

Monograph of invasive plants in Europe N°6: *Asclepias syriaca* L

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ABSTRACT

This work synthesizes all aspects of *Asclepias syriaca* L. (Apocynaceae) including the taxonomy, distribution, history of introduction and spread, ecology, biology, uses and benefits, impacts on biodiversity and agriculture, legislation, and management. *Asclepias syriaca* is a perennial broad-leaved species native to North America. Introduced for ornamental and various other purposes, such as a source of fibre and rubber, it has become established in many regions of Europe and it had increasingly spread in the last decades (>1980s). Its reproductive behavior is characterized by a high production of wind-dispersed seeds and by the propagation of creeping lateral rhizomes, which allows the species to proliferate rapidly. The species persists in a wide range of edaphic and climatic environments. It occurs particularly in anthropogenic and (semi-)natural habitats, such as roadsides, agricultural land, abandoned sites and grasslands, open shrubland, and forests, respectively. Studies have demonstrated negative impacts on the biodiversity and ecosystem processes in invaded regions, namely in open sand grasslands in Hungary. *Asclepias syriaca* occurs as a competitive weed in crop fields. Since 2017, the species is regulated by the European Union (EU) under the Regulation No. 1143/2014, which states that *A. syriaca* is subjected to restrictions such as a ban on importing, selling, breeding and that EU member states are required to place effective management measures. Awareness raising activities are important to inform the public, farmers and stakeholders about the risks of this invasive alien plant. Effective direct control options include mechanical control as well as herbicide application.

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Common milkweed; impact; invasion history; invasive alien plants; management; species distribution

1. Taxonomy and morphology

1.1. Names and classification Scientific name

Asclepias syriaca L., 1762 Synonyms: *Asclepias apocinum* Gaterau, *Asclepias cornuti* Decne., *Asclepias consanguinea* Kunze, *Asclepias capitellata* Raf., *Asclepias fragrans* Raf., *Asclepias globosa* Stokes, *Asclepias grandifolia* Bertol., *Asclepias illinoensis* Michx. ex Steud., *Asclepias intermedia* Vail, *Asclepias kansana* Vail, *Asclepias obtusifolia* Kunze, *Asclepias pubigera* Dumort., *Asclepias pubescens* Moench, *Asclepias serica* Raf., *Asclepias syriaca* L. f. *inermis* J.R.Churchill, *Asclepias syriaca* L. f. *leucantha* Dore, *Asclepias syriaca* L. f. *polyphylla* B. Bovin, *Asclepias syriaca* L. f. *syriaca*, *Asclepias syriaca* L. var. *kansana* (Vail) E.J. Palmer et Steyerl., *Asclepias syriaca* L. var. *syriaca* (POWO 2019) Taxonomic position: Dicotyledons, Order: Gentianales, Family: Apocynaceae Common names: cigansko perje

(Croatian), klejicha hedvábná (Czech), zijdeplant (Dutch), kæmpe-silkeplante (Danish), common milkweed (English), siidaskleepias (Estonian), mesisilkkijrtti (Finnish), herbe aux perruches (French), Echte Seidenpflanze (German), közönséges selyemkóró (Hungarian), albero della seta (Italian), sirinis klemalis (Lithuanian), trojeść amerykańska (Polish), ceara albinei (Romanian), ваточник сирийский (Russian), пустенолисна свиленица (Serbian), glejovka americká (Slovak), sirska svilnica (Slovenian), yerba de mariposas (Spanish), sidenört (Swedish) EPPO code: ASCSY

1.2. Morphological description

1.2.1. Species description

Asclepias syriaca is a herbaceous, perennial broad-leaved species. The main characteristics of the plant are its milky sap, seeds with silky hairs and its propagation by creeping lateral rhizomes (Bhowmik 1994;



Figure 1. *Asclepias syriaca*: (a) top of flowering plant; (b) open follicle showing layers of seeds; (c) entire flower; (d) sprouting plant; (e) seed with tufts of long, silky hairs (© Petra-Christin Meisel).

Dvirna 2018; Figures 1(d) and Figure 6). The species has simple, erect shoots, usually several together, growing up to 60 to 120(150) cm (Bhowmik and Bandeen 1976; Figure 1(a)). The leaf blade is usually ovate or elliptical with a rounded base and broadest at middle. Mature leaves are 10 to 26 cm long and 4 to 18 cm wide. Lateral leaf veins are prominent and are typically arranged oppositely (Gudžinskas et al. 2019). The flowers are in umbels at the top of the shoot or in the axils of the upper leaves (Figure 1(a)). The number of flowers in the inflorescence varies and ranges from a few to 130 flowers. The corolla is green-tinged purple or pink and the corona lobes are pink, pinkish or purple (Gudžinskas et al. 2019; Figure 1(c)). The follicles (pods) are greenish to grey, ovoid and pointed and covered with soft spiny projections up 3 mm high (Figure 1(b)). Follicles are 7 to 10 cm long and split open along one side exposing many seeds that are

dispersed by wind (Bhowmik and Bandeen 1976; Figure 1(b)). The shape of the follicles is reminiscent of a parrot's beak, a characteristic that is the origin of the common name of the plant in many countries. The seeds are brown and flat and almost 7 mm long and 5 mm wide with a tuft of silky hairs (6 to 10 mm long) coated with wax (Bhowmik and Bandeen 1976; Bhowmik 1994; Figure 1(e)).

1.1.2. Distinguishing features

Asclepias syriaca can be most likely confused with *A. speciosa* Torr. (showy milkweed) native to North America (Bhowmik and Bandeen 1976). At present, *A. speciosa* has only been recorded in southern Lithuania, where it occupies mesic grasslands, tall-herb fringe communities and agricultural land

Table 1. Principal features used to distinguish *Asclepias syriaca* from other *Asclepias* species present in Europe (adapted from Gleason and Cronquist 1991; Gudžinskas et al. 2019).

Species	Feature
<i>Asclepias syriaca</i>	Leaves: ovate or elliptical with a rounded base and widest at middle Flowers: corolla green-tinged purple or pink, corona lobes pinkish or purple, hoods 3.5–5 mm long, with rounded apex Follicle: erect, 7–10 cm long, tomentose and covered with soft, filiform to conic processes
<i>Asclepias speciosa</i>	Leaves: broadest in basal part, with shallowly cordate or almost rounded base Flowers: corolla deep purple or pink, corona pink or pinkish, hoods 10–13 mm long, with a tongue-like apex Follicle: erect, 11–13 cm long, the surface typically with soft, elongate tubercles
<i>Asclepias incarnata</i>	Leaves: narrow lanceolate or lanceolate Flowers: in cymes with 20–40 flowers, corolla pink to red (white), corona carmine or pink, hoods 2.5–3 mm, horn subulate, incurved, surpassing the hood Follicle: erect, narrow
<i>Asclepias curassavica</i>	Leaves: narrow lanceolate or lanceolate Flowers: in cymes with 10–20 flowers, corolla red to orange, corona yellow or orange Follicle: spindle-shaped, 5–15 cm long

(Gudžinskas et al. 2019). This species can be differentiated from *A. syriaca* by its leaf shape and size, at the flowering stage by the shape and size of flowers and the number of flowers in the inflorescence (Gudžinskas et al. 2019). Principal features used to differentiate *Asclepias* species present in Europe from *A. syriaca* can be found in Table 1. *Asclepias syriaca* may also be likely confused with *A. sullivantii* Engelm. ex A. Gray (Sullivant's milkweed), a species, however, that does not yet occur in Europe (for distinguishing features see e.g. Klips and Culley 2004). Other similar species belong to the genera *Apocynum* (dogbane) and *Vincetoxicum* (swallow-wort). They can also be distinguished by their leaf size, branching, flowers and fruits. For example, *Apocynum* species have small bell-shaped flowers and very narrow fruits (Bhowmik and Bandeen 1976).

1.1.3. Variations at the infraspecific level

No subspecies or varieties are currently recognized within the species (The Plant List 2020). However, studies have shown geographic variations among *A. syriaca* populations (Woods et al. 2012; Agrawal et al. 2015). The species shows adaptive phenotypic clines along its broad latitudinal distribution in eastern North America. Woods et al. (2012) found that plants from northern populations (New Brunswick/Canada) produced less aboveground biomass, more buds, clonal growth and latex, and had a higher root-to-shoot ratio than southern populations (North Carolina/United States). Moreover, Agrawal et al. (2015) identified several growth (e.g. specific leaf

area) and defense traits (cardenolides and latex) that have diverged, despite low neutral genetic differentiation between North American and European populations.

2. Distribution and status

2.1. Native range

The native range of *A. syriaca* encompasses the prairies and alluvial plain in North America (Woodson 1954). At present, it is also abundant on agricultural land and in ruderal habitats, such as roadsides and wasteland (Bhowmik and Bandeen 1976). Bhowmik (1994) stated that the geographical boundary of the distribution of *A. syriaca* in North America is 35° and 50° north latitude and 60° and 103° west longitude. *Asclepias syriaca* has been extending its range in particular into the southeastern regions of the United States in recent decades as shown by Wyatt et al. (1993). Today, in the United States, it occurs from Maine to Georgia and South Carolina and westward to North Dakota and Texas (EPPO 2020; USDA NRCS 2020; GBIF 2021; Figure 2). Recently, occurrences have been observed in Montana and Oregon (GBIF 2021). In Canada, *A. syriaca* occurs from Saskatchewan to the Atlantic Provinces, while the largest populations are found in the southern parts of Ontario and Quebec (Bhowmik and Bandeen 1976; EPPO 2020; USDA NRCS 2020; Figure 2).

2.2. Invaded range

The invasion history and current distribution of *A. syriaca* is well documented in Europe. *Asclepias syriaca* is a conspicuous species that has been included in European standard floras for a long time. Sampling efforts have increased in recent years, especially due to its categorization as “invasive” in some European countries and its recent inclusion in the List of Invasive Species of European Union Concern (Tsiamis et al. 2019; see section Legislation).

Asclepias syriaca is present in many European countries, though it is most widespread in central, eastern and southeastern parts of the continent (EPPO 2020; Figure 3). The species occurs up to latitude 50°, but it is largely confined to lowlands (e.g. Pannonian Basin, areas of the northern Italy basin) and hilly regions with favorable mild climates. It is rare at high altitudes, while it has been detected at altitudes of c. 880 m (Prášily/Šumava Mountains, Czech Republic; Kaplan et al. 2017). The species is almost absent from the Iberian Peninsula, Mediterranean countries such as Italy (southern part), Greece and Turkey. Further, *A. syriaca* is rare on the British Isles and in Northern Europe. In many of the cited references below, distribution

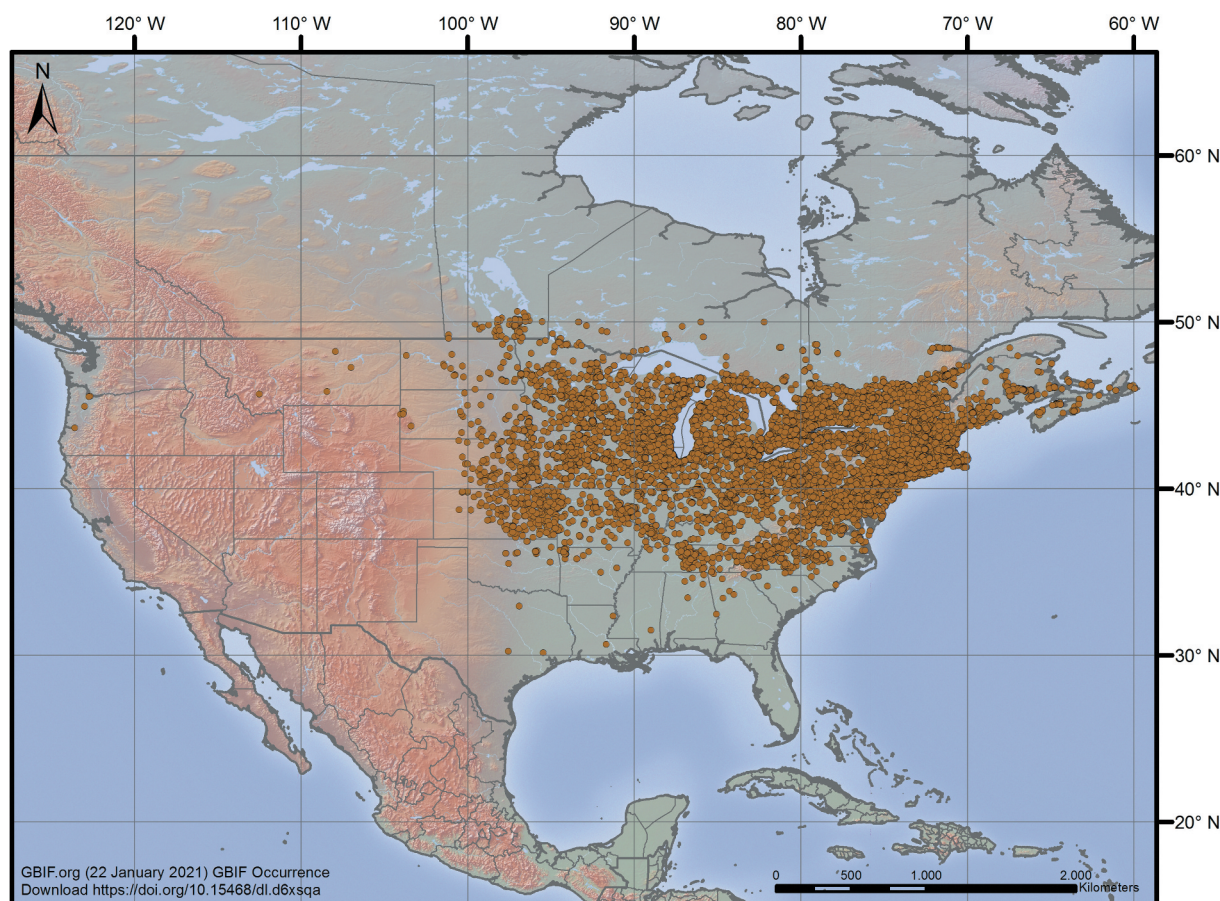


Figure 2. Distribution of *Asclepias syriaca* in the native range (North America). The data from USDA NRCS (2020) on the occurrence in the federal states of the United States and Canada was used as a basis. Distribution data (dots) of *A. syriaca* in the respective federal states are shown and were obtained from GBIF (2021).

maps of *A. syriaca* for the respective country can be found.

