Seedling dynamics and population structure of invasive Heracleum sosnowskyi (Apiaceae) in Lithuania

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Seedling dynamics and population structure of invasive *Heracleum sosnowskyi* (Apiaceae) in Lithuania

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We studied seedling dynamics and population structure of the invasive, monocarpic perennial *Heracleum sosnowskyi* (Apiaceae) in different habitats. The lowest seedling density was found in the managed anthropogenic herb stand, whereas in the unmanaged anthropogenic herb stand, mean seedling density was the highest and significantly different from that at the other studied sites. In all populations, a small fraction of the individuals were generative. In the managed anthropogenic herb stands, mature vegetative and generative individuals dominated in the population, whereas the unmanaged anthropogenic herb stands were dominated by immature vegetative plants. Our study confirmed that long-term abandonment of mesic meadows promotes development of denser stands of *H. sosnowskyi*. A short-time extensive management can reduce the density of monocarpic invasive species populations, especially their seedlings and immature vegetative plants. Significant reduction in seedling numbers occurred between April and May, with high seedling mortality rates in the following months until September. The mean seedling survival rate was 4.15%.

Introduction

Expansion of alien species creates complex challenges and poses a significant threat to biodiversity, society, economy and human health (Esch *et al*. 2001, Levine *et al*. 2003, Pyšek & Richardson 2008, Barney *et al*. 2015). Invasive plant species can change ecosystem functions and the structure of plant communities in invaded areas (Nielsen *et al*. 2008, Jeschke *et al*. 2014). Giant hogweeds *Heracleum mantegazzianum* and *H. sosnowskyi* (Apiaceae) are among the strongest competitive invasive plant species spread throughout large areas of Europe and they cause ecological, economic and social problems (Pyšek *et al*. 2007). They are on the lists of invasive species of many European countries (Gederaas *et al*. 2012, Gudžinskas *et al*. 2014, Pergl *et al*. 2016). The European Parliament and the Council of Europe adopted Regulation (EU) 1143/2014 on the prevention and management of the introduction and spread of invasive alien species. Currently, the List of Invasive Alien Species of European Union concern (cf. http://ec.europa.eu/environment/nature/invasivealien/list/index_en.htm) includes 49 species including *H. mantegazzianum*, *H. sosnowskyi* and *H. persicum*.

Introduction of *H. sosnowskyi* started soon after the species was described by Mandenova

(1944). It was first introduced to Russia in 1947 as a highly productive fodder plant for livestock. In the 1940s and 1950s, its cultivation began in Belarus, Estonia, Latvia, Lithuania, the Ukraine and former Eastern Germany (Nielsen *et al*. 2005, Jahodová *et al*. 2007a). Later, cultivation of this plant was largely avoided because of the health risk to humans and cattle (Nielsen *et al*. 2005).

Heracleum sosnowskyi was introduced to Lithuania in the 1950s and initially cultivated in the collection of the Experimental Scientific Station of the Institute of Biology (Vilnius). In the early 1970s, it was recommended as a fodder (silage) plant for cultivation in experimental farms (Jankevičius & Lugauskas 1977, Gudžinskas 1988, 1998). In the late 1970s, it became popular among gardeners and was grown as an ornamental plant. Later, in the 1980s, *H. sosnowskyi* was recommended as a bee-plant (Balvočiūtė *et al*. 1987). Gardeners and bee-keepers significantly contributed to the spread of this species via cultivation. However, first signs of the possible invasiveness of *H. sosnowskyi* in Lithuania were noted in the early 1980s, with its intense spreading into areas surrounding the places of cultivation (Gudžinskas 1988, 1998, Gudžinskas & Lančickas, 2007). This was the first alien plant species to be included in the Lithuanian list of legally recognised invasive species in 2002 (Gudžinskas *et al*. 2014). Currently, *H. sosnowskyi* is widely distributed throughout Lithuania. In some regions, it is extremely abundant and occupies significant land areas (Gudžinskas *et al*. 2014).

Studies on *H. mantegazzianum*, *H. persicum* and *H. sosnowskyi* in their native ranges in Asia and in Europe revealed that they are three distinct, although genetically close, species (Jahodová *et al*. 2007a, 2007b). Investigations on the genetic relationships revealed a high overall genetic variability and indicated that multiple introductions of all three species are likely to have occurred (Jahodová *et al*. 2007b). Some doubts related to the taxonomic position of *H. sosnowskyi* still exist because of the difficulties to identify certain individuals (Jakubska-Busse *et al*. 2013). Some authors suppose that problems in the identification may be due to hybridisation of closely related species and the existence of introgressive populations (Jahodová *et al*. 2007a, 2007b).

