A hitchhiker from the beach: the spread of the maritime halophyte *Cochlearia danica* along salted continental roads

Šíření přímořského halofytního druhu *Cochlearia danica* podél solených silnic

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The increase in road networks facilitates the dispersal of many species of plants along roadsides. In these special habitats, the use of deicing salt can provide suitable habitat conditions for the establishment of stress-tolerant halophytes. This study investigates the spread of an alien halophyte *Cochlearia danica* in continental Europe. This species is native to the Atlantic shores of Europe, has already spread in many countries along roadsides and was recently discovered in Hungary. We performed a literature review to track the European spread of this species, and investigated the Hungarian occurrences in detail. Then we determined the ability of this species to adapt to local soil conditions by means of soil analyses and germination tests using 19 different NaCl concentrations and alkaline soils. To estimate the rate of spread, we estimated the size of the four Hungarian populations in 2016 and 2017, and at the same time we measured the number of flowering stems, number of flowers in an inflorescence, number of seeds per fruit and seed mass. *Cochlearia danica* is recorded growing along roadsides in eight countries in continental Europe. Literature data indicate a rapid spread of this species along European roads, of 62–65 km/year. In Hungary this species is recorded at four roadside localities characterized by a high soil salt content. The relationship between NaCl concentration and percentage germination followed a sigmoidal curve. Germination tests revealed a significant negative effect of NaCl concentration on germination above 0.5% NaCl, but germination occurred even on extremely saline substrates with a 2% NaCl concentration. The area of the largest Hungarian population decreased by more than 99% and that of the second largest population increased by more than 30% between 2016 and 2017. Even though this species can adapt to high salinity in the soil, these rapid and marked changes in population size indicate that the population dynamics of this species may depend on interactions between the amount of local precipitation and soil type. Our study indicates that we should expect further occurrences of *C. danica* along roads.

K e y w o r d s: *Brassicaceae*, deicing salt, NaCl, plant invasion, roadside verges, seed dispersal

Introduction

The extent of road networks has increased remarkably during the past century worldwide. The total length of global road networks is more than 64 million km and a further marked increase is projected for the near future (van der Ree et al. 2015). The length of

paved roads in the European Union was recorded as 5,066,700 km in 2008 (Nicodeme et al. 2011). The mean size of areas without roads is 48 km^2, which means that Europe has one of the densest road networks in the world (Ibisch et al. 2016). The rapidly growing density of roads has a negative effect on the occurrence of many taxa and decreases biodiversity (Findlay et al. 2000) and the typical negative effects include fragmentation and edge effects on surrounding habitats, thus the communities affected are becoming more vulnerable to negative effects, such as the spread of alien species, which are more able to become established in new habitats (Forman & Alexander 1998, Spellerberg 1998, Zwaenepoel et al. 2006). Roads, as ecological corridors, play a significant role in the spread of plant species (Tikka et al. 2001), long-distance dispersal of native and alien species by vehicles is a frequent phenomenon, but is more common among alien species (von der Lippe & Kowarik 2007). Propagule export from cities to rural and suburban environments is likely to be more frequent than from rural to urban areas, thus it could increase the incidence of plant invasions, as more propagules, with a higher representation of seeds of alien species, were found along roads leading from urban areas (von der Lippe & Kowarik 2008). The spread of invasive species along roads is a worldwide phenomenon (Forman 2000, Gelbard & Belnap 2003, Kalwij et al. 2008, Essl et al. 2009, Follak et al. 2013, Skálová et al. 2017). Thus, roadsides are unique places, where often first occurrences of alien plants can be found. The construction and management of roads are usually associated with several types of anthropogenic disturbance, such as frequent mowing, deicing, use of herbicides, trampling by humans and vehicles, a range of pollutants and modified soils used for construction, the last of which may contain propagules of alien species (Šerá 2008, van der Ree et al. 2015). These all contribute to the spread of aliens, since native species are usually less able to adapt to the altered conditions in roadsides (Greenberg et al. 1997, Forman & Alexander 1998). In the case of lightweight seeds, dispersal may be facilitated by the air turbulence caused by cars (von der Lippe et al. 2013), and they may also travel long distances in mud attached to wheels (Ross 1986, Zwaenepoel et al. 2006), which can contain substantial numbers of seeds (Clifford 1959). For example, Schmidt (1989) sampled mud from a single car driven 15,000 km and found almost 4000 germinable seeds of more than 100 species. According to Ansong & Pickering (2013) more than 60,000 seeds were found in one ton of dry sludge collected from Australian cars. Machines used for mowing verges have also been shown to transport seeds (Strykstra et al. 1997, Vitalos & Karrer 2009).