In western European countries, such as Belgium and the Netherlands, *A. syriaca* has a limited and scattered distribution with a few established populations (NDFP 2015; Verloove 2020). In France, *A. syriaca* occurs predominately in the Rhone Valley and in the centre (Central-Val de Loire, Île-de-France) (GT IBMA 2017; Figure 3). In Switzerland, its distribution is confined to southern Ticino and the western (Romandy) and north-central part of the country (InfoFlora 2020). In Italy, the species is present in all northern regions (except Liguria and Aosta Valley), but it is almost absent from the southern part of Italy (Acta Plantarum 2020; Brundu et al. 2020).

In central and eastern Europe, the species is rather widespread (Figure 3). In Germany, *A. syriaca* occurs scattered throughout the country with a more clustered distribution in eastern Germany (Nehring and Skowronek 2017). The species can be found in the lower altitude parts of Poland, e.g. in the Gdańsk Lakeland, Toruń, the Greater Poland Lake District, the Lublin Upland, the Małopolska Upland, the Kraków-Częstochowa Upland, the North Podlasie Lowland and the Lithuanian Lakeland (Tokarska-Guzik et al. 2018; Zajac and Zajac 2019). New sites

of *A. syriaca* have been found in recent years in different regions of Poland (e.g. Tokarska-Guzik et al. 2010; Rutkowski et al. 2015). *Asclepias syriaca* occurs primarily in eastern Austria (Vienna, Lower Austria), while it has been rarely recorded in southern and western regions of this country. Large populations occur in parts of Lower Austria (Marchfeld region) (Follak et al. 2018). In the Czech Republic, the species currently occurs scattered in the lowlands of northwestern, central and eastern Bohemia. In Moravia, it grows mainly in its southern and central part, where it is locally abundant (Pyšek et al. 2012a; Kaplan et al. 2017). In Slovakia, the species is most commonly found in the south all along the border to Hungary, but records are also available from western and central regions (Kochjarová 2010; Mártonfi et al. 2014; Pauková et al. 2014). In Hungary, *A. syriaca* is widely distributed and established throughout the country in particular between the Danube and Tisza rivers (central Hungary), i.e. in the Great Hungarian Plain and parts of Transdanubia (Novák et al. 2009; Bartha et al. 2015; Csiszár and Korda 2017). In Bulgaria, Vladimirov and Georgiev (2019) summarized records of *A. syriaca* from many parts of the country such as the Thracian Lowland and the Danubian Plain. Dvirna (2018) showed that

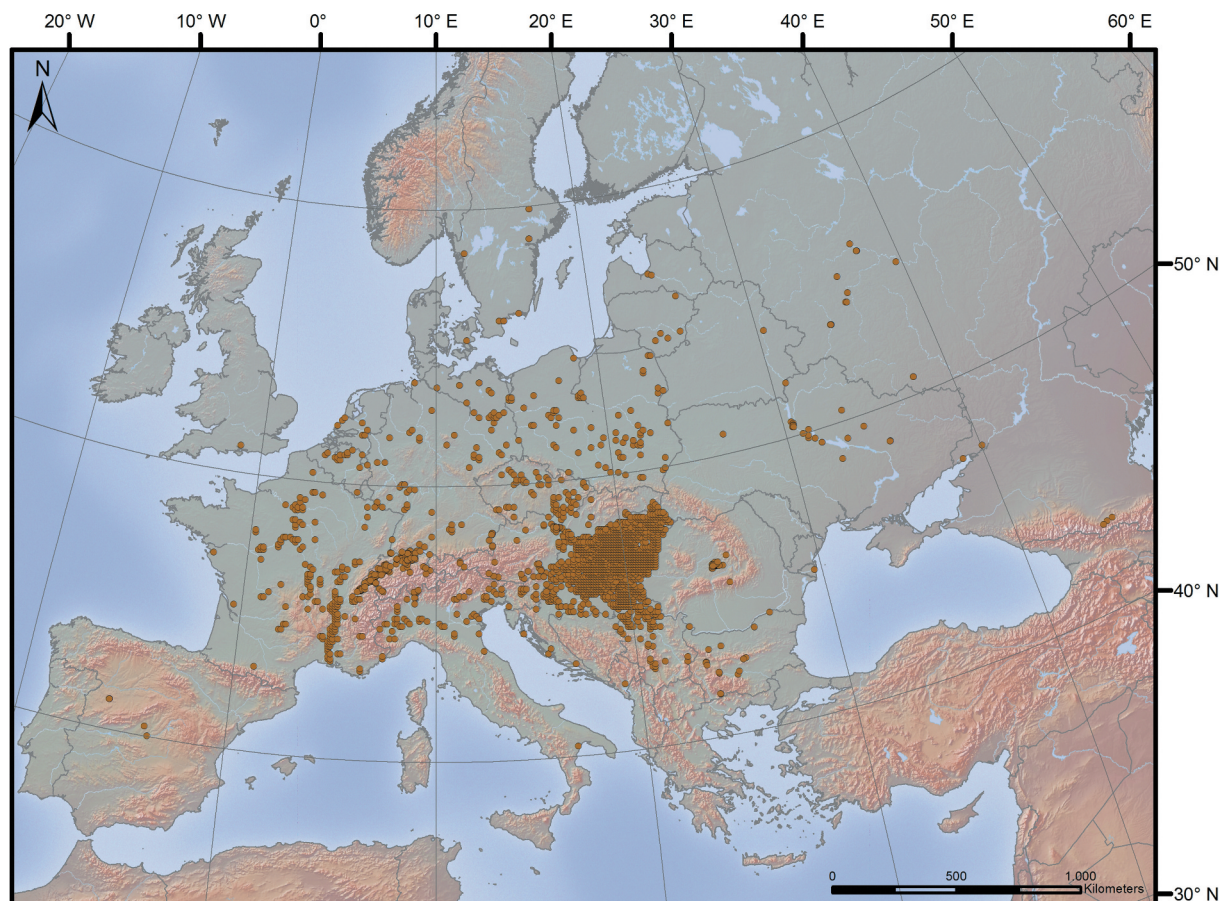


Figure 3. Distribution of *Asclepias syriaca* in Europe. Distribution data of *A. syriaca* were from Smekalova (2008), Stešević and Jovanović (2008), Vrbničanin et al. (2008), Bartha et al. (2015), Zimmermann et al. (2015), Follak et al. (2018, amended), Tsiamis et al. (2019), Vladimirov and Georgiev (2019), Nāburga and Evarts-Bunders (2019), GBIF (2021) and InfoFlora (2020).

A. syriaca occurs throughout the Ukraine, but it is most abundant in central regions around the cities of Kiev and Poltava. In Romania, the species is restricted to Transylvania (parts of Sibiu, Mureş and Braşov counties) according to Zimmermann et al. (2015). Further to the east, Smekalova (2008) detailed the scattered distribution of *A. syriaca* in Russia. Panasenkov et al. (2012) gave an overview of its distribution in the Bryansk Oblast (western Russia). Parfenov (1999) described the presence of the species in Belarus. Recently, Mialik (2018) confirmed the occurrence of *A. syriaca* in the central part of the Belarusian Polesye.

In some countries of the Balkan Peninsula, *A. syriaca* is regularly found (Figure 3). In Slovenia, records of *A. syriaca* are available from the surroundings of Ljubljana and in the eastern part of the country it is a common species (Ministrstvo za okolje in proctor 2018). Likewise, in Croatia, *A. syriaca* is distributed primarily in the surroundings of Zagreb, and in northeastern and eastern parts of the country, with rare records elsewhere (Boršić et al. 2018). In Serbia, large infestations are known from Vojvodina (Stanković-Kalezić et al. 2008; Vrbničanin et al. 2008; Figure 3). In Bosnia and Herzegovina (Posavski kanton) and Montenegro (city of

Podgorica), records are restricted to a few local populations (Stešević and Petrović 2010; Maslo 2016).

In northern Europe, established populations have been reported from southern Lithuania (Gudžinskas et al. 2018). In Latvia, Nāburga and Evarts-Bunders (2019) have reported local populations of *A. syriaca* in Riga and its vicinity. In Sweden, only a few records can be found in the literature (e.g. Tsiamis et al. 2019), though many recent observations of *A. syriaca* in southern regions are listed by the Swedish Species Observation System (<https://artportalen.se/>) indicating a much wider distribution.

Expansion of *A. syriaca* to higher altitudes or northern latitudes in Europe may accelerate with climate change. Using a niche-based habitat modelling approach, Kleinbauer et al. (2010) have shown that 30% of the area in Germany and Austria provides a suitable habitat for *A. syriaca* under current climatic conditions. They also reported that habitat suitability would increase up to 84 to 92% of the area depending on the climate change scenarios used. Finally, proceeding habitat degradation may facilitate the spread of *A. syriaca* (Szilassi et al. 2019).

The distribution of *A. syriaca* outside its native range is limited to Europe according to EPPO (2020). In the GBIF database (GBIF 2021), records for Mexico, Australia, and central Asia (Kazakhstan)

are given. However, the records for Australia and Mexico are erroneous or not ascertainable, respectively.

3. History of introduction and spread in Europe

Asclepias syriaca has been introduced to Europe as an ornamental plant in the 17th century (Bagi 2008; Rothmaler 2008). In some countries (e.g. France, Germany, Russia), the species has been (experimentally) cultivated in the 18th century for the use of the fiber and the floss for filling material and clothes (Whitening 1943). Meitzen (1862) already noted that the plant escaped from cultivation and gradually spread in Upper Austria, southern Russia and Germany. The use (e.g. for rubber production, paper production, beekeeping) and the experimental cultivation of the species has revived from time to time (e.g. Whitening 1943; see section *Uses and positive impact*) and subsequently, abandoned fields operated as source populations for the spread into surrounding areas (Dvirna 2015, 2018). In the early and mid-20th century, the number of escaped populations has increased considerably, although *A. syriaca* was still rare. In the last decades (>1980s), *A. syriaca* has spread further, with varying rates among countries (Figure 4). There are currently large established populations in many European countries (see section *Invaded range*).

In France, established *A. syriaca* populations were detected as early as in 1855 in the Botanical Garden of Montpellier and later in southwest and central France, as well as the along the Rhone River according to Thellung (1912). In the Netherlands, the oldest known documented records of established *A. syriaca* plants date back to 1866. The number of records has gradually increased after the year 2000 (Matthews et al. 2015). In Belgium, the species was first observed in 1987 and 1995 on ruderal places (province of Antwerp), and thereafter, also in other distinct locations, mainly as an escape from cultivation in gardens (Verloove 2020). In Switzerland, early records of *A. syriaca* were also from botanical gardens (Fribourg: 1854, Basel: 1886). Occasional occurrences in the wild were documented from 1922 onwards (InfoFlora 2020), while *A. syriaca* has been increasingly recorded in the last decade (Figure 4). The sharp increase of records in recent years (>2015) is most likely to a high sampling effort and reporting activity (specific floristic projects and monitoring studies).

In Germany, the earliest records date back to the 19th century (Nehring and Skowronek 2017). *Asclepias syriaca* was first found in the wild 1827 in Germany (Nehring and Skowronek 2017). Then, it has been recorded several times in the second half of the 19th century as a weed in gardens and parks as well as on arable land (e.g. Timm 1878; Büttner 1883). Timm (1878) stated that *A. syriaca* occurred in 1875 in Hamburg in a deserted garden area [“ ...