Although *H. sosnowskyi* is highly invasive and widely distributed in the eastern regions of central Europe and in eastern Europe, it is much less investigated than *H. mantegazzianum*, which is mainly distributed in central and western Europe (Nielsen *et al*. 2005).

Population dynamics and age structure are important characteristics of alien plants and especially of monocarpic perennial plants, such as *Heracleum* spp. Population structure and dynamics of *H. mantegazzianum* were studied in several European countries and in different habitats (cf. e.g., Tiley *et al*. 1996, Hüls 2005, Hüls *et al*. 2007, Pergl *et al*. 2007); however, the structure of *H. sosnowskyi* populations is much less known. Studies on the demographic structure of pure stands of *H. sosnowskyi* were performed in the Syktyvkar region of Russia (Dalke *et al*. 2015). Communities and habitats occupied by *H. sosnowskyi* and their changes following invasion were investigated in Latvia (Laiviņš & Gavrilova 2003) and, to some extent, in Lithuania (Gudžinskas & Rašomavičius 2005). Recently, studies on seed morphology and anatomy in different umbels of *H. sosnowskyi* were carried out in Lithuania (Jurkonienė *et al*. 2016).

Studies on the traits of invasive plants revealed that certain reproductive characteristics are crucial for their success (Rejmánek 1996, Moravcová *et al*. 2005). The life history, population structure and growth rate of invasive species are important for our understanding of the mechanisms of invasion as well as for the selection of control and eradication measures (Myers & Bazely 2003, Ramula *et al*. 2008, Thiele *et al*. 2009). Seedling emergence and survival indicate that established populations of alien species are not seed-limited, and survival of their seedlings is related to microclimatic conditions, interspecific competition and stochastic events (Pergl *et al*. 2007).

We studied population structure and seedling dynamics of *H. sosnowskyi* in different habitats. Our results are important from a theoretical point of view and can also be helpful in selection of effective measures for management and eradication of *H. sosnowskyi*.

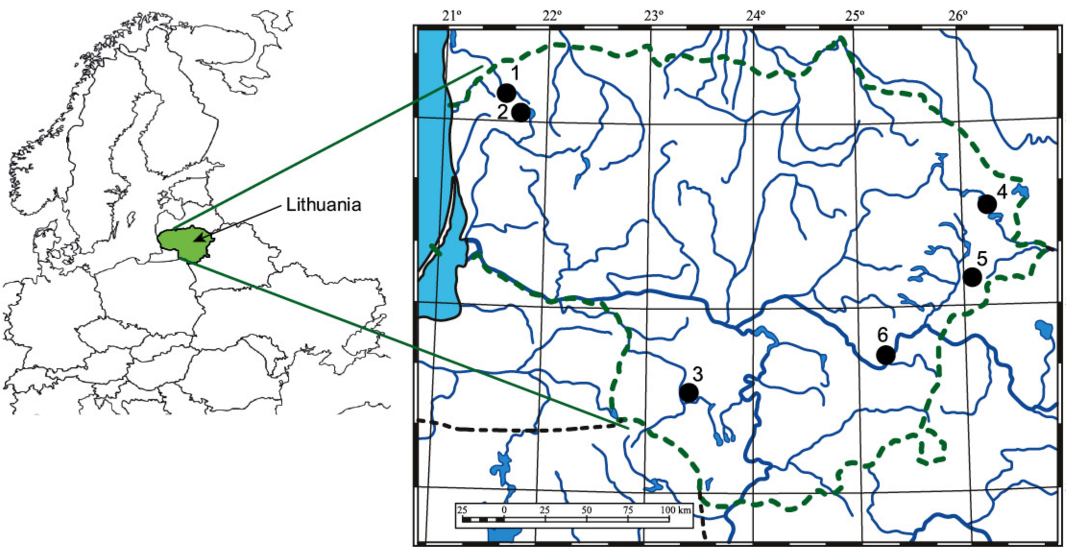

Fig. 1. Locations of the sites where population structure (1–5) and seedling survival (6) of *Heracleum sosnowskyi* were studied. Site numbers correspond to the numbers in Table 1.

Material and methods

Study species

Heracleum sosnowskyi is native to central and eastern Greater Caucasus as well as to western, central, eastern and southwestern Transcaucasia and northeastern Turkey (Jahodová *et al*. 2007a). It is a monocarpic perennial herb, 2.0–3.5 m high, occasionally up to 4.5 m, with a thick tap root. Leaves of mature individuals are compound, large, with 1.0–1.5-m-long, hollow petioles. Flowers are arranged in compound umbels up to 80 cm across, with the terminal umbel being the largest, surrounded by somewhat smaller satellite umbels. Flowers are hermaphrodite and insect-pollinated, although self-pollination has also been registered (Jahodová *et al*. 2007a). Flowering in the study area occurs from late June to late July (Gudžinskas 1998). Fruits (schizocarps) are oval-elliptical and split into two winged mericarps. Seeds germinate and seedlings start to emerge usually at the beginning of April.