Use of deicing salt has become widespread in Europe during the last five decades. Although winter road maintenance practices differ between countries according to climatic conditions, in most European countries the most frequently used material for deicing is salt (mostly NaCl, with a small proportion CaCl$_2$, rarely MgCl$_2$; Houska 2007). The two countries using the largest quantities of salt are the United Kingdom and Germany (2200 and 2000 metric tons respectively; Houska 2007). Deicing salts have complex effects on the roadside environment; they infiltrate ground-water (Amrhein et al. 1992) and damage the leaves of many species of trees (Hofstra & Hall 1971). The increased soil salt content can cause osmotic stress for plants, alter soil pH and the availability of nutrients, thereby altering the species composition of roadside vegetation and facilitating the spread of halophytic species of plants (Davison 1971). Halophytes constitute approximately 1% of the world's flora and are able to survive and reproduce in environments where salt concentrations are at least 200 mM NaCl (Flowers & Colmer 2008). Obligate

halophytes thrive best in saline circumstances (Flowers & Colmer 2008). Facultative halophytes are poor competitors and restricted to extreme environmental conditions (Barbour 1978).

Spread of a maritime halophyte species, *Plantago coronopus*, was first detected in Hungary in 2013 (Schmidt et al. 2014), and further occurrences were recorded in 2014, 2015 (Kovács & Lengyel 2015) and 2016 (Schmidt et al. 2016), which indicate an eastward spread of this species. Spread of native halophytes, such as *Plantago maritima* (Barina 2007), *Puccinellia distans* (Király & Hohla 2015), *Limonium gmelinii, Atriplex tatarica*, *Podospermum canum* (Schmotzer 2015), *Spergularia media, S. marina* and *Bupleurum tenuissimum* (Schmidt et al. 2016) has also been documented.

The motivation for this study was the recent discovery of an Atlantic coastal halophyte plant species, *Cochlearia danica* (Danish scurvygrass) in Hungary in 2016 (Molnár V. & Löki 2016). This discovery offered a unique opportunity to track the first stages of a potential plant invasion. Here, we analyse the spread of this species in central Europe, and assess its ability to bypass geographical, environmental and reproductive barriers during its spread.

We focused on the following stages of a potential invasion: (i) Transport. We tracked the dispersal of this species through continental Europe based on reports in the literature and investigated in detail its recent occurrences in Hungary based on a comprehensive field survey. (ii) Colonization. We examined soil parameters associated with the Hungarian roadside habitats of *C. danica* and tested the effect of soil salt content on its germinability in an in vitro germination experiment. (iii) Establishment. We estimated its ability to spread by studying its population dynamics and reproductive traits. Finally we estimated its invasion potential in continental Europe.

Material and methods

Surveying the spread of Cochlearia danica through Europe

To estimate the speed of spread of this species in continental Europe, we searched the literature using Google Scholar and the following keywords: the name of the species 'Cochlearia danica' AND 'roadside' OR 'road verge'. This returned 94 hits. After scanning these 94 papers, the number of studies dealing with roadside occurrences of *Cochlearia danica* was 13. Among these 13 papers, we found only one study dealing with continental Europe, and three more in the reference lists of the other 12 papers. We did not include the data on the occurrences of *C. danica* in the British Isles because this species there is already widespread along inland roads. Further searches with the following keywords: 'Cochlearia danica' AND 'autobahn' returned 38 papers (published mostly in German) and the number of relevant studies among these was eight with eight more referred to in their reference lists. We included two further papers not available on Google Scholar. Altogether there were 22 relevant publications. The following data were collected: locality of occurrence, classification of road, altitude at the locality and date of detection. These data were georeferenced using Quantum GIS 2.16.1 software.

In our field survey, we visited the recently discovered Hungarian populations and also searched for other occurrences. *Cochlearia danica* was first recorded in Hungary near Biharkeresztes (East-Hungary) and Győr (West-Hungary) in April 2016. After the first

discovery of this species, we made systematic surveys to detect the presence or absence of *C. danica* along the whole motorway system (~472 km) in April 2016 and 2017: we followed the M43/E79 between Oradea (Romania) and Berettyóújfalu (35 km), the M47/E79 from Berettyóújfalu to Debrecen (35 km), the M35/E79 from Debrecen to Polgár (50 km), M3/E71 from Polgár to Budapest (220 km) and M1 motorway (E60) from Budapest to Hegyeshalom (167 km). In this paper plant names follow the nomenclature used in the Euro+Med PlantBase (Euro+Med 2006).