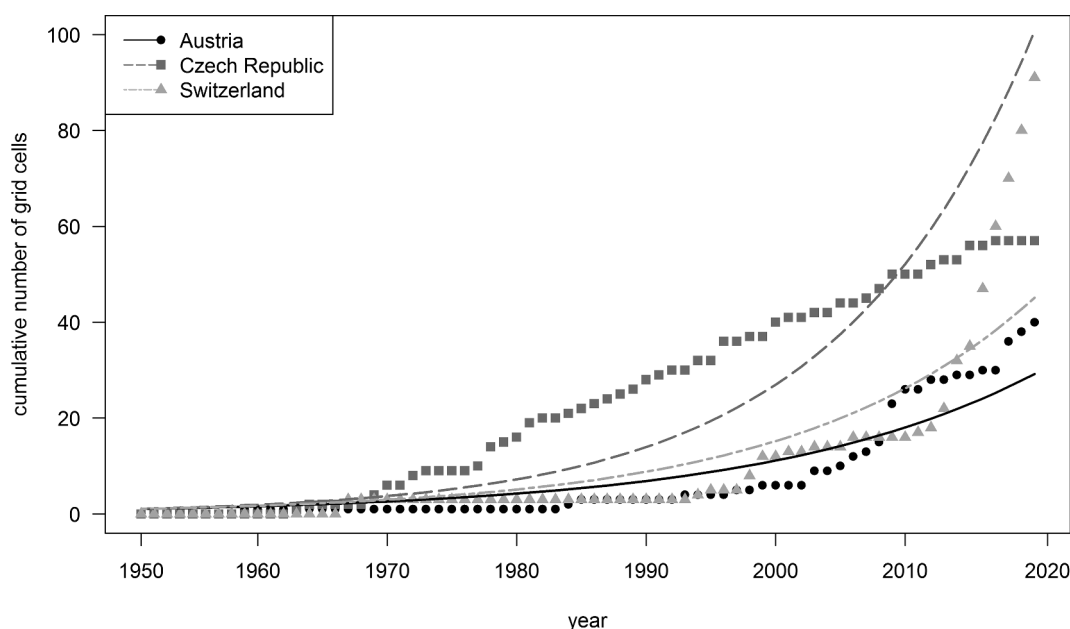


Figure 4. Observed cumulative number of grid cells (5×3 geographic minutes, $\sim 33 \text{ km}^2$) of the Floristic Mapping of Central Europe (FMCE) occupied by *Asclepias syriaca* in Austria, the Czech Republic and Switzerland for the observation period 1950 to 2019. Further given are the expected cumulative numbers of grid cells occupied by year derived from a Poisson regression model (lines). The increase in cumulative grid cells occupied per year was significant for each country ($P < 0.001$). The rate of spread (expressed as the estimated coefficients) was highest for the Czech Republic (0.065) followed by Switzerland (0.054) and Austria (0.048). The Tukey HSD post-hoc test showed a significant difference in annual increase between Austria and the Czech Republic and between the Czech Republic and Switzerland ($P < 0.001$). Distribution data were obtained from Kaplan et al. (2017), Follak et al. (2018, amended) and InfoFlora (2020).

on the often mentioned desert garden land before Teufelsbrück temporarily wild“]. Likewise, in Poland (in its contemporary borders), the species was observed since the 19th century (Rostafiński 1873; Abromeit et al. 1898–1940; Zajac and Zajac 2019). Rostafiński (1873) already stated that *A. syriaca* has become locally a weedy species because of its previous cultivation [“Now here and there as a result of the earlier cultivation an annoying weed”]. The number of localities increased from seven before 1950 to 62 in 2000 and up to 163 (in 105 10 × 10 km² grid cells) in 2019 (Tokarska-Guzik 2005; Zajac and Zajac 2019).

In Austria, the first records date back to the mid-19th century (e.g. Beck von Mannagetta 1893), followed by a very limited number of records during 20th century (Janzen 1977). *Asclepias syriaca* has locally spread after 1980 and in particular after the year 2000 as indicated by the increasing number of occupied grid cells (Figure 4). It is currently most abundant in a small part in the eastern lowlands (Follak et al. 2018). In the Czech Republic, *A. syriaca* was first recorded in the wild in the broad vicinity of the town of Krnov (Upper Silesia) at the beginning of the 19th century and then later in 1915 (Kaplan et al. 2017). Figure 4 shows the spread over time in the Czech Republic >1950. The data reveals a continuous, almost linear and significant increase in the area occupied by *A. syriaca*. In Hungary, *A. syriaca* has been known since the end of the 18th century and later, it was also cultivated for the production of fiber/silk or honey (beekeeping). In this country, the spread of *A. syriaca* owes to land use changes e.g. due to arable land abandonment and increased areas with transitional woodland/shrub (Csontos et al. 2009; Szilassi et al. 2019). Medvecká et al. (2012) stated that the first occurrence of *A. syriaca* in Slovakia was much later, namely in 1917. The species was then found in isolated occurrences in warmer regions of southwestern Slovakia in the end of the 1980s along roadsides, railways and on waste places. Populations were considered remainders of abandoned plantations for fibre and beekeeping (Valachovič 1989). In Bulgaria, early records were from 1948 (railway station in Plovdiv) and 1957 (Momin Prohod town) (Vladimirov and Georgiev 2019). *Asclepias syriaca* was then found locally in different regions of Bulgaria including few large and established populations. In Ukraine, the cultivation of *A. syriaca* has already been mentioned in the mid-19th century, but first escaped plants were recorded for the first time much later, namely near Kiev in 1914 (“in a ravine near the village of Novoselki”; Dvirna 2018).

Similarly, in southeastern European countries, early records from *A. syriaca* were made in the 19th century. For example, in Croatia, Schlosser and Vukotinovic (1869) noted its occurrence at a few locations along

the Sava River in Zagreb, most likely due to an escape from nearby garden. In Serbia, its distribution is currently mainly confined to Vojvodina, while early escaped populations have been described from the town of Bečej (center of Vojvodina) by Kovács (1929).

4. Ecology

4.1. Response to abiotic factors

4.1.1. Climate

Asclepias syriaca is adapted to a wide range of climatic conditions. In its native range, *A. syriaca* occurs between northern latitudes of 35 to 50° and western longitudes of 60 to 103° (Woodson 1954; Bhowmik 1994; see section *Native range*). According to the World Map of Köppen-Geiger Climate Classification, *A. syriaca* occurs mainly in the following climatic regions: warm temperate climate, fully humid with hot summers (Cfa) and continental climate, fully humid with hot and warm summers (Dfa, Dfb), respectively (Kottek et al. 2006). Bhowmik (1994) noted that the distribution of *A. syriaca* is limited by 18°C and 32°C mean July temperatures in the north and south, respectively. Doyon (1958) noted that *A. syriaca* is nearly absent from the western part of North America most likely due to low precipitation during the summer.

In Europe, *A. syriaca* occurs in regions with a warm temperate climate, fully humid with warm summers (Cfb), and with a continental climate (Dfb) (Kottek et al. 2006). Large populations can be found in particular in the continental Carpathian Basin (Hungary, Serbia, see section *Invaded range*). Using this broad climatic classification, large areas of Europe are potentially climatically suitable for *A. syriaca*. Suboptimal climatic conditions (e.g. low temperatures) are supposed to limit the altitudinal and northward distribution in Europe (e.g. in Scandinavia). In northern countries, *A. syriaca* escaped from cultivation in gardens and wild populations preferentially occur in urban centres (e.g. Năburga and Evarts-Bunders 2019), which constitute “thermal islands”. However, in Central Europe, for example in Poland, favourable climatic conditions for this species include regions with harsher climates like the Suwałki region (north-eastern Poland; Tokarska-Guzik et al. 2015, 2018).

4.1.2. Temperature

The optimal temperature for growth is 27°C, while limited growth of young plants was observed at 15°C (Bhowmik 1994). Mild late frosts with temperatures from – 1°C to – 2°C kill young shoots whereas they may be harmless to mature ones (Varga 2003 as quoted in Sárkány et al. 2008). Seeds and rhizomes of *A. syriaca* also are able to tolerate temperatures below 0°C. Low winter temperatures are necessary to break

seed dormancy. Suboptimal thermal conditions can limit the effectiveness of sexual reproduction, germination, and vegetative growth (Evetts and Burnside 1972).

High temperatures (35°C in comparison to 25°C) stimulate the growth of shoots under short-day (8 h), but inhibited it under long-day conditions (16 h). These differences do not apply to root growth, which intensified at higher temperatures regardless of the photoperiod (Campbell 1985).

Available data on the influence of temperature and photoperiod on seed germination is ambiguous. The minimum germination air temperature is from 15 to 20 °C and the maximum one from 35 to 40°C according to Evetts and Burnside (1972). Radivojevic et al. (2016) tested the germination of seeds at 20°C, 25°C, 30°C and 35°C. They found the highest share of germinated seeds at a temperature of 30°C (64.4% in sandy soil, and 51.9% in loamy soil); however, optimum conditions for germination were day/night temperatures altering from 26°C to 21°C. Likewise, according to other authors, the highest germination rate occurred under alternating temperatures. Farmer et al. (1986) observed a germination rate of 56% with 30/20°C (16 h/8 h), while Baskin and Baskin (1977) observed 94% germination rate in conditions of 35/20°C or 30/15°C and its decrease to 70% at 20/10°C (see section *Seed production and germination*).

The germination is also positively affected by seed stratification in low-temperature water. Optimal effects were observed at stratification from 7 to 28 days at 5°C (Evetts and Burnside 1972). Seeds have the ability of after-ripening in winter and show a higher germination capacity at temperatures corresponding to the period of the turn of May and June in its native range. Seeds stratified in the presence of light or in the dark, and then incubated at variable temperatures of 30–35/15–20°C for 2 to 3 weeks germinated in 68 to 75%. Germination efficiency decreases below 20% at stratification at 20/10°C. Extending stratification to 9 weeks increases germination to >70% (Bhowmik 1994).

Temperature significantly affects the emergence of seedlings of *A. syriaca*. Maximum seedling emergence is observed at an air temperature of 27°C. The increase in temperature results in shortening the time necessary for emergence of young plants (Bhowmik 1994).

4.1.3. Light

Although *A. syriaca* is considered to be a generalist for most habitat factors (Bhowmik 1994), this does not apply to its requirements for light. Optimal conditions for *A. syriaca* development are provided by full insolation or slight shade (Berkman 1949 as quoted in Bhowmik 1994). It usually grows in fully open areas, frequently on the edges of forests and thickets (see *Habitats and syntaxonomy*). *Asclepias syriaca* has

a C₃ photosynthetic pathway (McWhorter and Patterson 1980). Delaney and Higley (2006) reported photosynthetic and transpiration rates for *A. syriaca* at a level of $17.7 \pm 1.22 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and $5.56 \pm 0.30 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$, respectively, which are characteristic for heliophytes (sunlight loving species). It should be noted, that there is also data available indicating alternative preferences of the species for light. For example, Alvarado-Miller (2018) described *A. syriaca* as a sciophyte (shade loving species). This conclusion was supported by a complex set of parameters assumed to be typical for sciophytes: lower photosynthetic rate ($5.28 \pm 1.28 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), light compensation point ($33.3 \pm 6.3 \mu\text{mol m}^{-2} \text{ s}^{-1}$), stomatal conductance ($0.038 \pm 0.000 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ at $2000 \mu\text{mol m}^{-2} \text{ s}^{-1}$), respiration rate ($1.11 \pm 0.52 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and transpiration rate ($1.29 \pm 0.302 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$). These results, so divergent from others, were obtained under laboratory conditions (in the greenhouse), while the majority of other authors (e.g. Delaney and Higley 2006; in Nebraska/United States) based their conclusions on data from field conditions in which various environmental factors (temperature, relative humidity, water stress, time of day, etc.) interact with each other.

In the initial period of growth, higher photosynthetic photon flux density (PPFD, $310 \mu\text{mol s}^{-1} \text{ m}^{-2}$) contributes to an increase in height of shoots, leaf surface and the production of large amounts of dry matter (Campbell 1985). Insolation significantly affects not only the growth and physiological processes of *A. syriaca*, but also its response to herbivorous insects. Changes in the ratio of the amount of red (R) to far-red (FR) light (R: FR) can strongly influence the secondary chemistry of *A. syriaca* (Agrawal et al. 2012). Plants growing in partial shade produce fewer stems and they develop longer internodes, with larger, softer and less hairy leaves. Moreover, herbivores damage their leaves about half as much compared to plants growing in full sun. Changes in insolation during plant life affect the induction of hormones and resistance traits of *A. syriaca* (see section *Herbivory*). Individuals growing in shade were characterized by a 50% weakened impulse of jasmonate hormone in response to herbivory of *Danaus plexippus* Linnaeus (Lepidoptera: Nymphalidae). Conversely, latex induction was 17% higher in plants growing in the sun as well as the concentration of cardenolides (+27%) and secretion of other hormones (Agrawal et al. 2012).