Study sites

Population structure of *H. sosnowskyi* was studied at five sites: Mosėdis, Plateliai, Mokolai, Rojus, Cirkliškis (sites 1–5; cf. Table 1 and Fig. 1), situated in areas with the heaviest

Table 1. Location of the study sites and characteristics of their habitats.

Site no.	Site name and location	Elevation (m a.s.l.)	Habitat type (duration of abandonment in years) and code*
1	Mosėdis (Skuodas District, 56.16167°N, 21.58000°E)	58	unmanaged mesic grassland (2), E2.7
2	Plateliai (Plungė District, 56.03833°N, 21.81167°E)	170	anthropogenic herb stand, E5.1
3	Mokolai (Marijampolė District, 54.59417°N, 23.32139°E)	66	unmanaged mesic grassland (3), E2.7
4	Rojus (Ignalina District, 55.52417°N, 26.36944°E)	160	unmanaged mesic grassland (7), E2.7
5	Cirkliškis (Švenčionys District, 55.11639°N, 26.13417°E)	209	anthropogenic herb stand, E5.1
6	Visoriai (city of Vilnius, 54.75242°N, 25.25554°E)	161	unmanaged mesic grassland, E2.7

* cf. Davies *et al.* 2004 and later corrections and amendments at https://www.eea.europa.eu/data-and-maps/data/eunis-habitat-classification.

invasion of this species. The sites in Mosėdis, Mokolai, Rojus were in unmanaged mesic grasslands (formerly cultivated meadows abandoned for 2, 3 and 7 years, respectively), and in Plateliai, Cirkliškis in anthropogenic herb stands on wastelands (Table 1). The habitats were identified and named after the *EUNIS Habitat Classification* (Davies *et al*. 2004), with later corrections and amendments (https://www.eea.europa.eu/data-and-maps/data/eunis-habitat-classification).

The most abundant herb species at the Mosėdis, Mokolai and Rojus sites, apart from the dominant *H. sosnowskyi*, were *Dactylis glomerata*, *Festuca pratensis*, *F. rubra*, *Phleum pratense*, *Poa pratensis*, *Ranunculus repens*, *Taraxacum officinale* and *Vicia cracca*. At the Plateliai and Cirkliškis sites, again excluding *H. sosnowskyi*, the most abundant were *Aegopodium podagraria*, *Anthriscus sylvestris*, *Chaerophyllum aromaticum*, *Chelidonium majus*, *Geum urbanum* and *Urtica dioica*. The site in a wasteland in Cirkliškis was situated in an area where *H. sosnowskyi* was cultivated in the 1970s. The *H. sosnowskyi* stand in Plateliai was mowed once a year (at the end of June) during two years prior to the investigation; this site was therefore selected to reveal the effect of mowing on the population structure of this species.

The total herb-layer coverage values (including coverage of *H. sosnowskyi*) at the Mosėdis, Mokolai and Rojus sites ranged from 95% to 98%, whereas at the Plateliai and Cirkliškis sites, they were 85% and 90%, respectively. The coverage of bryophytes in all communities was insignificant (ca. 1%), except at the Cirkliškis site, where they covered about 10% of the soil surface. Mean coverage of *H. sosnowskyi* at the study sites ranged from 45% to 60%.

Survival of *H. sosnowskyi* seedlings was studied at Visoriai (site 6; cf. Table 1 and Fig. 1). The area was densely covered by herbs (mean coverage 93%) and sparsely of bryophytes (ca. 1%). The most abundant herb species in the community were *Achillea millefolium*, *Carex pallescens*, *Dactylis glomerata*, *Deschampsia cespitosa*, *Galium mollugo*, *Poa pratensis*, *Rumex acetosa*, *Stellaria graminea*, *Veronica chamaedrys* and *Vicia cracca*. The meadow was not mown for at least three years prior to the investigation.

Population structure

Heracleum sosnowskyi population structure studies were carried out between 2 and 19 July 2014 (sites 1–5; cf. Table 1 and Fig. 1). Based on their morphological features, individuals were assigned to one of the four groups: seedlings, immature vegetative, mature vegetative and generative.