Germination experiments and soil analyses

We tested the ability of *C. danica* seeds to germinate in vitro at room temperature at different NaCl concentrations from 14 October 2016 to 14 January 2017. Since the seeds do not require cold stratification (Bakker & de Vries 1992), we stored the seeds (collected on 2 May 2016, near Biharkeresztes) at room temperature. We tested germination on a 1% agar substrate in Petri-dishes with the following 19 NaCl concentrations (mass percent): 0 (control), 0.03%, 0.05%, 0.07%, 0.10%, 0.20%, 0.30%, 0.40%, 0.50%, 0.75%, 1.00%, 1.50%, 2.00%, 2.25%, 2.50%, 3.00%, 3.50%, 4.00% and 5.00%. We used these concentrations to determine whether this species requires salt for germination and to assess the maximum % of NaCl at which it is able to germinate. The chosen salt concentrations are comparable to those in the following soil types: soils with salt content < 0.10% are not saline and these salt levels do not inhibit the growth of agricultural plants, 0.10–0.25% are slightly saline and cause a slight decrease in the growth of salt-sensitive plants, 0.25–0.50% are moderately saline and the yields of most cultivated plants decline in these soils, 0.50–1.00% are saline, in which only the growth of halophytes is unaffected, and soils with >1.00% salt content are strongly saline, in which only a few obligate halophytes are able to persist (Stefanovits et al. 1999). Germination was tested in plastic containers filled with alkaline soils originating from Zsadány, East-Hungary (46.93589°N, 21.52886°E). In each treatment (germination at 19 NaCl concentrations on agar and alkaline soil), 50 seeds with three replicates were germinated (in total 3000 seeds). Seeds were sterilized by washing them with 20% sodium hypochlorite (NaClO) solution for two minutes and then with sterile water three times, beforehand, in order to avoid fungal infestation. During germination tests we stored the Petri-dishes and the plastic containers near the window in a laboratory, under natural light conditions at room temperature and monitored germination for 60 days. Emerging seedlings were counted daily during the experiment.

Soil salt content (mass percent), pH (KCl), $CaCO_3$ (mass percent), organic matter content (mass percent), N (mg/kg), P (mg/kg) and K (mg/kg) content were measured in the case of the two largest known Hungarian populations (Biharkeresztes and Győr). We collected soil samples at root depth (1.5–6.5 cm) at 10 points at three different distances (1, 2, 3 m) from the road on 4 April 2016 in Biharkeresztes and 18 April 2016 in Győr. Alkaline soil used in the germination experiments was also analysed. Total soluble salt content was quantified by measuring electric conductivity of a saturated paste of soil and water using a conductivity meter (Tetra Con 325) (Hungarian technical standard MSZ-08-0213:1978 2.2). Soil analyses were carried out by the accredited laboratory of the Research Institute of Karcag of the Centre for Agricultural and Applied Economic Sciences of University of Debrecen.

Measuring the area occupied by each population and determining the reproductive traits

The geographical positions of the Hungarian populations were determined using a Garmin E-Trex Legend handheld GPS recording in WGS84 format. The spatial extent of populations at Biharkeresztes and Ártánd was measured in both years (2016 and 2017). The area of populations and number of individuals at Győrújbarát and Győr were measured only in 2016 because the size of the populations decreased markedly in 2017 and it became more practical to estimate both the area and the number of individuals. For each patch of *C. danica*, we measured the length and width, the distance of the closest and the furthest individuals from the road, and the distance from the road margin to the nearest and furthest edge to estimate their average distance from the road margin. To estimate the number of individuals in each population, we counted the individuals in 11 randomly designated plots (10 × 10 cm), used the median of these numbers to calculate values per $1m^2$, and multiplied this by the area of the stand.

To estimate the potential individual seed production, the number of flowering stems per individual and number of flowers per inflorescence (in five inflorescences per individual) were counted on 4 April 2016 and 10 April 2017 for 30 individuals from Biharkeresztes. The number of seeds per fruit was counted on 2 May 2016 (50 fruits) and on 13 May 2017 (100 fruits). The mass per thousand seeds was calculated in 2016 based on weighing 3 × 100 seeds following the method described by Török et al. (2013).