4.1.4. Water

Asclepias syriaca is tolerant to a wide range of soil moisture conditions. Growth of *A. syriaca* is limited by rainfall at the level of 50 mm in minimum combined during three summer months (Evetts 1977 quoted in Bhowmik 1994). The species even

tolerates prolonged drought periods. In an experiment, over half (up to 60%) of plants survived below the permanent wilting point in soils with 9% moisture. However, the water deficiency resulted in a decrease of shoot and seedling growth as well as it impedes the development of young plants (Minshall 1977 quoted in Bhowmik 1994). According to Couture et al. (2015) simulated water stress decreased total plant growth by 76% under-controlled conditions (25/18°C, day/night) in an environmental chamber experiment. A recent study under-controlled conditions in the greenhouse showed that soil moisture significantly affects the relationship of *A. syriaca* with conspecific soil fauna and flora (Snyder and Harmon-Threatt 2019). Seedlings of *A. syriaca* showed reduced growth in well-watered soils, which promoted the development of microbial communities of pathogens (especially fungal ones). However, such negative impacts weakened and disappeared under drought conditions.

4.1.5. Substratum and nutrient availability

Asclepias syriaca tolerates a wide range of soil types and pH values. It can grow well in light, dry, sandy soils as well as in loamy, fertile and even moist soils (Bhowmik 1994; Bennett et al. 2006; Kelemen et al. 2016). For example, in many locations in its native range, *A. syriaca* is observed on deep and loamy soils (Bennett et al. 2006). In its introduced range, in central Hungary, it occurs on dry sandy old-fields (Kelemen et al. 2016) and in north-central Poland, populations of the species were found on dry, poor to moderately fertile soils or moderately moist and rich in nutrients ones (Puchalka et al. 2013).

The species is able to occur on soils with low nitrogen and phosphorus content, with varying degrees of mineralization of organic carbon and nitrogen compounds. The average content of total nitrogen in the upper levels of the soil profile ranged from 0.107 to 0.123% at the localities of *A. syriaca* in its native range (Bennett et al. 2006). Total nitrogen content ranged from 0.07 to 0.15% at the sampling sites in north-western Poland. The content of soil organic matter, humus, organic carbon and the C:N ratio varied in the range of 1.79 to 3.61%, 1.04 to 2.5%, 0.61 to 1.45%, 7.6 to 11.4%, respectively (Baciczko and Borcz 2015).

Average content of exchangeable elements observed in sampled soils in its native range (southern end of Lake Michigan) was as follows (in kg/ha): 23.9–26.1 phosphorous, 66–112 potassium, 1172–1189 calcium, 144–289 magnesium, 4.34–7.95 exchangeable Ca/Mg ratio. The average total content of other macro- and microelements were as follows (in ppm): 151–161 sulfur, 6.63–16.3 copper and 271–401 manganese (Bennett et al. 2006). In north-western Poland, a high content of digestible

potassium (K_2O) as well as magnesium was found at habitat of the species, namely 16.1 to 21.4 and 5.2 to 8.9 mg/100 g soil, respectively, but a low content of digestible phosphorus (P_2O_5). It ranged from 4.7 to 18.2 mg/100 g. The content of $CaCO_3$ varied in a wide range between 0.2 to 6.9% in sampled soils (Baciczko and Borcz 2015). In Hungary, higher humus content as well as available phosphorus and nitrate-nitrogen in the soil was observed in areas invaded by *A. syriaca*, while the content of $CaCO_3$ was reduced (Bagi 2008).

Deficiencies of nutrients negatively affect plant biomass, both underground parts and aboveground shoots. Plants growing in nutrient-rich soils have a larger shoot (809%) and root (435%) biomass compared to plants growing under low-nutrient conditions. Limited access to nutrients reduces the ratio of shoots to roots by 85%. It affects also the allocation of cardenolides and latex, which in turn influences the effectiveness of plant defense traits on herbivory (Züst et al. 2015).

Asclepias syriaca grows on both alkaline and acidic soils. In the native range, it is reported from localities with pH 4 to 5 (Spurway 1941), pH 6.29 to 6.33 on average (Bennett et al. 2006) as well as pH over 7 (Groh 1943 quoted in Bhowmik 1994). The data from northwestern Poland showed that the species occurs mostly on slightly alkaline soils with a pH from 7.3 to 7.6 (Baciczko and Borcz 2015).

Optimal germination conditions are observed at a pH in the range of 4 to 8, while the germination rate decreases at a pH lower than 4 and above 8. Seedlings are able to tolerate pH in an extremely wide range from 2 to 12 (Evetts and Burnside 1972) although, according to other sources, seedling development was impaired on dry and acidic soils (Valachovič 1991 quoted in Sárkány et al. 2008). Plants tolerated salinity up to a level of 2,500 ppm NaCl (Cramer and Burnside 1982). A reduction of seed germination was observed at 85.4 mM NaCl, however, seedlings tolerated salinity up to 42.7 mM NaCl (Evetts and Burnside 1972). Seeds collected from roadsides (high salt exposure) and old-field populations (low salt exposure) in Ontario (Canada) were treated with 70 mM NaCl. The results showed that both populations had shorter roots when exposed to salt levels compared to the control and thus, that roadside populations were not better adapted to high salt levels than populations from old-fields (Beaton and Dudley 2004).

4.2. Response to biotic factors

Asclepias syriaca can either originate from seed or adventitious root buds. Seedling recruitment is susceptible to competition with other plant species. In experiments under greenhouse conditions, Evetts and

Burnside (1975) showed that the shoot weight of *A. syriaca* was significantly reduced by light, soil, and full competition (light + soil) with *Setaria viridis* (L.) Beauv., *Amaranthus retroflexus* L. and *Sorghum bicolor* (L.) Moench. Moreover, plant height was significantly decreased by soil and full competition with the three species.

Established populations that regenerate from adventitious buds can be highly competitive in particular in open grassland habitats or agricultural land suppressing native or crop species, respectively (see section *Negative impacts*). High growth rates and drought tolerance of *A. syriaca* are regarded as the key to its high competitiveness. Literature reports also indicate that the interference of *A. syriaca* with neighbouring plants includes biochemical interactions (allelopathy) (Nádasy et al. 2018). However, under conditions of competition for light, *A. syriaca* reacts with a strong elongation of shoots (Agrawal et al. 2012). It decreases or even disappears from habitats with high canopy coverage by shrubs and trees (due to low light conditions) and during the course of succession (Bagi 2008; Albert et al. 2014). These latter authors showed that the cover of *A. syriaca* decreased significantly with increasing age (>20 years) of abandoned agricultural land in Hungary, most likely due to increasing competition from native perennials and the decline in soil nitrogen content.

4.3. Habitats and syntaxonomy

Asclepias syriaca is adapted to a wide range of climatic and edaphic conditions (see sections *Climate* and *Response to abiotic factors*) and thus it can persist in many habitats (Bhowmik 1994). In North America, *A. syriaca* colonizes “prairies and alluvial bottoms, spreading to meadows, fields, roadsides, and railways” (Woodson 1954; Cramer and Burnside 1982). Likewise, in its invaded range in Europe, *A. syriaca* can be found in a broad range of open anthropogenic to (semi-)natural habitats that are subjected to a high level of natural or human disturbance (Pyšek et al. 2012a; Figure 5). The species colonizes abandoned agricultural land and vineyards (Pál 2007; Csontos et al. 2009; Csiszár and Korda 2017), dry and mesic grasslands (Gudžinskas et al. 2018), raised flood defense levees and meadows (Jarić et al. 2011), late successional old-fields (Kelemen et al. 2016), shrublands and open dry forests (Follak et al. 2018), pine and poplar plantations (Sztár et al. 2014; Gallé et al. 2015; Csiszár and Korda 2017) as well as fire-damaged areas (Sztármári et al. 2016). *Asclepias syriaca* has become an abundant species in open sand grasslands in the Great Hungarian Plain (Bagi 2008; Bakacsy 2019). Occasionally, it occurs in habitats with tall herb fringe communities (Gudžinskas et al. 2018). The species also invades habitats of high conservation

value (i.e. Natura 2000 sites), such as dunes and open sand steppes (Šefferova Stanová et al. 2008; Matthews et al. 2015; Bakacsy 2019; see section *Colonization of high conservation value habitats*). Moreover, ruderal habitats (waste places), roadsides and railway embankments are regularly colonized (Dvirna 2015; Rutkowski et al. 2015; Follak et al. 2018). *Asclepias syriaca* also occurs in crops, such as maize, soybean, legumes and cereals (Bagi 2008; Vrbničanin et al. 2008; Pauková et al. 2014; Dvirna 2015; Follak 2018a). Moreover, it can be found in small-scale ornamental and allotment gardens (Follak 2018b). Szilassi et al. (2019) investigated factors (climatic factors, soil characteristics, land use) shaping the occurrence of *A. syriaca* in the southern Great Plain area in Hungary. They concluded that current land cover (complex cultivation patterns and natural grassland areas) as well as physical properties of soils (soil texture, such as sandy loam, and loamy sand) are factors that significantly influence the presence of *A. syriaca* in a given area. These factors provide a suitable habitat for *A. syriaca* (i.e. optimal light conditions and soils in which the rhizomes can easily reach to the groundwater).

Asclepias syriaca occurs in plant communities from the classes *Artemisietea vulgaris* (xerophilous ruderal vegetation), *Stellarietea mediae* (annual vegetation of arable land and ruderal habitats), *Festuco-Brometea* (sandy steppes), *Bidentetea tripartitae* (vegetation of annual nitrophilous wetland herbs) and *Molinio-Arrhenatheretea* (meadows and mesic pastures) (e.g. Valachovič 1987, 1989; Pál 2007; Stanković-Kalezić et al. 2008; Jarić et al. 2011; Panasenکو et al. 2012; Bacieczko and Borcz 2015; Dvirna 2015; Rutkowski et al. 2015; Bakacsy 2019). In southeastern Europe, for example in Serbia, *A. syriaca* was recorded in the associations *Arctietum lappae* Felföldy 1942, *Sambucetum ebuli* Felföldy 1942 and *Convolvulo arvensis-Elytrigietum repentis* Felföldy 1943 (class: *Artemisietea vulgaris*) (Stanković-Kalezić et al. 2008). Dvirna (2018) noted that *A. syriaca* grew along a forest belt within the association *Rudbeckio laciniatae-Solidaginetum canadensis* Tüxen et Raabe ex Anioł-Kwiatkowska 1974 (class: *Artemisietea vulgaris*). Rutkowski et al. (2015) stated that the floristic composition of the invaded plant communities varied significantly in central Poland (Toruń). *Calamagrostis epigejos* (L.) Roth, *Elymus repens* (L.) Gould and *Poa angustifolia* L. co-occurred with a high frequency in the studied plots. Panasenکو et al. (2012) detailed the phytosociological affiliation of *A. syriaca* in the Bryansk Oblast (western Russia) within the class *Artemisietea vulgaris*. *Asclepias syriaca* can reach very high cover values in plant communities. In the Czech Republic, such communities have been assigned to the *Asclepiadetum syriacae* Lániková in



Figure 5. Habitats invaded by *Asclepias syriaca* in Europe: (a) crop fields (cereals), (b) and (c) roadsides, (d) railway embankments, (e) shrubland and open dry forests and (6) abandoned sites (Photos: Swen Follak).

Chytrý 2009 association (class *Artemisietea vulgaris*) (Láníková 2009). Popov et al. (2016) and Dvirna (2015) confirmed the presence of this association in Serbia (Bačka region) and central Ukraine, respectively.

The cover and densities of *A. syriaca* are variable and depend largely on the invaded habitat and local factors (e.g. disturbance, soil and nutrient conditions, accompanying plant species; see section *Vegetative growth*). For example, the average cover of *A. syriaca* was approximately 16% in a sand dune grassland (following the removal of a pine plantation), while its average maximum cover was around 40% in abandoned agricultural land in Hungary (Szitár et al. 2014; Kelemen et al. 2016). Bacieczko and Borcz

(2015) reported cover values >25% in semi-natural turf meadows of the *Molinio-Arrhenatheretea* class in northern Poland (West Pomerania). It occupied an area of about 0.165 ha. Likewise, in central Slovakia, *A. syriaca* densities of max. 33 shoots/m² and 18 shoots/m² were found in an abandoned vineyard and along a roadside, respectively (Pauková et al. 2013). Valachovič (1987) observed a density of 45 shoots/m² on a ruderal site in western Slovakia. Csontos et al. (2009) described a density that varied between 7.4 (abandoned vineyard) and 18.1 (abandoned agricultural land) shoots/m² (stand height 70 to 110 cm) in Hungary near Budapest. Here, *A. syriaca* has infested an area of 0.2 ha (vineyard) to 20 to 30 ha (agricultural land), respectively.