Seedlings included individuals grown from seeds in the study year. Most of the seedlings during the study still had green, occasionally already wilted, seed leaves, developed from the cotyledons. Immature vegetative individuals included plants grown from seeds of at least one year before (i.e., 2013 or earlier). Immature vegetative individuals were notably smaller than the mature ones, and had simple leaves with lobate margins or small compound leaves, which were still substantially different from the leaves characteristic for mature vegetative or generative plants. Individuals with large compound leaves, which were at least half of the size or of the same size as leaves of generative plants, but without inflorescences, were treated as mature vegetative. This group included plants being at least two years old. Plants with large leaves, developed stems and inflorescences were treated as generative individuals. The same developmental stages but named differently were also used in other studies: e.g. small, middle, or large vegetative and reproductive individuals in Hüls *et al*. (2007); or seedlings, juveniles, rosette plants and flowering plants in Pergl *et al*. (2007).

At each site, 20 sampling plots (100 in total) of 1 m^2 (1 × 1 m), delimited with a wooden frame and arranged in transects from the edge of the *H. sosnowskyi* stand towards its centre were established. Prior to counting the individuals, percentage covers of *H. sosnowskyi* and other herb and moss species were visually evaluated in each sampling plot divided for that purpose into 10 × 10 cm subplots. The numbers of individuals belonging to each of the four groups mentioned above group were recorded in each sampling plot of each site.

Seedling survival

Seedling survival was evaluated in 2014 at the

Visoriai site in ten permanent, 0.25 m^2 (0.5 × 0.5 m) sampling plots arranged in a line, and located 1 m apart from each other. The area for the plots was 2 m from the edge of a dense stand and was free of both mature vegetative and generative individuals. The aim was to eliminate the effect of large individuals of *H. sosnowskyi* and to estimate the rate of seedling survival in a newly invaded area. Sampling plots were marked with plastic sticks placed in each corner. Seedlings in each sampling plot were counted from spring to autumn at approximately one-month intervals (21 April, 20 May, 23 June, 22 July, 19 August and 12 September). For counting purposes, each plot was divided with 0.5-m-long sticks into 25 equal subplots. Almost all *H. sosnowskyi* plants wilted in October so further counting was therefore not possible.

Statistical analyses

The normality of data distribution was evaluated using Shapiro-Wilk's test. As all data sets were non-normally distributed, non-parametric tests were applied. Pairwise comparisons were carried out using a Mann-Whitney *U*-test. Differences between several samples were tested with a non-parametric Kruskal-Wallis (K-W) χ^2-test. Spearman's rank-order correlation was used to test for dependencies between data sets (density of seedlings, density of immature and mature individuals and the coverage of native herbs). Differences (correlations) were considered significant at $p < 0.05$. In the following, numerical results are reported as means ± SDs. All calculations were performed in PAST 3.10 (Hammer *et al*. 2001).

Results

Seedling density and population structure

Seedling density

Seedling density of *H. sosnowskyi* varied among the sites, habitat types (managed *vs*. unmanaged) and sampling plots within the same site (cf. Table 2). The highest number of seedlings in a 1-m^2 sampling plot, 222, was found at the Cirkliškis site, while the minimum, 1 seedling, was recorded in the sampling plots in Plateliai and Mokolai (cf. Table 2). The seedlings were more evenly distributed and their overall density was lower in the unmanaged mesic grassland habitats than in the anthropogenic herb stands (cf. Table 2).

In the recently abandoned mesic grasslands in Mosėdis and Mokolai (cf. Table 2), seedling densities did not differ (Mann-Whitney *U*-test: $p > 0.05$; Table 2). However, seedling density in the unmanaged mesic grassland abandoned for a longer time (Rojus site; abandoned for 7 years; cf. Table 1) was significantly higher than at Mosėdis (Mann-Whitney *U*-test: $U = 109.5$, $n = 20$, $p < 0.05$) and Mokolai (Mann-Whitney *U*-test: $U = 116.0$, $n = 20$, $p < 0.05$). The lowest seedling density (4.65 ± 3.98 per m^{-2}) was found in the managed anthropogenic herb stand at in Plateliai, whereas in the unmanaged habitat of the same site type in Cirkliškis, seedling density was the highest (79.65 ± 45.53 per m^{-2}) and differed significantly (Mann-Whitney *U*-test: $U = 0$, $n = 20$, $p < 0.001$) from that at the Plateliai and other study sites.

There was no correlation between seedling density and herb coverage (Spearman's $r = 0.06$,

Table 2. Seedling densities at the study sites.