Statistical analyses

Data analyses were carried out in the R statistical environment (R Core Team 2016). Differences in percentage germination in relation to NaCl concentration were evaluated using a one-way ANOVA. Tukey test (honestly significant differences, HSD) was used to estimate pairwise significances. We performed sigmoidal curve fitting to reveal the nature of the relationship between NaCl concentration and percentage germination using Boltzmann non-linear curve fit and graphical program package OriginPro (OriginLab Corp., Northampton, MA, US).

Results

Spread of Cochlearia danica in Europe and its occurrences in Hungary

Cochlearia danica is native to coastal habitats in the following countries in Europe: Belgium, Denmark, United Kingdom, France, Finland, Netherlands, Ireland, Germany, Norway, Portugal, Russia, Spain and Sweden, but can also be found in disturbed inland habitats (Tutin et al. 1993). In the UK it occurs in a range of maritime habitats such as rock-crevices, in therophyte communities, coastal grasslands, salt-marshes and drift-line communities (Fitter & Peat 1994).

Excluding the British Isles, the spread of *C. danica* along roads was documented in eight European countries between 1986 and 2016. In the literature review, we found 63 occurrences, of which 44 were along motorways, 13 along highways and four along side roads (no information on the type of road was available for two localities) (Electronic Appendix 1). A few studies mention the spread of this species along lower-class roads (Zonderwijk & Groen 1996, Jagel & Gausmann 2009, Klug 2012). The highest altitude
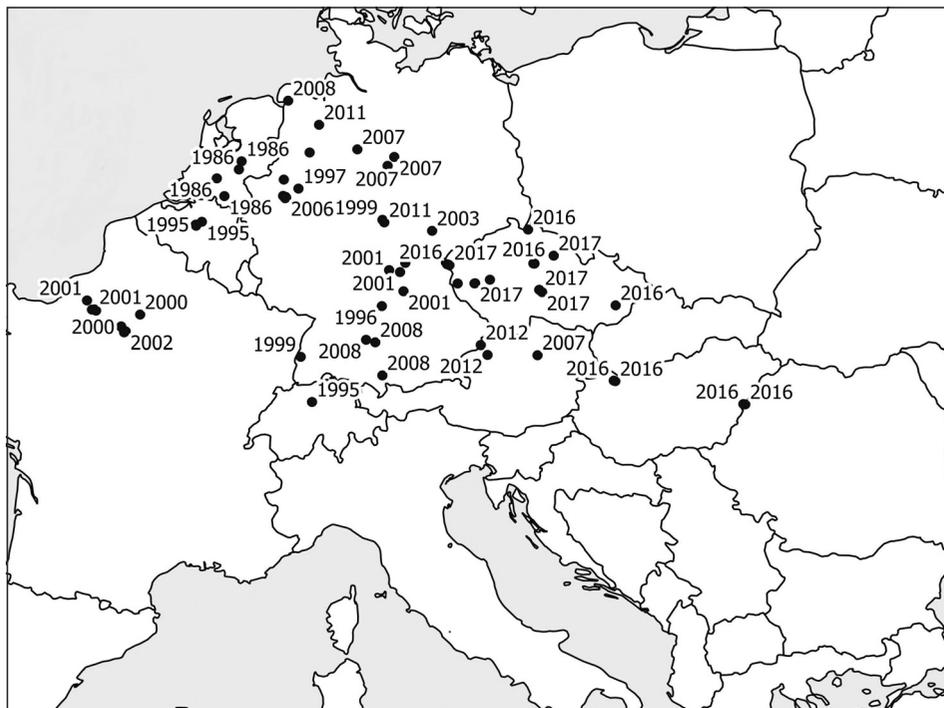
Fig. 1. – Occurrences of *Cochlearia danica* and the date of first detection in roadside locations in continental Europe based on a review of the literature and the authors observations.

record for this species was 700 m (Austria) and the lowest 4 m a.s.l. (Germany). In the mid-1990s only a few localities were known from roadsides in Europe but this had increased to 63 by 2017 (Fig. 1). Only one study (Ducháček et al. 2017) includes information on the population size of *C. danica,* varying from five individuals to hundreds of individuals in different localities suggesting recent colonization.