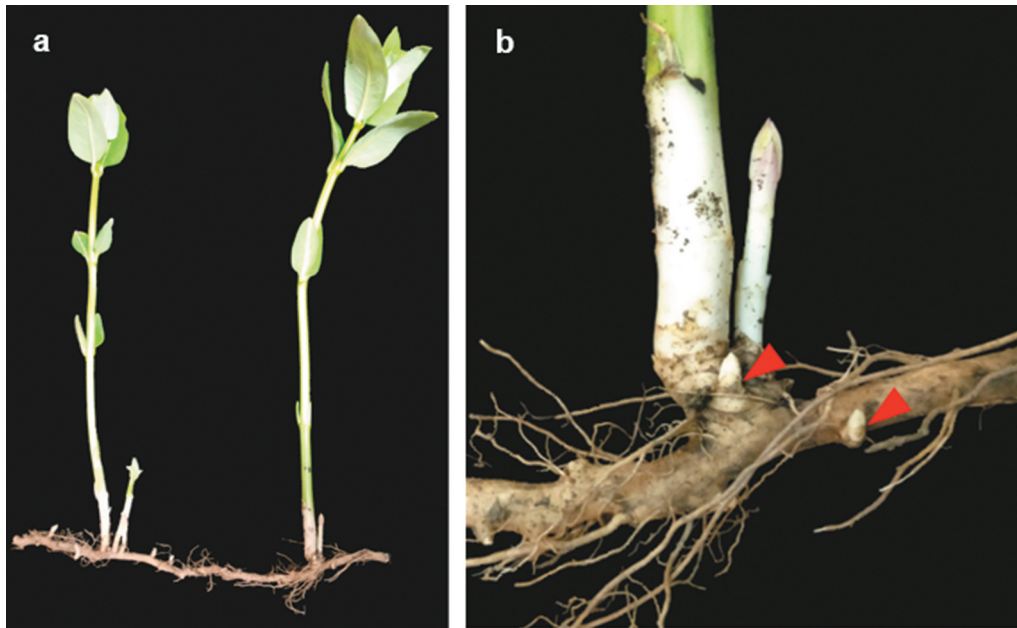


Figure 6. Clonal structure of *Asclepias syriaca*: (a) shoots (ramets) remain interconnected by rhizomes (spacers) and (b) the red arrows show the dormant adventitious buds (Photos: László Bakacsy).

4.4. Ecological interactions

4.4.1. Herbivory

Asclepias syriaca has developed defence traits, such as the production of cardenolides and latex, limiting the herbivore community to mostly host-specific chewing, leaf mining and phloem sucking insects. Cardenolides make *A. syriaca* toxic and bitter-tasting, while latex engulfs small herbivores and inhibits the feeding of larger ones (Agrawal 2005). Although these specialist herbivores on *A. syriaca* have evolved resistance to cardenolides and latex, both traits can still impose negative effects on them (Tao et al. 2016).

Studies of *A. syriaca* herbivore fauna in the United States (central Illinois and the greater Chicago region) were made by Price and Willson (1979) and Betz et al. (2000) (Table 2). Most important in terms of abundance and damage are *Oncopeltus fasciatus* Dallas (large milkweed bug; Hemiptera: Lygaeidae), *Labidomera clivicollis* Kirby (milkweed leaf beetle; Coleoptera: Chrysomelidae), *Tetraopes tetraophthalmus* Forster (red milkweed beetle; Coleoptera: Cerambycidae), *Rhyssomatus lineaticollis* Say (milkweed stem weevil; Coleoptera: Curculionidae) and *Liriomyza asclepiadis* Spencer (milkweed leaf-miner fly; Diptera: Agromyzidae). *Tetraopes tetraophthalmus* is an univoltine and monophagous herbivore of *A. syriaca*. Adult beetles feed on flowers and foliage while larval beetles feed on the rhizomes (Matter 2001). In contrast, *R. lineaticollis* larvae feed upon pith parenchyma in shoots of *A. syriaca* (Fordyce and Malcolm 2000). Recently, harsh damage has been found on *A. syriaca* by the polyphagous, non-native scarab *Popillia japonica* Newman (Japanese

beetle, Coleoptera: Scarabaeidae) in central Kentucky (United States). It feeds on the flowers reducing fruiting and seed set by >90% (Baker and Potter 2018b). In Europe, *P. japonica* (A2 quarantine pest in the EU member countries) already occurs locally in Portugal (Azores) and in Switzerland and Italy (EFSA Plant Health Panel 2018).

In Europe, *A. syriaca* has escaped most of its specialist herbivores attacking it in its native range (Table 2). However, *A. syriaca* is attacked by aphid species, some of them, such as the cosmopolitan *Aphis nerii* Boyer de Fonscolombe (oleander aphid; Hemiptera: Aphididae) heavily sucks on the plant leading to die-back of shoots as observed in Hungary (Bagi 2008). This phloem-feeding specialist was reported in some other countries in Central Europe (Austria, Serbia, Ukraine), recently also in Slovakia (Purkart et al. 2020). A few insects native to Europe attack the plant, such as the bug *Lygaeus equestris* Linnaeus (black-and-red-bug; Hemiptera: Lygaeidae) that is found on *A. syriaca* in some European countries (Table 2). Its main damage is caused by sucking on the flower buds (Bagi 2008). Moreover, Bagi (2008) observed feeding of the polyphagous weevils *Peritelus familiaris* Boheman (Coleoptera: Curculionidae) and *Omophlus proteus* Kirsch (Coleoptera: Tenebrionidae) on young shoots and foliage in Hungary.

4.4.2. Plant parasites and diseases

Bhowmik and Bandeen (1976) and Bhowmik (1994) noted several parasitic fungi associated with *A. syriaca* in North America, such as *Uromyces asclepiadis* Cooke, *Cercospora clavata* (Gerard) Cooke, *Puccinia bartholomaei* Dietel, *Golovinomyces cichoracearum*

Table 2. Herbivores (selection) attacking *Asclepias syriaca* in North America and Europe.

Taxon	Country	Source ^a
Insecta		
Hemiptera		
<i>Aphis nerii</i> (Boyer de Fonscolombe, 1841)	Austria, Hungary, Serbia, Slovakia	1, 2, 5, 8
<i>Aphis fabae</i> (Scopoli, 1763)	Austria, Serbia	5, 15
<i>Aphis asclepiadis</i> (Fitch, 1851)	United States	13
<i>Aphis gossypii</i> (Glover, 1877)	Hungary, United States	2, 9
<i>Myzocallis asclepiadis</i> (Monell, 1879)	Canada, United States	13, 14
<i>Lygaeus equestris</i> (Linnaeus, 1758)	Austria, Hungary	5, 10
<i>Lygaeus kalmii</i> (Stål, 1874)	Canada, United States	1, 2, 4, 14
<i>Myzus persicae</i> (Sulzer, 1776)	United States	2
<i>Oncopeltus fasciatus</i> (Dallas, 1852)	United States	1, 2, 3
<i>Tropidothorax leucopterus</i> (Goeze, 1778)	Czech Republic, Germany, Slovakia	12
-		
Coleoptera		
<i>Labidomera clivicollis</i> (Kirby, 1837)	Canada, United States	1, 2, 14
<i>Omophlus proteus</i> (Kirsch, 1869)	Hungary	10
<i>Peritelus familiaris</i> (Boheman, 1834)	Hungary	10
<i>Popillia japonica</i> (Newman, 1838)	United States	6
<i>Rhyssomatus lineaticollis</i> (Say, 1824)	United States	1, 2, 11
<i>Tetraopes tetraophthalmus</i> (Forster, 1771)	Canada, United States	1, 2, 14
<i>Tetraopes femoratus</i> (LeConte, 1847)	United States	1, 2
-		
Diptera		
<i>Liriomyza asclepiadis</i> (Spencer, 1969)	United States	2
-		
Lepidoptera		
<i>Cynia tenera</i> (Hübner, 1818)	United States	2
<i>Danaus plexippus</i> (Linnaeus, 1758)	Canada, United States	1, 2, 14
<i>Euchaetias egle</i> (Drury, 1773)	United States	1, 2
-		
Thysanoptera		
<i>Frankliniella occidentalis</i> (Pergande, 1895)	United States	2

^a(1) Price and Willson (1979), (2) Betz et al. (2000), (3) Dingle et al. (1980), (4) Wheeler (1983), (5) S. Follak & A. Moyses (personal observations 2018, 2020), (6) Baker and Potter (2018b), (7) Matter (2001), (8) Purkart et al. (2020), (9) Molnár et al. (2010), (10) Bagi (2008), (11) Fordyce and Malcolm (2000), (12) Kment et al. (2009), (13) Smith et al. (2008), (14) Bhowmik (1994), (15) Tomanović et al. (2003).

(DC.) Heluta and different *Fusarium* species (e.g. *Fusarium acuminatum* Ellis et Everh.). However, further information on these fungi, their epidemiology, impact and distribution is scarce. Likewise, in Europe, limited information has been reported on parasitic fungi attacking *A. syriaca*. For example, Tóth (2017) found severe leaf spot incidence on *A. syriaca* in eastern Hungary and identified two

fungi as causal agents, namely *Fusarium sporotrichioides* Sherb. and *Alternaria alternata* (Fr.) Keissl. The species is also colonized by cosmopolitan arbuscular mycorrhizal fungi (AMF), such as *Rhizophagus irregularis* (Błaszk., Wubet, Renker et Buscot) C. Walker et A. Schüßler and *Rhizophagus aggregatus* (N.C. Schenck et G.S. Sm.) C. Walker (Bagi 2008; Vannette et al. 2013; Tao et al. 2016).

The species is a host of different virus and bacterial diseases. For example, alfalfa mosaic virus (AMV), cucumber mosaic virus (CMV) and tobacco mosaic tobamovirus (TMV) have been isolated from naturally infected *A. syriaca* plants in Hungary and former Yugoslavia (Salamon et al. 1989; Kazinczi et al. 1999, 2002). Moreover, Flynn and Vidaver (1995) have described an infection by *Xanthomonas campestris* pv. *asclepiadis* (bacterial blight of milkweed) in Nebraska (United States). This bacterial disease reduced vitality of infected *A. syriaca* populations.

5. Biology

5.1. Phenology

Asclepias syriaca is a perennial, sexually-reproducing and polycarpic plant (i.e. flowering and fruiting occurs many times during its life) with a high capacity for vegetative growth. In phenological terms, the following phenophases can be distinguished in the development of *A. syriaca*: initial growth, vegetative stage, flowering, fruit ripening and leaf/shoot senescence.

Initial growth of *A. syriaca* is influenced by the length of the photoperiod in addition to temperature (Campbell 1985; Radivojevic et al. 2016). New shoots grow from the adventitious buds on the rhizomes in spring depending on local weather conditions (Bhowmik and Bandeen 1976; Tokarska-Guzik et al. 2018). Simultaneously, under suitable conditions, the buried seeds, which sustain their germination ability for at least five years, germinate (Bagi 2008). Individuals are able to produce shoots from their root system within a few weeks after germination. According to Jeffery and Robison (1971), seedling survival and regrowth increased as the seedlings developed additional leaf pairs. To sum up, plants do not produce flowers in the year of germination; only their rhizomes develop (Bagi 2008).

At the beginning of the next growing season, single buds develop on each lateral rhizome. Aboveground shoots sprout at the end of April to mid-June. In the case of plants that are several years old, new shoots also grow from places (referred to as crowns) where shoots developed in the previous year, usually in numbers of 1 to 3 (max. 6). The intensive development of the rhizomes starts again during July and August and lasts until mid-September (Bagi 2008). With each successive stage of growth, the buds, which were capable

of producing new shoots, were found in increasing soil depths (Jeffery and Robison 1971). The buds forming on them remain dormant throughout the winter. Shoots will stay in physiological contact for many years.

In the native range, shoots of *A. syriaca* start developing numerous flowers in June, ending in July or early August (Bhowmik and Bandeen 1976; Wilbur 1976). In the invaded range, *A. syriaca* has a prolonged flowering season ending in August (Bagi 2008; Pauková et al. 2013; Tokarska-Guzik et al. 2018). The flowers form on the shoots as a series of umbellate cymes (inflorescences) that bloom chronologically along the shoots in a basal to apical manner (Kephart 1987; Liede and Weberling 1995; Howard 2018; Figure 1(a)). The nectariferous flowers are pollinated by a large group of insect pollinators (see section *Floral biology*).

The fruiting period lasts from July to August/September (Bagi 2008; Tokarska-Guzik and Pisarczyk 2015). Fruits ripen by late August or early September. Seeds, which bear a cluster of long, white hairs, are released in September to October in the native range and in late September to November in the introduced range (Bhowmik and Bandeen 1976; Tokarska-Guzik et al. 2015, 2018) at which time the shoots become senescent. In autumn, the plant sheds leaves and its shoots die back. Fruits of *A. syriaca* can remain on the shoots throughout the winter. In some parts of Europe (mainly the northeastern regions, e.g. in Poland) the species probably reproduces mostly vegetatively (Puchałka et al. 2013), which does not preclude the development of numerous populations in the wild (Tokarska-Guzik and Pisarczyk 2015; Dvirna 2018).