Site	Total number	Minimum	Maximum	Mean ± SD (per 1 m^2)
1. Mosėdis (unmanaged mesic grassland; abandoned for 2 years)	447	4	50	22.35 ± 14.47
2. Plateliai (managed anthropogenic herb stand)	93	1	16	4.65 ± 3.76
3. Mokolai (unmanaged mesic grassland; abandoned for 3 years)	469	1	56	23.45 ± 15.23
4. Rojus (unmanaged mesic grassland; abandoned for 7 years)	776	9	77	38.80 ± 20.52
5. Cirkliškis (unmanaged anthropogenic herb stand)	1593	27	222	79.65 ± 45.53
Unmanaged mesic grasslands (sites 1, 3, 4 pooled)	1692	1	77	28.20 ± 18.31
Anthropogenic herb stands (sites 2, 5 pooled)	1686	1	222	42.15 ± 49.59

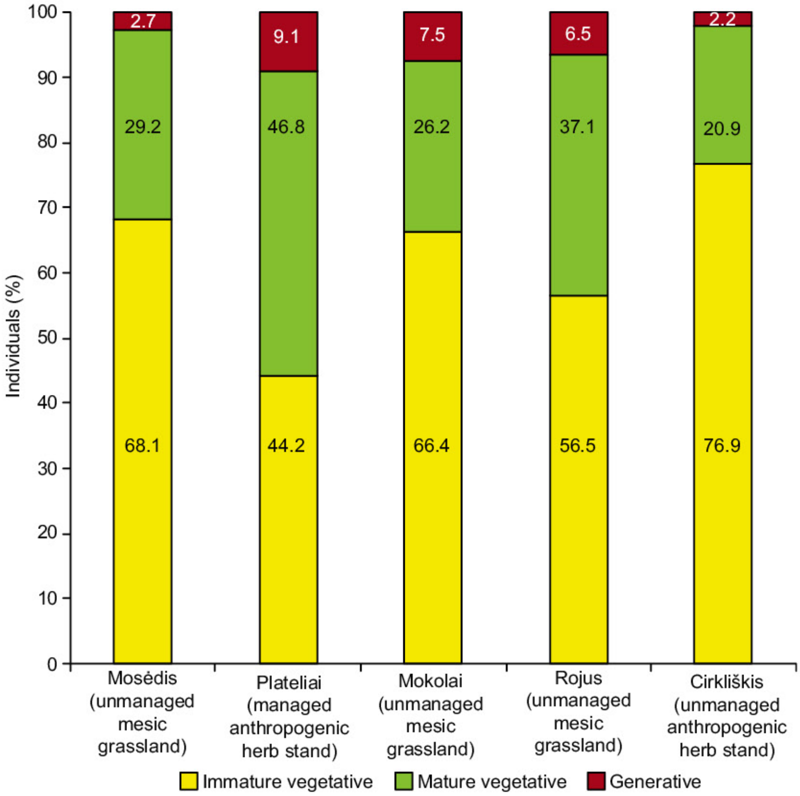

Fig. 2. Proportions of immature vegetative, mature vegetative and generative individuals in the studied populations of *Heracleum sosnowskyi*. Numbers in the bars are percentages of individuals in each stage.

$n = 100$, $p > 0.05$). However, we found a positive correlation between seedling density and the density of *H. sosnowskyi* individuals at higher developmental stages (Spearman's $r = 0.44$, $n = 100$, $p < 0.001$).

Population structure

A total of 939 individuals of *H. sosnowskyi* in all development stages (except the seedling stage) were recorded at the study sites, their density in the unmanaged mesic grasslands (sites 1, 3 and 4) being 8.38 ± 6.52 indiv. m^{-2}, and in anthropogenic herb stands (sites 2 and 5), 10.90 ± 10.25 indiv. m^{-2}, with no significant difference between the habitat types.

There was a significant difference (Mann-Whitney U-test: $U = 13.5$, $n = 20$, $p < 0.001$) in the density of all individuals between the managed and unmanaged anthropogenic herb stands (sites 2 and 5: 3.85 ± 2.34 and 17.95 ± 10.27 indiv. m^{-2}, respectively). The densities in the unmanaged mesic grasslands (sites 1, 3 and 4) were smaller, and a significant difference was found among habitats, depending on the duration of abandonment (K-W χ^2-test: $\chi^2 = 8.41$, df = 2, $p < 0.05$).

In the entire *H. sosnowskyi* populations, a small fraction of individuals was in a generative phase (Fig. 2). In the managed anthropogenic herb stands (site 2), mature vegetative and generative individuals dominated (46.8% and 9.1%, respectively), whereas in the unmanaged anthropogenic herb stand (site 5), 76.9% of all *H. sosnowskyi* individuals were immature vegetative plants.

Immature vegetative individuals

The total number of immature vegetative individuals ranged from 34 to 276 per site, and from 0 to 34 per sampling plot (cf. Table 3). Their overall density in the unmanaged mesic grasslands (sites 1, 3 and 4) was 5.35 ± 4.71 indiv. m^{-2}, and in the anthropogenic herb stands (sites 2 and 5) 7.75 ± 8.94 indiv. m^{-2}. Although the latter value was higher, the difference was not significant (Mann-Whitney U-test: $p > 0.05$). However, the density in the unmanaged anthropogenic herb stand alone (site 5) differed significantly (Mann-Whitney U-test: $U = 261.5$, $n = 20$, $p < 0.001$) from the overall density in the unmanaged mesic grasslands (sites 1, 3 and 4).