Based on our literature review, the spread of *C. danica* along the road networks in continental Europe can be traced as follows. The first record of this species on a roadside was 1986 in Belgium. The locations in the Netherlands and Germany are the closest roadside occurrences of this species to the coast in continental Europe. The species reached its easternmost locality (Hungary, Ártánd, E60) 30 years later, between 1986 and 2016, which is around 1866 km from the westernmost known locality (France, Saint-Aubin-sur-Gaillon, A13). The distance between the first known occurrence in Austria (Pöchlarn) and the easternmost Hungarian locality (Ártánd) is 589 km, and time that elapsed between their detection is 9 years. Based on this information, the average dispersal speed of this species along roads is 62–65 km/year.
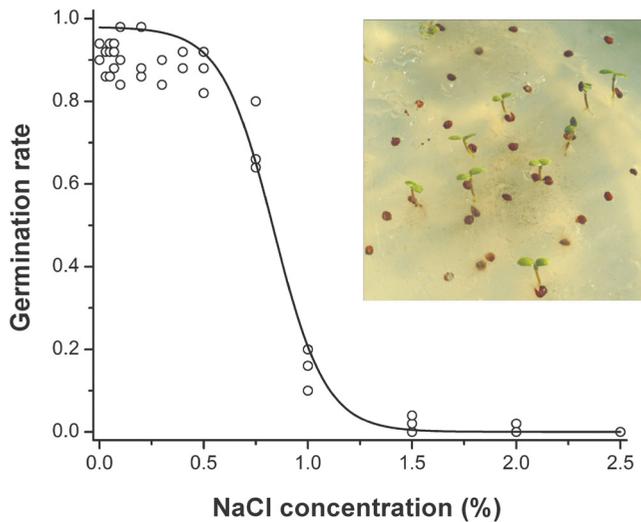
This species was found in Hungary at four localities in 2016 (Table 1) on roadsides of highways and motorways with high traffic intensity (Fig. 2A). Dense patches of *C. danica* (Fig. 2B) were found between 0.95±0.66 and 1.65±0.75 (mean±SD) meters from the road edge. The distance of the nearest individual to the edge of the road was at 0 m (Biharkeresztes, Ártánd), and the farthest was at 4.7 m (Biharkeresztes).

Table 1. – Characteristics of Hungarian occurrences of *Cochlearia danica*.

Municipality	Road	Coordinates	Side of road	Date of first detection
Győr	M1 (E60)	47.64594°N, 17.61641°E	Budapest–Hegyeshalom	30 March 2016
Győrújbarát	M1 (E60)	47.63456°N, 17.66468°E	Budapest–Hegyeshalom	8 April 2016
Biharkeresztes	M42 (E79)	47.13529°N, 21.69858°E	Berettyóújfalu–Borş, Borş–Berettyóújfalu	29 March 2016
Ártánd	M42 (E79)	47.12871°N, 21.75849°E	Berettyóújfalu–Borş, Borş–Berettyóújfalu	4 April 2016

Fig. 2. – *Cochlearia danica* on the side of road E79 near Biharkeresztes (Hungary). A – roadside habitat; B – patches with high density of flowering individuals; C – sporadic occurrence of individuals at the edge of a roadside.

Fig. 3. – In vitro percentage germination of seed of *Cochlearia danica* on substrates with different salt concentrations and sigmoidal curve fitted to the percentage that germinated.

In vitro seed germination and soil analyses

Seed germination on 1% agar substrate began on the third day after sowing, and by the fourth day more than 60% of the seed had germinated. A one-way ANOVA showed a significant effect of NaCl concentration on percentage germination, with a moderate increase between 0% and 0.10% NaCl concentration, a peak of 98% germination at 0.10% NaCl concentration (Electronic Appendix 2), and a significant decrease at 0.5% (Electronic Appendix 3). At maximum concentration of 2.00% NaCl only one seed germinated producing a seedling which lacked a radicle and died before developing cotyledons and no seeds germinated at concentrations above 2.00% NaCl. A post-hoc test showed that percentage germination did not differ significantly between 0% and 0.5%. The relationship between NaCl concentration and percentage germination was sigmoidal with a high goodness of fit and a low residual sum of squares (Boltzmann non-linear curve fit, $R^2 = 0.99$; $P < 0.001$; RSS = 0.06; Fig. 3). On alkaline soil percentage germination in the three plastic containers was 88%, 90% and 96%. By the seventh day after sowing, more than 90% of the seeds had germinated.

Soil analysis showed, that water-soluble salt content decreased with distance from the edge of the road at both localities (Biharkeresztes and Győr). At Biharkeresztes it decreased from 0.15% (1 m distance from road edge) to 0.08 % (3 m distance from road edge), while at Győr it decreased from 0.14% to < 0.02% (Table 2).

