both ranges, but its influence was stronger in North America versus in Europe. Soil texture also proved to be an important variable that determined species composition in several other studies (Pinke et al. 2011; 2012; 2016; Pal et al. 2013).

All studied heavy metals in North America, and two out of three heavy metals in Europe exerted a significant impact on species composition. The experienced lower effect of heavy metals in the non-native range is probably due to the fact that invasive plants are able to tolerate heavy metals and can accumulate both macronutrients and heavy metals very effectively. (Hulina and Đumija 1999; Jadia and Fulekar 2008; Širka et al. 2016). Furthermore, Willscher et al. (2017) suggest that *H. tuberosus* is a suitable candidate for performing phytoremediation by extracting Mn, Zn, Cd and Ni from contaminated soils.

In our study, pH as well was a significant factor in North America, but not in Europe. This is probably due to the fact that *H. tuberosus* thrives in a wide range of pH levels, the optimal range being pH 4.5-8.6 (Duke 1983; Kosaric et al. 1984).

In conclusion, our results indicate strong biogeographical differences in the impact of *Helianthus tuberosus* in the field. There are several climatic and soil properties which can influence the species composition of *H. tuberosus* communities, but *H. tuberosus* itself can exert a strong impact on species composition, too.

6.2.3. Arbuscular mycorrhizal fungi (AMF) colonization

Our results verified that *H. tuberosus* had arbuscular mycorrhizal fungi (AMF) colonization both in the native and non-native range. Our results provide novel insights into the AMF colonization of *H. tuberosus*, since previous studies discussed the mycorrhizal relationships of the plant only as a crop species (Püschel et al. 2011; Zubek et al. 2011; Sennoi et al 2013). To our best knowledge our study reported for the first time

the AMF colonization of the wild *H. tuberosus* populations in both the native and non-native ranges.

The research of Štajerová et al (2009) is the first which gives information about AMF colonization of *H. tuberosus* in the non-native range (Czech Republic). Moreover, Zobek et al. (2011) analyzed the AMF colonization of the plant, when it was collected from a botanical garden in the non-native range. They suggest that AMF colonization of *H. tuberosus* was low, and its morphology was *Arum* type (intercellular, forming arbuscules terminally in cortical cells). In contrast, our results showed that AMF colonization of the plant was much higher in both the native and non-native range. These results corresponded with the study of Tawaraya (2003), which indicated that cultivated plant species showed a lower mycorrhizal dependency than wild plant species.

Our results indicated that introduced European and native North American populations of *H. tuberosus* differed in their arbuscular mycorrhizal (AM) fungi colonization, which was found to be significantly lower in the non-native range. As discussed previously, our field study demonstrated that stem density of *H. tuberosus* was around twice as high in European plots as in North America. The above two observations fit well with other studies which have shown that AMF colonization of roots decreases with decreasing light intensity (Hayman 1974; Daft and El-Giahmi 1978; Gehring 2003; Johnson 2010).
Furthermore, the reduced mycorrhizal associations may even benefit invaders in a competitive environment (Pringle et al. 2009; Seifert et al. 2009; Vogelsang and Bever 2009; Bunn et al. 2015; Waller et al. 2016). Pringle et al. (2009) suggest that exotic plants without obligate dependence on an AMF symbiont have greater chance to become invasive in the new community compared to those with strong AMF associations. The study of Seifert et al. (2009) also supports this theory, because they found that the introduced North American populations of *Hypericum perforatum* responded less to inoculation with AM fungi than did native European populations.
We did not study the mycorrhizal status of *H. tuberosus*, however, there is a group of plants considered to be facultative symbionts, which form arbuscular mycorrhizae in some cases, but lack AMF association at other times. Although the background of such sporadic colonization has not been researched yet to a sufficient degree, it may be related to the availability of inoculum, particularly in disturbed environments, as well as environmental conditions (Smith and Read 2008). Furthermore, the study of Hempel et al. (2013) suggests that facultatively mycorrhizal species show wide geographic and

ecological amplitude, and plants that are able to form mycorrhizal associations most effectively, would benefit most from the symbiosis (Grman 2012).

In conclusion, we provide evidence on AMF colonization of *H. tuberosus* in the native and non-native ranges. The detected significant differences in colonization between the two continents suggest that AMF colonization of the plant could be an important factor of plant invasion. Further studies need to clarify the role of AMF colonization in the process of plant invasion.

7. SUMMARY

Helianthus tuberosus (L.), a perennial plant native to North America, is a significant invasive species in Europe. We organized our research around three main aspects : **(1)** distribution of *H. tuberosus* in its non-native range (Carpathian Basin), based on herbarium data; **(2)** allelopathic effect of *H. tuberosus* as a complex mechanism for *H. tuberosus* invasion, studied by bioassays, chemical analysis of phenolic compounds and pot experiment; and **(3)** biogeographical study to acquire field evidence of interactions between *Helianthus* and neighboring species, to clarify which factors can influence the species composition and to get more information about arbuscular mycorrhizal fungi (AMF) colonization of *H. tuberosus* at home and away. Our results revealed that:

1. • *H. tuberosus* has been constantly present in the Carpathian Basin from the first part of the 19th century, at first as a profitable crop, and later also as a noxious invasive species in the Carpathian Basin

• herbaria serve as remarkable sources to evaluate the distribution of invasive plants in the Carpathian Basin

2. • *H. tuberosus* can interfere with other species through allelochemical interactions

• higher amounts of allelochemicals accumulated in the leaf versus the root

• the concentration of some allelochemicals in *H. tuberosus* was the highest at the beginning and at the end of the vegetation period, when they can be more effective

• seasonal dynamics of allelochemicals seems to be a significant factor in plant competition and is likely to play an important role in the spread of the invader into new areas

• allelopathy could be an important factor in *H. tuberosus* invasion

3. • there are strong biogeographical differences regarding the impact of *H. tuberosus* in the field, species number and diversity being reduced in the non-native range (Europe)

• there are several climatic and soil properties which can influence the species composition of *H. tuberosus* communities

• *H. tuberosus* itself can exert a strong impact on species composition, too.

• *H. tuberosus* has AMF association both in the native and non-native ranges

• AMF colonization of *H. tuberosus* was higher in the native range

• the stem density of *H. tuberosus* did not influence the AMF colonization of the species

• the lower AMF colonization in the non-native range could be an important factor in plant invasion.

Overall, we demonstrated that herbaria can substantially contribute to the research of invasive plants in the Carpathian Basin. Our results suggest that allelopathy and AMF colonization can be significant factors in the spread of invasive plant species into new areas. Furthermore, because the impact of *H. tuberosus* is stronger in its non-native range than its native range, our results are in accordance with a growing body of quantitative studies that demonstrate a strong biogeographic context to exotic plant invasions.

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