Howard (2018) demonstrated the shift of the flowering date of *A. syriaca* in response to climate change. Rising temperatures may influence the period and the duration of flowering. Consequently, the author argues that changes in flowering time may negatively influence the reproduction of *A. syriaca* by disrupting the match between the timing of its flowering and the flight seasons of its pollinators.

5.2. Reproductive biology

Asclepias syriaca is a highly successful colonist compared to other species of the same genus, because of its vegetative habit and reproductive strategy. It reproduces both sexually and vegetatively. Self-sterile and entomophilous flowers are formed in groups of 10 to 130 in the form of umbellate inflorescences (Morse 1982; Anderson 1999; Zalai et al. 2017; Tokarska-Guzik et al. 2018; Figure 1(a)). The species produces large amounts of seeds, which are spread by wind (anemochorically) (Bhowmik and Bandeen 1976; Pleasants 1991; Moravcová et al. 2010), and under favorable conditions, due to corky

margins, the seed can also float for considerable time on water (Jeffery and Robison 1971). As a clonal plant, it presents a large capacity for vegetative reproduction through rhizome growth and fragmentation (Anderson 1999; Nowiński and Latowski 2003; Podbielkowski and Sudnik-Wójcikowska 2003; Borders and Lee-Mäder 2015), which is an important element to support its spread. Once established, plants develop into persistent clones (Wilbur 1976).

5.2.1. Floral biology

Morgan and Schoen (1997) and Bagi (2008) provided a detailed description of the flower structure of *A. syriaca* based on a broad literature review. Individual white through pinkish/purplish and rarely, also to red flowers are androgynous and pentamerous (Willson and Rathcke 1974; Bhowmik and Bandeen 1976; Tokarska-Guzik and Pisarczyk 2015, Figure 1(c)).

Asclepias syriaca pollen is produced in paired packages (pollinia) and pollination occurs when a pollinium is inserted by a pollinator into a stigmatic chamber (Pleasants 1991). Kephart and Theiss (2004) detected definitive evidence of mechanical barriers between *A. syriaca* and its congeners in common garden experiment. Pollinia attach differentially to the arolium on insect legs for *A. syriaca* but to the tarsal hairs in other asclepiads, which suggest morphological specialization.

Effective sexual reproduction is associated with flower biology and nectar production as described by Kevan et al. (1989). They showed that pollinators and environmental conditions have both positive and negative influences on its sexual reproduction. Pollinators alter the amount of nectar present in flowers and contaminate it with enzymes and microbes. Environmental conditions influence the sugar concentration of the nectar. Eisdowitch et al. (1990) concluded that nectar has two functions: (i) it is a carbohydrate reward for pollinating insects required by the plants for sexual reproduction and (ii) it is the germination medium for pollen at the onset of pollen tube growth. For example, they discovered that *Metschnikowia* spp. – i.e. yeasts that are widespread in nature, which are vectored from flower to flower by pollinators – produce a substance that inhibits pollen germination in *A. syriaca* (at least in vitro). This fact may be important in limiting fertilization and perhaps fruit set in *Asclepias* species. Further, the reproductive phase of individual flowers of *A. syriaca* – lasting more than 5 days (Kephart 1987) – is long, compared with most other flowering plants (Wyatt and Broyles 1990).

The fragrant, nectariferous flowers are arranged in umbellate, 5 to 10 cm long, cymes, situated terminally and/or under the leaves (Figure 1(a)). The inflorescence size is related to local abiotic conditions or, as suggested by Willson and

Rathcke (1974), numerous-flower inflorescences may develop where a larger target for pollinators is required. In the populations studied by the above-mentioned authors, the lower inflorescences had an average size of 98 flowers, the middle ones 74, and the upper ones 51. Inflorescences on a shoot usually bloom in sequence up the shoot. Observations carried out by Moore (1946) showed that all the flowers in one inflorescence open within 2 to 3 days, while about 7 days pass from the moment of full bloom of the lower inflorescence to the flowering of the highest on the shoot. A high percentage of flowers fell off 10 to 12 days after opening (Bhowmik and Bandeen 1976).

The flowers produce large amounts of nectar both during day and at night, so there are many pollinators, especially in the native range (Wyatt and Broyles 1994; Anderson 1999). They are pollinated by insects, mainly bees, bumblebees, wasps, beetles, butterflies, and ants, but the effectiveness of pollination is over very low distances and varies in different types of habitats (Morse 1982; Pleasants 1991; Theiss et al. 2007; Bagi 2008; Csontos et al. 2009). According to studies by Willson and Bertin (1979), the main pollinia vectors in the native range were noctuid moths at night and honeybees – including the non-native *Apis mellifera* Linnaeus (Howard 2018) – in the afternoon. Southwick (1983) reported that wasps (Vespidae and Sphecidae) and bumblebees (*Apidae* spp., *Bombus* spp.) were the most abundant visitors in northern Michigan, while in New York honeybees were the principal nectar feeders.

In the introduced range, *A. mellifera* was found to be the main pollinator. In addition, bumblebees (e.g. *Bombus vagans* Smith and *Bombus terricola* Kirby) are of importance in pollinating *A. syriaca* flowers besides other wasps, bees, butterflies and flies (Bagi 1999, 2008; Zalai et al. 2017). The “trap” structure of flowers (sticky gaps in the anthers) means that some small insects are unable to free themselves from the flowers and die in them (Tokarska-Guzik et al. 2018). According to Judd (1968), the ant *Formica fusca* Linnaeus and *A. mellifera* were the insects trapped in the largest numbers in Ontario (Canada). Moreover, as reported by McNeil (1977), *Thymelicus lineola* Ochsenheimer aggregates on *A. syriaca* and their legs and (or) proboscis often become entangled in the flowers (Quebec/Canada). Thanks to entomophily, genetic diversity is maintained within populations. Ovaries of *A. syriaca* are fertilized by the insertion of a single pollinium into a flower; hence, all seeds from a single fruit pod (follicle) typically represent a full-sibling genetic family (Gold and Shore 1995; Agrawal 2005; Bingham and Agrawal 2010). Short-distance pollen dispersal can have important implications for *A. syriaca* (Pleasants 1991). The biology of *A. syriaca* flowers, including the interaction with pollinators,

have been the subject of many studies (Macior 1965; McNeil 1977; Dailey et al. 1978a, 1978b; Bertin and Willson 1980; Morse 1982, 1986, 1994; Southwick and Southwick 1983; Eisikowitch et al. 1987; Eisdcowitch et al. 1990; Jennersten and Morse 1991; Kahn and Morse 1991; Theiss et al. 2007).

Experiments carried out by Willson and Rathcke (1974) have shown that the inflorescence size above a certain size is not correlated with seed set or pollination rates. The number of follicles matured by each inflorescence is limited, and a minimum number of flowers appear to be necessary to ensure that follicle production, within this limit, is maximized. Willson and Bertin (1979) reported that large inflorescences attracted more pollinators and more nectar thieves. A higher proportion of all visits was made by pollinators, but the species composition of visitors did not usually change with inflorescence size. Moore (1946) suggested that the inflorescence size of *A. syriaca* is a heritable trait, because the author found that inflorescence size was uniform within the same clones, but was significantly different between clones collected from different areas.

5.2.2. Hybrids

Hybridization among *Asclepias* species is quite uncommon as physiological barriers and pollinator fidelity are mechanisms that largely prevent hybridization (Klips and Culley 2004). In its native range, natural hybridization occurs throughout areas of sympatry for *A. syriaca* with other *Asclepias* species, even though the formation of F₁ hybrids is a rare event (Broyles 2002). *Asclepias syriaca* is known to hybridize with *A. exaltata* L. (poke milkweed), *A. purpurascens* L. (purple milkweed), *A. sullivantii* and *A. speciosa* (Broyles 2002; Klips and Culley 2004).

5.2.3. Seed production and germination

Asclepias syriaca produces large amounts of fluffy seeds. The brownish seeds are flat, measure 7 × 5 mm, with a tuft of white, flossy hairs, approximately 6 to 10 mm (Ujvárosi 1973; Bhowmik and Bandeen 1976; Moravcová et al. 2010; Figure 1(e)) and their thousand seed weight is 7 to 8 g (Bagi 2008) or 4 to 9 g according to Zalai et al. (2017). The seeds occur in large fruits, which are oblong-ovate shaped follicles with a white pericarp (Bagi 2008; Petrova et al. 2013; Tokarska-Guzik et al. 2015; Figure 1(b)). Morse and Schmitt (1985) have found variation in seed morphology both among clones and follicles within clones.

In the native range, a single shoot of *A. syriaca* may produce as many as 25 follicles (Jeffery and Robison 1971). However, the studies of Bhowmik and Bandeen (1976) revealed an average number of 4 to 6 follicles per shoot. In Europe, reproductive shoots produce about two to three (rarely four or five) follicles, and

each of them contains up to 200 seeds (B. Tokarska-Guzik personal observations 2018, 2019), 300 (Jeffery and Robison 1971), 385 (Moravcová et al. 2010) or 150 to 425 seeds (Bhowmik and Bandeen 1976).

Asclepias syriaca, in comparison with some other species of the genus, produces a low number of follicles per umbel and few umbels per shoot (Wilbur 1976). However, according to Wilbur (1976) it had a comparable high number of seeds per follicle. That author assumed that some *A. syriaca* clones with many shoots produce tens of thousands of seeds per year. Bhowmik and Bandeen (1976) and more recent studies report that with an average population density equal to 1 to 3 shoots/m² (i.e. up to 60,000 shoots/ha), each of which can produce 4 to 6 follicles with 150 to 425 seeds each (an average of 1450 seeds/shoot), local populations can produce approx. 87 million seeds/ha. Most of the seeds have been shed within about 10 days after the follicles had opened. The seeds form a persistent seed bank (Bagi 2008). However, a number of environmental and biocenotic factors limit seed survival and germination (Tokarska-Guzik et al. 2018). The main mode of spread in *A. syriaca* includes the numerous seeds, which possess a flight-supporting apparatus and can be dispersed over relatively large distances by wind (Sacchi 1987; White 1996; Csontos et al. 2009; Moravcová et al. 2010; see section *Dispersal*).

Moravcová et al. (2010) and Dvirna (2018) demonstrated that the viability of the seeds was high (99% and 100%, respectively); however, the germination ability of the seeds under laboratory conditions was low (25 to 50%). Morse and Schmitt (1985) have found that heavy seeds had superior germination, survivorship, and seedling mass. Under favourable conditions, seeds are characterized by high (90%) germination ability and they remain viable for up to 5 years. Germination of *A. syriaca* seeds takes place at temperatures above 15°C, i.e. in spring, which usually covers April to mid-May depending on the geographical location. Under optimal circumstances – at 27°C, after cold treatment lasting at least 15 days at 5°C – the success rate of germination can be as high as 99% (Bagi 2008). The results of Radivojevic et al. (2016) indicated that *A. syriaca* has the ability to germinate under a broad range of temperatures, with optimal temperatures of 26/21°C.

As reported by Oegama and Fleitcher (1972), seeds of *A. syriaca* have an inherent dormancy and germination can be induced by various treatments including stratification, cutting or removal of the seed coat, alternating temperature, and a number of chemicals. Jeffery and Robison (1971) have shown that seed dormancy of *A. syriaca* is broken by a few days of moist low-temperature after-ripening and that the duration of low-temperature after-ripening of the seeds is temperature-dependent. In turn, Baskin and Baskin

(1977) confirmed that stratification is effective in overcoming dormancy, and non-dormant seeds germinated in both light and darkness.

In summary, germination is strongly correlated with seed source (population), temperature, and substrate type, and was poorly correlated with seed size. No association was found between geographical origin and germination response (Farmer et al. 1986). Another condition is that seeds are situated at shallow soil depths of about 0.5 to 1 (5) cm, because if they lie on the surface, they will not germinate (Bagi 2008). According to Yenish et al. (1996), seedling emergence of *A. syriaca* averaged 80% for seeds buried 0.5 to 4 cm deep and emergence was negligible for seed on the surface or buried deeper in soil. Mojzes and Kalapos (2015) demonstrated a smoke-enhanced germination of *A. syriaca* (laboratory experiment). This mechanism may support this species to colonize new habitats after fire. The effectiveness of proliferation via seeds (including the germination of seeds in the wild and ability of seedlings survival) have not yet been the subject of the research in northeastern Europe (i.e. Poland). Moravcová et al. (2010) determined seedling establishment at the level of 46.2% (36–68% mean-range).