Table 2. – Soil parameters recorded for the Hungarian roadside habitats of *Cochlearia danica* and the alkaline soil used in the germination experiment.

Locality	Distance from road	pH (KCl)	Total salt content (mass %)	CaCO₃ (mass %)	Organic matter (mass %)	(nitrate+ nitrite)-N (mg/kg)	P (mg/kg)	K (mg/kg)
Győr	1 m	7.7	0.14	3.18	2.9	10.2	156	176
Biharkeresztes	1 m	7.4	0.15	8.01	6.4	93.2	201	206
Győr	2 m	6.8	0.09	< 0.05	7.9	4.4	217	311
Biharkeresztes	2 m	6.9	0.09	0.05	4.1	52.3	170	287
Győr	3 m	7.3	< 0.02	7.53	4.9	2.7	149	307
Biharkeresztes	3 m	6.8	0.08	< 0.05	7.6	27.9	155	140
Alkaline soil (Zsadány)	3 m	5.8	0.07	< 0.05	3.7	6.4	183	608

Changes in population abundance and reproductive traits of the species

In 2016 the largest *C. danica* population was at Győrújbarát, the second largest at Biharkeresztes and the smallest at Győr. In 2017 the Győrújbarát population had decreased remarkably both in area and number of individuals, whereas the Biharkeresztes population increased in area and number of individuals (Table 3).

Measurements indicate that the reproductive capacity of *C. danica* is 3.6±2.3 (mean±SD, range = 1–9) flowering stems per individual, 10.6±3.3 (4–15) flowers per inflorescence (Electronic Appendix 5) and 8.5±2.4 (2–13) seeds per fruit (Electronic Appendix 6). The mass of 1000 seeds was 0.233±0.009 g (mean±SD).

Table 3. – Changes in the area and number of individuals in the populations of *Cochlearia danica* in Hungary from 2016 to 2017.

	Year	Győr	Győrújbarát	Biharkeresztes	Ártánd
Population area (m^2)	2016	1.0	364	277	10
	2017	0.1	1	426	20
Number of individuals	2016	3,000	1,201,000	579,000	21,000
	2017	50	1,000	890,000	42,000

Discussion

Occurrences of Cochlearia danica in Hungary

The differences in the areas of the four Hungarian populations could be explained by the time that elapsed between their colonization. Since the area occupied by the population at Győrújbarát was the largest in 2016, this was probably the first site colonized by this species in Hungary in 2014–2015. According to Dávid Schmidt, who carefully investigated this section of the road in 2013–2014 (searching for *Plantago coronopus*), *C. danica* was not present. Based on the number of individuals in the populations at Biharkeresztes and Ártánd they were probably established in 2015. Two of the Hungarian populations are at motorway exits, and two are near parking places. In these localities the traffic moves slowly and as a consequence it is easier to notice *C. danica* populations. There are populations at similar localities in Germany (Hohla & Raabe 2012) and Austria (Klug 2012). The occurrence of *Cochlearia danica* in Hungary is obviously due to road maintenance practices such as winter deicing that increases soil salinity and creates free surfaces on road verges. Furthermore, due to regular mowing small herbaceous plants with low competitive ability are more successful on roadside verges (Sýkora et al. 2002).

Cochlearia danica occurs in large monodominant patches at all the Hungarian sites, but it is also associated with some native disturbance-tolerant annual ruderal species (such as *Atriplex tatarica* and *Lepidium ruderale*), native weeds (*Cardaria draba*, *Plantago major* and *Portulaca oleracea*), annual aliens (*Ambrosia artemisiifolia*, *Plantago coronopus* and *Tragus racemosus*), ruderal, annual, native pioneers (*Polygonum aviculare*, *Cerastium dubium, Cerastium glutinosum* and *Spergularia maritima*) and stress-tolerant generalists (*Podospermum canum*; categorization follows Borhidi 1995, Király 2009). Similar annual, disturbance-tolerant species occur with *C. danica* at other sites (Hohla & Raabe 2012) along with common species of the Hungarian and Czech localities including *Cerastium dubium*, *Lepidium ruderale*, *Plantago coronopus* and *Polygonum aviculare* (Ducháček et al. 2017). Other halophytes such as *Plantago coronopus* and *Puccinellia distans* also occur in habitats with *C. danica* on road verges.