The lowest and highest densities (1.70 ± 1.30 and 13.80 ± 9.23 indiv. m^{-2}, respectively) were recorded in the managed and unmanaged anthropogenic herb stands (Plateliai and Cirkliškis), respectively.

In the unmanaged mesic grasslands (sites 1, 3 and 4), the densities ranged from 3.55 ± 3.53 to 7.70 ± 6.22 indiv. m^{-2} (Table 3), the only significant difference being that between the values for the Mosėdis and Mokolai sites (Whitney U-test: $U = 113$, $n = 20$, $p < 0.05$).

Mature vegetative plants

The total number of mature vegetative individuals at the study sites ranged from 28 to 75, in the sampling plots being from 0 to 12. The numbers in the unmanaged mesic grasslands (sites 1, 3 and 4) and in the anthropogenic herb stands (sites 2 and 5) were rather similar (2.62 ± 2.48 and 2.77 ± 2.44 indiv. m^{-2}, respectively). However, the numbers and densities differed significantly between the managed and unmanaged anthropogenic herb stands (sites 2 and 5) (Mann-Whitney $U = 109$, $n = 20$, $p < 0.05$), the values being twice lower for the managed than for the unmanaged anthropogenic herb stands (Table 3).

The density of mature vegetative plants in the unmanaged mesic grassland in Mokolai significantly differed (Whitney U-test: $U = 113$, $n = 20$, $p < 0.05$) from that of the other two studied sites in the same habitat type (Mosėdis and Rojus).

Generative individuals

The number of generative individuals of *H. sosnowskyi* was similar at all the sampled sites and ranged from 6 to 11 (Table 3). In the sampling plots, 0–1 generative plants were recorded. The

Table 3. Numbers of *Heracleum sosnowskyi* plants at the study sites (mean ± SD per plot (20 plots per site) in parentheses).

Site	Immature vegetative	Mature vegetative	Generative
1. Mosėdis (unmanaged mesic grassland)	154 (7.70 ± 6.22)	66 (3.30 ± 3.33)	6 (0.30 ± 0.57)
2. Plateliai (managed anthropogenic herb stand)	34 (1.70 ± 1.30)	36 (1.80 ± 1.54)	7 (0.35 ± 0.67)
3. Mokolai (unmanaged mesic grassland)	71 (3.55 ± 3.53)	28 (1.40 ± 1.57)	8 (0.40 ± 0.99)
4. Rojus (unmanaged mesic grassland)	96 (4.80 ± 2.86)	63 (3.15 ± 1.81)	11 (0.55 ± 0.76)
5. Cirkliškis (unmanaged anthropogenic herb stand)	276 (13.80 ± 9.23)	75 (3.75 ± 2.81)	8 (0.40 ± 0.75)
Unmanaged mesic grasslands (sites 1, 3, 4 pooled)	321 (5.35 ± 4.71)	157 (2.62 ± 2.48)	25 (0.42 ± 0.79)
Anthropogenic herb stands (sites 2, 5 pooled)	310 (7.75 ± 8.94)	111 (2.77 ± 2.44)	15 (0.37 ± 0.70)

Table 4. Numbers of seedlings in sampling plots, their total numbers and seedling survival (%) until the end of the trial.

Date	Sampling plot										Total
	1	2	3	4	5	6	7	8	9	10	
21 April	169	215	84	162	116	157	218	327	271	305	2024
20 May	116	65	48	134	64	113	128	288	112	262	1330
23 June	102	62	41	122	60	102	112	117	99	111	928
22 July	74	50	38	76	39	67	58	94	63	71	630
19 August	32	28	23	30	24	27	29	36	32	41	302
22 September	5	3	9	12	3	9	7	11	9	16	84
Survival (%)	2.96	1.40	10.71	7.41	2.59	5.73	3.21	3.36	3.32	5.25	4.15