5.2.4. Vegetative growth

The clonal structure of *A. syriaca* is organized as follows: shoots (ramets) originate from subterranean buds, which develop on rhizomes (spacers) (Polowick and Raju 1982; Stamm-Katovich et al. 1988; Klimešová and Klimeš 2006; Bagi 2008; Figures 1(d) and Figure 6). Although numerous adventitious buds develop on rhizomes, the majority remains dormant due to unfavourable conditions and the apical dominance of the shoots (Bhowmik and Bandeen 1976; Polowick and Raju 1982; Hsiao and McIntyre 1984; Figure 6). Its shoots can grow solitary or in small groups (2 to 5 shoots). The shoots live only for one year, but the plant keeps sprouting every year in the same place (Bagi 2008). The whole clone (genet) of *A. syriaca* remains physiologically connected through the rhizomes for years (Klimešová and Klimeš 2006; Bagi 2008). It is a so-called integrator strategy (Oborny and Kun 2002). Moreover, *A. syriaca* is able to change its clonal structure in a very flexible way, thus adapting to different environmental conditions: under favourable conditions, it develops shorter rhizomes and therefore, the location of the shoots is denser (*phalanx-type*). On the contrary, longer rhizomes and thus sparser shoots can be found under less favourable conditions (*guerrilla-type*) (Bagi 2008; Bakacsy and Bagi 2020). The average growth rate of the rhizomes is 0.01 to 0.25 m/year, but it can reach up to 3 m/year

depending on the climatic conditions (Klimešová and Klimeš 2006; Bagi 2008; Bagi and Bakacsy 2012).

Due to this vigorous vegetative growth, *A. syriaca* often develops extensive and dense stands. The rhizomes usually grow horizontally 10 to 40 cm below the soil surface, but they can penetrate up to 1 to 1.5 m deep as well (Bagi 2008; Bagi and Bakacsy 2012). These long rhizomes can reach the groundwater and they transport water to shoots (Hsiao and McIntyre 1984; de Kroon et al. 1998; Bakacsy 2019; Bakacsy and Bagi 2020). Several studies pointed out, that the death of a complete clone is a rather rare event and clones can become very large and old (Oborny and Bartha 1995; Klimešová and Herben 2015; Scherrer et al. 2017; Klimešová et al. 2018; Bakacsy and Bagi 2020). The potential lifetime of *A. syriaca* clones may exceed one hundred years (Bagi and Bakacsy 2012).

5.3. Dispersal

5.3.1. Natural spread

Natural long-distance spread of *A. syriaca* is contingent on sexual reproduction, while short-distance spread is further assisted by vegetative spread. The seeds are light (8.82 mg per seed; Platt and Weis 1977; see section *Seed production and germination*), have plumes and thus are easily dispersed by wind, often over substantial distances (Csontos et al. 2009). Platt and Weis (1977) reported rather low terminal velocity of diaspores (24.9 cm/s) and mean seed dispersal distances of 13.8 m at wind speeds of 10 to 15 km/h. Likewise, Moravcová et al. (2010) reported a terminal velocity of 35.3 cm/s underlining the high capability of the diaspores for anemochory. Morse and Schmitt (1985) found that seed morphology varies substantially among different clones of *A. syriaca*, and thus also propagule falling times and dispersal velocity shows substantial variation among clones. Similarly, there is also variation in seed traits within single follicles, and this variability of morphological attributes of seeds increases the likelihood to colonize sites at different dispersal distances (Sacchi 1987). This author showed that seeds are variable in hair length (plume length) and seed mass. Hair length is related to the location of the seed within a follicle, while seed mass is not. In strong winds, seeds with relatively long hairs dispersed considerably farther than those with short hairs when paired and released simultaneously.

Moreover, *A. syriaca* also spreads vegetatively via rhizomes. Clonal growth allows the species to build up dense clonal aggregations and it is most important for local expansion of already established populations (see section *Vegetative growth*). It has been shown that the rhizomes of *A. syriaca* have allelopathic effects on co-occurring plant species, which may facilitate spread by vegetative means (Nádasy et al. 2018).

5.3.2. Human-assisted spread

The spread of *A. syriaca* is assisted by a variety of intentional and unintentional human activities. *Asclepias syriaca* occurs often along roads and railways (Dvirna 2015; Rutkowski et al. 2015; Follak et al. 2018). In a case study from eastern Austria, Follak et al. (2018) showed that roadsides were important habitats for *A. syriaca*. The authors argue that suitable site conditions (i.e. rarely mown ruderal grasslands on road embankments) and the high connectedness of roads jointly contribute to the high prevalence of *A. syriaca* along roads.

In Europe, *A. syriaca* is a popular ornamental plant, and is still cultivated in gardens today (Tokarska-Guzik and Pisarczyk 2015). In addition, it has been cultivated on moderate scales as fibre plant and by beekeepers because it is a good source of nectar (Bagi 2008). Cultivation for economic purposes started in the 1870s, but has ceased in the mid-20th century. Recently, new efforts to exploit the potential of *A. syriaca* for bio-economic uses have been made (see section *Uses and positive impacts*). The listing of *A. syriaca* as an invasive alien plant in the EU legally restricts its trade and cultivation within its borders. However, invasive alien plants can be purchased easily via the internet (Lenda et al. 2014) and this applies to *A. syriaca*. When plants of *A. syriaca* are mechanically fragmented (e.g. due to tillage or soil removal), the individuals are often able to regenerate shoots from rhizome fragments (Bagi 2008). This high regenerative capacity facilitates spread when fragments are transported to new sites (e.g. via contaminated soil) (S. Follak personal observation 2019). Similarly, seeds can be transported to new sites with agricultural machinery, the more so, as many infested habitats are located adjacent to (e.g. roadsides) or even in crop fields (Yenish et al. 1996; Novák et al. 2009). Moreover, land use changes, such as the abandonment of agricultural land, create new opportunities for the spread of *A. syriaca*, as the species thrives well in degraded grasslands and old fields (Szilassi et al. 2019; see section *Habitats and syntaxonomy*).

6. Economic importance and impacts

6.1. Uses and positive impacts

Gaertner (1979) and Small (2015) provided detailed information on medicinal, technical and various other uses of *A. syriaca*. In the past, however, work on the utilization of *A. syriaca* for natural rubber and fibre production was the most important one (Gaertner 1979). Numerous studies on potential uses had already been conducted in the 18th and 19th century e.g. in Germany and Russia and are summarized by Whitening (1943). Although it exudes copious

amounts of white milky latex, it has low natural rubber content and thus, there was no economic success for this purpose. *Asclepias syriaca* yields two kinds of fibre, namely the bast fibre of the shoot and the seed hairs (floss) from the follicles. However, fibres have not been successfully commercialized due to drawbacks in large-scale cultivation of *A. syriaca*. Far more important, the quality of the bast fibres varied greatly with the environmental conditions and the seed hairs were too brittle for spinning (Gaertner 1979). Recently, *A. syriaca* has received attention again due to the use of the hypoallergenic seed hair in pillows and comforters. Research is going on in handling, drying and floss-processing systems of the seed hair and at the same time in investigating further alternative uses in areas such as clothing, lightweight composites, thermal and acoustic insulation, paper production as well as a source for biofuel (e.g. Von Bargen et al. 1994; Spiridon 2007; Roşu et al. 2011; Karthik and Murugan 2016).

In Europe, the species was commonly cultivated as an ornamental as well as for beekeeping as the flowers of *A. syriaca* are an important nectar source for honeybees (Bagi 2008). For example, Farkas and Zajácz (2007) detailed the utilization of *A. syriaca* for honey production in Hungary. In its native range, *A. syriaca* is the main oviposition site for the endangered *D. plexippus*, as well as a food plant and nectar source for many other insect species (Southwick 1983; MacIvor et al. 2017; see sections *Herbivory* and *Floral biology*). In the United States, it is even being discussed to increase *A. syriaca* in the landscape in its breeding range again in order to support the recovery of the population of *D. plexippus* (Luna and Dumroese 2013; Thogmartin et al. 2017).

Interestingly, some studies reported a positive side effect in the invaded range. Namely, *A. syriaca* played a protective role (nurse effects) in the germination and establishment of *Festuca vaginata* Waldst. et Kit. ex Willd. in open sand grasslands (Szitár et al. 2018). This result can be explained by the fact that *A. syriaca* is able to use the groundwater, which is not reached by the roots of the native species, so there is no competition (or very weak) between the species (Szitár et al. 2016).

6.2. Negative impacts

6.2.1. Effects on biodiversity and ecosystem functioning

Asclepias syriaca has a set of traits that make it a very competitive species: tall, shading canopy, vegetative spread, drought tolerance and allelopathic potential (Bagi 2008; Tokarska-Guzik and Pisarczyk 2015). It can actively modify its environment, thus the species is also called a transformer species (Török et al. 2003; Balogh et al. 2004; Szitár et al. 2018).

The invasion of *A. syriaca* is most dynamic in habitats that have already been degraded by some effects (Szilassi et al. 2019). In Hungary, numerous studies have shown that *A. syriaca* can effectively spread from disturbed habitats to surrounding (semi-)natural ones (Csontos et al. 2009; Csecserits et al. 2011; Albert et al. 2014; Szitár et al. 2014; Bakacsy 2019). As such, degraded areas are increasing, and remaining valuable (semi-)natural habitats are also threatened by the invasion of *A. syriaca*. Effective clonal growth and drought tolerance make it suitable for a slow but persistent expansion into natural open sand grasslands (Bagi 2008; Bagi and Bakacsy 2012; Szatmári et al. 2016; Szilassi et al. 2019). The examinations of (semi-)natural open sand grasslands (old fields) revealed, that *A. syriaca* was able to slow down their regeneration processes or maintain their degraded conditions (Bagi 2008; Csecserits et al. 2011; Albert et al. 2014; Kelemen et al. 2016). The impacts on native species are related to its significant shading (Kelemen et al. 2016) and the release of allelopathic compounds (Kazinczi et al. 2004; Csiszár et al. 2013).

Kelemen et al. (2016) detected a significant negative effect of *A. syriaca* on the cover of grassland species, but it did not have any effect on total species richness. Native species with low specific leaf area, low seed mass and low vegetative spreading ability were especially susceptible to *A. syriaca* invasions. Jurová et al. (2019) strengthened Kelemen's study (2016) as they also found that the cover of smaller native species (such as *Trifolium repens* L., *Bromus commutatus* Schrad. and *Dactylis glomerata* L.) was reduced in Slovakia. Therefore, it is likely that the plant size is an important feature when competing with *A. syriaca*.

Bakacsy (2019) showed that the presence of *A. syriaca* affects the pattern of beta diversity in open sand grasslands. The species reduces the beta-diversity of the grassland community through changes in assembly rules and therefore, its invasion lead to biotic homogenization of open sand grasslands. In contrast, some studies have found that the species does not affect the establishment of dominant grass species (*Stipa borysthena* Prokudin and *Festuca vaginata*) after a pine plantation removal or burning during primary succession (Szitár et al. 2014, 2016).

Asclepias syriaca can also affect higher trophic levels. Some studies have demonstrated that *A. syriaca* has substantial, but mixed effects on native fauna assemblages (Gallé et al. 2015; Somogyi et al. 2017; Jurová et al. 2019; Kapilkumar et al. 2019). Spider diversity was less diverse in the presence of *A. syriaca* (Gallé et al. 2015; Somogyi et al. 2017; Kapilkumar et al. 2019). However, ant abundance was positively influenced by *A. syriaca* due to ants that feed on aphids (e.g. *Aphis nerii* Boyer de Fonscolombe) which live on the plant (Gallé et al. 2015; Somogyi et al. 2017). The species did not have

negative effects on soil nematode diversity in natural grasslands (Jurová et al. 2019). Pyšek et al. (2012b) showed that often soil fauna, soil water and nutrient content increase due to plant invasions. This phenomenon can also be observed in the case of *A. syriaca* invasions in open sand grasslands in Hungary. Soils under stands of *A. syriaca* are characterised by higher humus, phosphorus and nitrate contents, and lower pH and carbonated lime compared to uninvaded stands in Pannonic open sand grasslands (Bagi and Bakacsy 2012). On the contrary, Jurová et al. (2019) found that these soil parameters were not markedly different in the comparison of invaded and non-invaded stands in abandoned vineyards and permanent grasslands in south-central Slovakia. In a recent study, Szigeti et al. (2020) showed that the invasion of *A. syriaca* has a neutral effect on pollinator communities, such as wild bees, honey bee (Hymenoptera: Apoidea: Api-formes) and hoverflies (Diptera: Syrphidae) as most of the parameters (abundance, species richness and diversity) did not show significant difference between the invaded and control sites.

According to available studies, the species has negative impacts on biodiversity and ecosystem processes. However, relatively few studies have been published so far combining the impact of *A. syriaca* and the management itself (e.g. herbicide treatment) on the natural habitat. More studies based on a holistic approach (Barney 2016) are needed to improve the knowledge about the impact of *A. syriaca* on plant and animal communities.

6.2.2. Colonization of high conservation value habitats

Asclepias syriaca is an invader of disturbed semi-natural habitats rather than intact natural habitats (see *Habitats and syntaxonomy*), where topsoil disturbances (treading, ploughing, erosion) or a decrease in native plant species cover facilitate its establishment (Bagi 2008; Bakacsy 2019). *Asclepias syriaca* can colonize natural habitats after disturbances or by spread from adjacent infested areas.