Ability of Cochlearia danica to survive roadside soils conditions

Our soil analyses showed that due to the use of deicing salts, roadside habitats of *C. danica* are characterized by high salt content. Since this species has not been detected in other habitats, it seems likely that roadside conditions, such as high soil salt content and open vegetation structure provide optimal conditions for its establishment. In the germination

experiment, we confirmed the ability of this species to survive roadside soil conditions. According to Stefanovits et al. (1999) soils with more than 1% soluble salt content are highly saline, and can support only a few halophyte plant species. We recorded germination of *C. danica* on even higher salt concentrations, highlighting its tolerance of elevated salt levels.

We recorded similarly high percentage germination in the salt-free control and low salt concentrations (0.10%). Percentage germination was significantly lower at the higher salt concentrations (from 0.5%). Based on our results, *C. danica* may not be an obligate halophyte, but a poor competitor and a good stress-tolerator. This is supported by previous studies, which show that the survival of seedlings of *C. danica* is positively related to the percentage of bare soil (Bakker & de Vries 1992) and their ability to accumulate heavy metals (Reeves 1988).

Soil analyses show a decrease in salt content with distance from roads (see also Zehetner et al. 2009). Our germination tests showed germination on even higher salt concentrations than recorded in roadside soil. Thus, it seems, that occurrences of *C. danica* closer to road margins is limited not by the increased salt content, but possibly by mechanical impacts from wheels of vehicles leaving the road.

Our results show that the high soil salt content typical of roadsides provides suitable conditions for *C. danica*. The distance of the patches from roads was similar in the case of *Plantago coronopus*, an established halophyte, which also spreads along roads in Hungary (Schmidt et al. 2014). Presumably both species prefer open microhabitats on soils with elevated salt concentrations close to roads, which facilitates the occurrence of halophytes and gives them a competitive advantage over other species. Several studies have documented the spread of maritime species (e.g. *Cochlearia officinalis*, *Halimione portulacoides*, *Plantago maritima*, *Hordeum marinum*, *Suaeda maritima*) along roads in Great Britain, which includes species that had not been documented from continental regions of the island before (Scott & Davison 1982, 1985). It is also a well-known phenomenon in continental regions of Europe, such as in the case of the halophyte *Puccinellia distans*, which was recorded growing in roadsides several times in the last few years (Bozena 2010) or another halophyte, *Suaeda salsa*, which was first recorded from roadside verges in the Czech Republic (Kaplan et al. 2017). The spread of another continental halophyte, *Limonium gmelinii*, along motorways in the Czech Republic has also recently been documented (Kocián et al. 2016). Our study shows that *C. danica* can be added to the list of halophytes that are dispersed along road networks.

Population dynamics and potential future spread of the species

Changes in the area and number of individuals in the Hungarian populations between 2016 and 2017 may be due to the different type of soils at Győrújbarát and Biharkeresztes. It is possible that the very dry first three months of 2017 in Hungary (Metnet 2017) had a greater effect on the sandy soil at Győrújbarát, which resulted in the decrease there of the *C. danica* population. Despite the dry period, the population at Biharkeresztes increased, possibly due to higher soil water capacity of the loamy soil compared to the sandy soils at Győrújbarát (Stefanovits et al. 1999, Gyalog & Síkhegyi 2000). This information indicates that the population dynamics of this species may depend on interactions between rainfall and soil type.

We assume that initially only a few individuals introduced by traffic occurred at all four Hungarian localities. According to our measurements an average individual of *C. danica* has four flowering stems and 11 flowers per inflorescence. When all flowers bear fruit, the 44 fruits of an average individual produce a total of 396 seeds. When all the seeds germinate and develop into adult plants, a population of 100 individuals could have 35,000 offspring in one year and more than 12 million offspring in two years. Small seeds could contribute to the success of *C. danica*, since it is among the most important traits of invasive species, usually associated with significant seed production, persistent seed bank and effective wind dispersal (Westoby et al. 1996, Bekker et al. 1998).