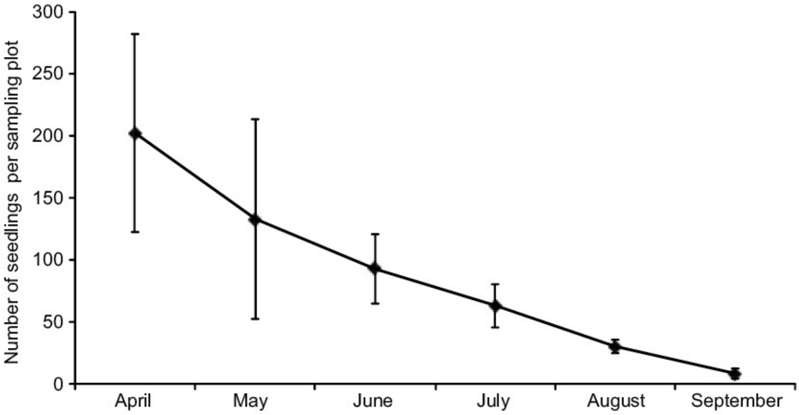

Fig. 3. Decrease in the seedling number (mean ± SD) per sampling plot (0.25 m^2) between April and September 2014.

densities of generative individuals in the unmanaged mesic grasslands and in the anthropogenic herb stands were rather similar (0.42 ± 0.79 and 0.37 ± 0.70 indiv. m^{-2}, respectively). They did not differ between the managed and unmanaged anthropogenic herb stands (sites 2 and 5) (Mann-Whitney *U*-test: $p > 0.05$) as well as among the unmanaged mesic grasslands (sites 1, 3 and 4) (K-W χ^2-test: $\chi^2 = 1.23$, df = 2, $p > 0.05$).

Seedling survival

At the start of the study in April, in the ten sampling plots the total number of seedlings was 2024 (range = 84–327, mean ± SD = 202.40 ± 79.90 per plot, and mean ± SD = 809.60 ± 319.59 per m^{-2}) (cf. Table 4 and Fig. 3).

The first significant decrease in the number of seedlings occurred between April and May (Mann-Whitney *U*-test: $U = 22.5$, $n = 10$, $p < 0.05$) when their numbers decreased from 2024 to 1330 (by 34.29%). During the following two months, seedling mortality rates were similar: from May to June 30.23%, and from June to July 32.11%. During the next two months, the decrease was more pronounced (52.06% from July to August and 72.19% from August to September).

Seedling survival rates at the end of the study (in September) ranged from 10.71% to 1.40%, whereas the overall survival rate was 4.15% (Table 4). Thus, the numbers of seedlings that survived until the second half of September were 8.40 ± 4.09 per plot or 33.60 ± 16.35 per m^{-2}.

Discussion

Seedling density

Studies of the closely related *H. mantegazzianum* revealed significantly higher seedling densities than those found for *H. sosnowskyi* in our study in Lithuania (Table 2). The maximum density of 3700 seedlings m^{-2} was recorded in the Czech Republic, with mean density values ranging from 671.80 ± 439.2 to 1613.9 ± 1322.1 per m^{-2} (Pergl *et al*. 2007). Seedling densities of *H. mantegazzianum* in Germany (Hüls 2005) and Scotland (Tiley *et al*. 1996) were 504.0 ± 363.3 per m^{-2} and 400 per m^{-2}, respectively. The mean density of *H. sosnowskyi* seedlings in spring in the Syktyvkar region in Russia was 791.7 per m^{-2} (median 509 per m^{-2}) (Dalke *et al*. 2015).

Differences in the density of *H. mantegazzianum* seedlings in central Europe and of *H. sosnowskyi* seedlings in Lithuania might be due to different conditions at the study sites. In the Czech Republic, studies were carried out in dense stands of *H. mantegazzianum* (Moravcová *et al*. 2007b, Pergl *et al*. 2007), whereas the sampling plots in Lithuania were arranged from the edge of the stand towards its centre with the densest part of the population.

The seedling numbers and densities found in our study are probably lower as compared with those in the populations of *H. mantegazzianum* studied in the Czech Republic, Germany and Scotland also because of the time when the study was performed. We conducted our research in the first half of July, whereas in the Czech

Republic, seedlings were counted in April (Pergl *et al*. 2007).

In our study, the most intense decrease in seedling numbers occurred between April and June (Fig. 3 and Table 4). The number of *H. sosnowskyi* seedlings in April in Lithuania was 532.00 ± 322.30 per m^{-2}, which is close to the values recorded for of *H. mantegazzianum* in Germany (Hüls 2005) and Scotland (Tiley *et al*. 1996).