One of the most exposed valuable habitats to the invasion of the species are sand dune-type habitats, such as the Pannonic sand steppes or closed sand steppes (Natura 2000 code: 6260) and Pannonic inland dunes or open dry grasslands (Natura 2000 code: 6340). These habitats exist particularly in Hungary and Serbia and are home to many endemic or threatened plant species (e.g. *Colchicum arenarium* Waldst. et Kit., *Dianthus diutinus* Kit., *Onosma arenaria* Waldst. et Kit., and also the lichens *Cladonia magyarica*, *Xanthoparmelia pokornyi*) (Bagi 2008; Bölöni et al. 2011). Therefore, these habitats are of particular importance for the European Union Habitats Directive (Commission Implementing Council Directive 92/43/EEC). The species has also invaded

two Serbian protected areas, the sand and steppe habitats Deliblato and Subotica-Horgos Sands (Igić et al. 2002), which are home to several endemic or relict-endemic species and communities (e.g. *Festucetum vaginatae deliblaticum* Stjep.–Ves. 1953). *Asclepias syriaca* has already appeared in dune habitats in the Netherlands. These colonized Natura 2000 habitats are located in the fixed coastal dunes with herbaceous species (South-Kennemerland; Natura 2000 area, code: 2103) and dunes with *Hippophae rhamnoides* L. (Natura 2000 code: 2160) (Matthews et al. 2015). According to Matthews et al. (2015), the species poses a medium threat to native species and ecosystem functions in these habitats in the Netherlands.

6.2.3. Agriculture and other economic impacts

In its native range, *A. syriaca* can be found in many types of crops but infestation frequencies varied greatly by crop (Bhowmik and Bandeen 1976; Cramer and Burnside 1982; Hartzler and Buhler 2000). Yenish et al. (1997a) noted that *A. syriaca* has increased in cereals due to the adoption of reduced tillage systems in Minnesota (United States). In Iowa (United States), *A. syriaca* was found in approximately 50% of the surveyed maize and soybean fields (Hartzler and Buhler 2000). Over 70% of the soybean, oat and sorghum were infested with *A. syriaca*, while infestation frequencies for maize, wheat and alfalfa were 36, 28, and 6% respectively in Nebraska (United States). However, recent observations in the Midwestern United States, showed a reduction of *A. syriaca* populations in crop fields, most likely due to the extensive cultivation of herbicide-resistant maize and soybean crops. In 1999, *A. syriaca* was observed in 51% of the crop fields (maize and soybean) surveyed in Iowa (United States), whereas in 2009 only 8% of the fields were infested with the species (Hartzler 2010; Pleasants and Oberhauser 2013).

In Europe, *A. syriaca* has emerged locally as a weed in crop fields (maize, soybean, cereals, legumes), orchards and (abandoned) vineyards in Austria (Follak 2018a; Figure 5), Slovakia (Pauková et al. 2013, 2014), Czech Republic (Kaplan et al. 2017) and Serbia (Vrbničanin et al. 2008). In contrast, in Hungary, the species is more widely distributed in agriculture, particularly in central Hungary, the Great Hungarian Plain and parts of Transdanubia (Novák et al. 2009). As in its native range, *A. syriaca* has a patchy distribution in crop fields and high growth rates are important factors for its competitive success (Bagi 2008; Follak 2018a). In Europe, quantitative data on the impact of *A. syriaca* on crop yield losses is not yet available. Some interference data are available from North American studies (e.g. Evetts and Burnside 1973; Cramer and Burnside 1982; Yenish et al. 1997a), but these results can only be transferred with caution to the European situation because of

different climatic conditions and cropping practices. For example, wheat yield was reduced by 47% at a density of 12 shoots/m² of *A. syriaca* in Minnesota (United States). Yield reductions of 10, 19, and 29% in corn, soybean and sorghum, respectively, have been reported by Cramer and Burnside (1982) in Nebraska (United States). A previous study found that *A. syriaca* interference decreased sorghum yield by 21% and the number of sorghum heads per hectare by 14% (Evetts and Burnside 1973). *Asclepias syriaca* acts also as a reservoir for different virus diseases of crops and insect pests (Bhowmik 1994; Bagi 2008; see section *Plant parasites and diseases*).

6.2.4. Health

Asclepias syriaca contains cardioactive steroids, specifically asclepiadin, gomphoside and afroside (Simpson et al. 2013). All plant parts are toxic with follicles and seeds being most toxic. Poisoning in humans is rare, but it has been reported to occur after consuming plant parts of *A. syriaca* (Simpson et al. 2013). Follicles and young shoots are sometimes included as “wild food” in edible plant guides, though inadvertent poisoning may occur due to such recipes (Simpson et al. 2013). Symptoms include nausea, dilated pupils and rapid and weak pulse. Literature reveals scant livestock experience with ingestion of this plant (Wagstaff 2008; Burrows and Tyrl 2013). An occasional episode of intoxication of cattle following ingestion of large amounts of *A. syriaca* has been described in Hungary (Sályi and Petri 1987 as quoted in Wagstaff 2008). The bitter, milky sap and leathery leaves would be most likely distasteful to animals. It may be only eaten in large amounts when livestock is forced to, e.g. due to food shortage. In North America, however, most poisoning occurs in livestock that fed on narrow-leaved milkweed species, such as *A. verticillata* L. (whorled milkweed) (Wagstaff 2008).

7. Legislation and management

7.1. Legislation

The effective establishment and spread across various grassland ecosystems and agricultural areas within the introduced range has been the motivation for several assessments of the invasiveness of *A. syriaca* and associated risks across Europe (Spain, France: Maillet and Zaragoza 2003; Bulgaria: Petrova et al. 2013; EU: Tokarska-Guzik and Pisarczyk 2015; Poland: Tokarska-Guzik et al. 2012; Tokarska-Guzik et al. 2018; Luxemburg: Ries et al. 2020). At the national level, *A. syriaca* was classified as a noxious, harmful, quarantine species, and its use is regulated by national law in Canada (1996), Hungary (2007), Mexico (2000), Serbia (2010), Poland (2011), Croatia (2015) and Slovakia (2014) (ECOLEX 2020). Several legally non-

binding instruments such as “watch lists” or “grey lists” were used to monitor the species’ introduction and spread (e.g. Wittenberg et al. 2006; Henderson 2007; Petrova et al. 2013; Zavialova 2017). Since 2017, *A. syriaca* has been included in the Union List and keeping, importing, selling, breeding, and growing of the species in the European Union is therefore banned as required under Article 7 of the Invasive Alien Species regulation (Commission Implementing Regulation (EU) 2017/1263).

7.2. Management

7.2.1. Prevention

Measures for preventing *A. syriaca* from being introduced intentionally or unintentionally include legal restrictions and awareness-raising campaigns for stakeholders, e.g. garden owners, as well as the public. Citizen science activities have been found to be a cost-effective tool for engaging with the public to collect records of *A. syriaca* and to educate the public about risks and management options (Prysby and Oberhauser 2004; Oberhauser and LeBuhn 2012; Lewandowski and Oberhauser 2017; Baker and Potter 2018a; Purkart et al. 2020). Ongoing awareness raising activities inform about the risks and share recommendations, such as not to use the species, to dispose the cutting material in residual waste, or to be incinerated e.g. in Germany and Austria (Korina 2020; ÖBF 2020).

Furthermore, preventing unintentional spreading of diaspores by restricting contaminated soil movements is an effective measure for mitigating the spread of invasive alien plants. The seeds and rhizomes pose a risk of unintentional spreading through movement of the topsoil layer (Bhowmik 1994; Yenish et al. 1997b; Lapin 2017). Especially in sites at risk of invasion within protected areas, such as dry grasslands and areas close to roads, monitoring of *A. syriaca* helps to detect, report, and eradicate individuals at an early stage (Bagi 2008). However, monitoring programs are labor-intensive and costly due to the number of trained staff needed to collect field data. Expert knowledge is also required to develop action plans and process the data (Lapin 2017).

7.2.2. Chemical control

Herbicides are effective control measures but exhibit negative environmental side effects. The use of herbicides requires consultation of the respective legal registration and they must be applied strictly according to the product label. Selective spraying of herbicides is used in crop fields and grasslands to halt the further spread of *A. syriaca* (Bhowmik 1994; Bagi 2008).

In crop fields, herbicides usually did not kill (established) *A. syriaca* populations. They cause

foliar damage and frequently, growth resumes after application; however, in some cases the above-ground shoot are killed (Cramer and Burnside 1981; Lizotte-Hall and Hartzler 2019). Thus, in cropping systems, the species is difficult to control (Yenish et al. 1997b; Colbach et al. 2000). For example, the latter authors showed an increase in *A. syriaca* prevalence in continuous no-till soybean with annual application of herbicides (post-emergence: bentazone, imazethapyr) over five years (Minnesota/United States). In Nebraska (United States), *A. syriaca* was difficult to control (efficacy: average 26%) with different postharvest herbicides applied (Wicks et al. 2003). Auxin-type herbicides (e.g. 2,4-D, dicamba) provided not much control of *A. syriaca* (Bhowmik 1982; Ontario, Canada). The non-selective glyphosate appears to be the most effective herbicide (Cramer and Burnside 1981; Bhowmik 1982). In field experiments, control of 70% (or better) of *A. syriaca* was obtained with glyphosate at 2.2 kg/ha applied at the early or late bud growth stage (Cramer and Burnside 1981). Soil-applied herbicides (e.g. metribuzin) can limit the establishment of *A. syriaca* from seeds (Vangessel 1999). In general, *A. syriaca* control in the field with herbicides is variable, and it appears to be dependent on growth stage, application rate and time of application (Bhowmik 1982).

The approach of chemical control in (semi-)natural habitats was tested in Hungary (e.g. Csiszár and Korda 2017; Zalai et al. 2017; Bakacsy and Bagi 2020). Zalai et al. (2017) observed that glyphosate (treatment before flowering, repeated) and dicamba + tritosulfuron (20 to 30 cm height or before flowering, repeated) had an effect on *A. syriaca* with no visible shoots at the last rating date (September) and the almost no regrowth in the following year (Bükk National Park/Hungary). In the long term, any chemical control measure is effective, when herbicides are applied repeatedly to suppress the regeneration of the species in the following growing seasons (Bakacsy and Bagi 2020). Herbicidal treatments need to be monitored over the following years to evaluate their success and potential side effects (Mason and French 2007; Szitár and Török 2008).

7.2.3. Physical control

Manual and mechanical control include a diverse set of techniques such as hand pulling, cutting and mowing. Manual harvesting and root removal, aims at physical elimination of individuals and their root systems in order to control the perennial rootstock, which bears adventitious buds. For a complete removal of the rhizomes of *A. syriaca*, it is recommended to start digging around 30 to 40 cm from

the base of the shoot, digging all the way around and as deeply as possible (Morse and Schmitt 1985; Bhowmik 1994). Other mechanical control measures include the removal of shoots by clipping or mowing, which induces the sprouting of lateral buds (Bhowmik 1994). Despite repeated mowing, Zalai et al. (2017), observed a strong regrowth of *A. syriaca* populations. Although mowing and cutting showed limited effectiveness, it has been shown to be effective for limiting seed dispersal. The production of seeds can also be limited by cutting the inflorescences before flowering (Stevens 2003). The frequency of mowing and the population size of *A. syriaca* are important parameters. Studies in the native range of the species conclude that a single mowing treatment in the early summer period does not necessarily prevent it from re-flowering later in the summer (Knight et al. 2019). Prescribed burning should be avoided, as fire can favour *A. syriaca* (e.g. Szatmári et al. 2016).

7.2.4. Alternative control measures

Although the species is toxic for the majority of mammalian herbivores, it has been found that European rabbits are capable of digesting *A. syriaca* (Ducs et al. 2016). Due to the possibility of adapting food preferences according to the dietary traditions in a habitat, grazing by European rabbits may be considered for the control of *A. syriaca* (Ducs et al. 2016). Cultural control in the sense of the management of crop fields can also assist in managing *A. syriaca* when it invades agricultural land (Hartzler and Buhler 2000). The spread of *A. syriaca* has been controlled by including forage grasses or legumes, small grains, and irrigated corn in the crop rotation (Bhowmik 1994). In conventional cropping systems, soybean-winter wheat rotation best suppressed the establishment of *A. syriaca* seedlings (Yenish et al. 1997b). The planting of competitive crops, such as cereals or alfalfa (*Medicago sativa* L.) can limit *A. syriaca* emergence and growth (Bhowmik 1994).

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László Bakacsy contributed to the sections of effects on biodiversity and ecosystem functioning, vegetative growth and reviewed the final draft.

Franz Essl contributed to the section dispersal and commented on other sections of the manuscript.

Lisa Hochfellner contributed to the section history of introduction and spread in Europe and performed statistical analyses.

Katharina Lapin contributed to the section on legislation and management.

Michael Schwarz contributed to the section distribution and status and created the distribution maps.

Barbara Tokarska-Guzik contributed to the section biology, in particular, phenology, reproductive biology: floral biology and seed production and germination and commented on other sections of the manuscript.

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