Based on the literature, it seems that *C. danica* is spreading rapidly along European roads. Our estimates of the dispersal speed (62–65 km/year) exceeds the estimated dispersal speeds reported in previous studies from the United Kingdom, which are 10–20 km/year (Leach 1994) and 40 km/year (Welch 2001). Development of the road network, increasing traffic intensity, increasing number of individuals, and increasing seed production in the western-European populations may all contribute to increasing dispersal speed (see also Pyšek & Hulme 2005). The implications of the spread of *C. danica* along roads for conservation has yet to be considered, but this may change in the near future. There has been no consideration of the potential threat posed by *C. danica* to inland alkaline plant communities, which are present in large areas in the Pannonian Basin (Eliáš et al. 2013, Deák et al. 2014). This species has so far not reached these habitats, but it is approaching them in Hungary. Furthermore high percentage germination was recorded on alkaline soils, with a high salt content. In Hungary several motorways and higways pass over alkaline plant communities so there is a possibility that this species may colonize natural habitats further from its native distribution. In alkaline habitats there are only a few invasive species (Molnár & Borhidi 2003) possibly due to the high soil salt content, but *Cochlearia danica* may represent a new threat to these habitats of special importance.

It seems unlikely that continental cold winters pose a barrier for *C. danica*. This was confirmed by its survival in the extremely cold winter in Hungary in 2016/2017, with more than 31 frost days and monthly average temperature of –6°C in January at Debrecen, the closest meteorological station to Biharkeresztes (Metnet 2017).

There are several effects of human-mediated long distance dispersal of plant propagules. After a species is introduced into an area far from its native distribution, it can remain a casual, able to reproduce but unable to maintain its population for long periods. When species overcome local environmental barriers and reproduce regularly, they may be considered naturalized, but they may be unable to colonize natural, seminatural or anthropogenic environments. Invasion can only occur when a naturalized species colonizes areas far from its introduction, and this may mean it invades disturbed, seminatural plant communities, by increasing its population size (Richardson et al. 2000). According to previous studies alien species, spreading along roads, are able to successfully colonize natural habitats from roadsides (Tyser & Worley 1992, Gelbard & Belnap 2003). *Cochlearia danica* should be considered an alien, because without human-mediated dispersal it could not have overcome the geographic barrier. It is common that occurrences of native species outside their native range within a country are also categorized as alien occurrences, such as in the cases of the roadside occurrences of *Spergularia marina* in the Czech Republic (Kaplan et al. 2016) and *Limonium gmelinii* in Hungary (Bartha et al. 2015).

Based on the spatial and temporal distribution of *C. danica* in continental Europe, it can be considered as a naturalized alien species. In the near future we will be able to assess whether it will become a naturalized species in Hungary and Czech Republic (i.e. having self-replacing populations for at least 10 years without direct human intervention; Richardson & Pyšek 2006), or it will remain a casual alien species. Considering its huge potential reproductive ability and the widespread availability of suitable open habitats, we assume that it has a good chance of becoming a naturalized alien element of the Hungarian and Czech floras. Taking into account the current trend, we should expect further occurrences of this species along roads in countries where the spread of other halophyte species has also been detected, e.g. Slovakia (Dítě & Dítětová 2016), Slovenia (Grašič et al. 2016) and Poland (Wróbel et al. 2006). Further occurrences will largely depend on the method used for winter deicing. Thus, in countries (e.g. Ireland; Biological Records Centre 2017) where grit is used for winter deicing, the spread of this species is less likely. However, this species may reach coastal regions of the Adriatic Sea and/or the Black Sea, and threaten maritime plant communities there in the near future.

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Souhrn

Silniční síť a budování nových komunikací usnadňují šíření mnoha druhů rostlin. Jedná se o speciální stanoviště, kde zimní solení vytváří vhodné podmínky k růstu halofytů, tolerujících stres. Článek popisuje šíření nepůvodního halofytního druhu *Cochlearia danica* v kontinentální Evropě. Druh je původní na atlantickém pobřeží Evropy, odkud se rozšířil do mnoha zemí, a nedávno byl zaznamenán i v Maďarsku. Pomocí literárních údajů jsme rekonstruovali šíření druhu po Evropě a experimentálně jsme testovali jeho schopnost adaptace k růstu na zasolených půdách. *Cochlearia danica* je udávána z osmi zemí kontinentální Evropy a v současnosti se šíří průměrnou rychlostí 62–65 km/rok. V Maďarsku se vyskytuje na čtyřech silničních lokalitách s vysokým obsahem solí v půdě. Při koncentracích NaCl vyšších než 0.5 % se klíčivost snižuje, určitá frakce však klíčí i při koncentracích 2 % NaCl. Největší maďarská populace se meziročně (2016–2017) zmenšila o 99 %, druhá největší naopak o 30 % vzrostla. Populační dynamika druhu závisí na interakcích mezi úhrnem srážek a vlastností půdy. Naše výsledky naznačují, že v budoucnosti lze očekávat další šíření *C. danica* podél silnic.

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