Seedling density depends on the availability of viable seeds in the soil seed-bank. Studies on the soil seed-bank of *H. sosnowskyi* in Lithuania showed the non-dormant seed densities at Santariškės, Bajorai and Visoriai to be 7986 ± 3035 seeds m^{-2} in spring, 255 ± 180 seeds m^{-2} in summer and 4851 ± 1616 seeds m^{-2} in autumn after seed release (Moravcová *et al*. 2007a). Thus, over time, seed density changes significantly depending on the density of mature individuals, weather conditions during seed release, habitat characteristics, etc. Seed density directly affects the density of seedlings in spring (Moravcová *et al*. 2007b, Pergl *et al*. 2007), which explains the significantly lower seedling density at the Plateliai site (anthropogenic herb stand; Table 2). This site was mown once a year at the end of June for two years prior to the study. Thus, the soil seed-bank was supplied by seeds from regrown individuals or through seed wind-dispersion from unmanaged neighbour stands 60–100 m from the study site. The local soil seed-bank is significantly depleted each spring because the seeds of *H. sosnowskyi* break dormancy at almost the same time and massively germinate in early spring. Furthermore, 98.2% of the total seed-bank of *H. sosnowskyi* are located in the upper soil layer (0–5 cm), with only a small percentage in the deeper soil layers (Moravcová *et al*. 2007a). A reduced seed supply significantly influences the seedling density within a population.

Habitat abandonment significantly contributes to the spread and invasion of alien plant species (cf. e.g., Meiners *et al*. 2001, Hüls *et al*. 2007, Kuhman *et al*. 2011, Wang *et al*. 2016). Our study confirmed that the long-term abandonment of mesic meadows promotes development of denser *H. sosnowskyi* stands. In contrast, extensive management for even a relatively short time can reduce the density of monocarpic invasive species, especially that of young individuals.

Population structure

The overall density of *H. sosnowskyi* plants (immature vegetative, mature vegetative and generative individuals; seedlings were excluded) in the studied populations in Lithuania was 8.20 ± 7.58 indiv. m^{-2}. At individual sites it ranged from 3.85 to 17.95 indiv. m^{-2}. Studies on population structure and density of *H. mantegazzianum* in the Czech Republic revealed the mean density (across different years and sites) of 5.40 indiv. m^{-2} (Pergl *et al*. 2007), whereas in Germany, the mean density was 7.70 indiv. m^{-2} (Nehrbass *et al*. 2006). Although the density of the studied *H. sosnowskyi* populations in Lithuania was higher than the density of *H. mantegazzianum* in central Europe, the differences are not great and can be explained by differences in the structure of individual stands of *Heracleum* species. Populations of the tall *Heracleum* species are usually densest in their centres and sparser towards the margins (Hüls *et al*. 2007). Thus, selection of sampling plots may affect the results.

We found the highest and lowest densities of immature *H. sosnowskyi* individuals in the anthropogenic herb stands at Cirkliškis and Plateliai, respectively (Table 3). Mowing of the Plateliai site during a period of two years before our study, possibly led to the depletion of the soil seed-bank, which may explain the fact that the proportion of immature vegetative individuals substantially decreased, comprising 44.2% of all individuals (Fig. 2). On the other hand, this population was characterised by a significantly higher proportion of both mature vegetative and generative individuals (46.8% and 9.1%, respectively). In the unmanaged habitat of the same type in Cirkliškis, immature vegetative individuals dominated (76.9%), whereas the share of mature vegetative and generative individuals was lower (Fig. 2). The increase in the proportion of mature vegetative and generative individuals in the managed anthropogenic herb stand was determined by the biological traits of the species. Under unfavourable conditions (e.g. shaded or dry sites, regularly mown or grazed, etc.), flowering of the closely related *H. mantegazzianum* was postponed until sufficient reserves were accumulated; under such conditions, plants can live for at least 12 years until flowering (Nielsen *et al.* 2005, Pergl *et al.* 2006). This may also be typical to *H. sosnowskyi*. Thus, while recruitment because of a limited seed-bank is low, the proportion of mature individuals in the population increases. Therefore, adequate management of *H. sosnowskyi* populations via cutting can reduce recruitment rates and inhibit the spread of the species. However, this method will not eliminate the species rapidly, even in cases where there is no seed supply from other areas.

Population density and age structure in the studied unmanaged mesic meadow sites were less contrasting than in the anthropogenic herb stands. Two of the studied populations, in Mosėdis and Mokolai, were established quite recently, as meadow habitats were abandoned for 2–3 years. Therefore, these populations were at the phase of intense expansion and took an intermediate position between dense and open stands (Hüls *et al.* 2007). The proportion of immature vegetative and mature vegetative individuals at both sites was similar (Fig. 2). A higher density of *H. sosnowskyi* individuals was recorded in the Rojus site. This population occupied almost all suitable areas of the unmanaged mesic grasland, which had been abandoned for more than five years. Almost the entire area of the meadow was occupied by a dense stand of *H. sosnowskyi*, and the proportion of mature vegetative individuals was higher (37.1%; Fig. 2) than in the other two studied grassland populations. The increase in numbers of mature vegetative individuals was probably a result of infraspecific competition and, therefore, prolonged the pre-generative period of the development (Nielsen *et al.* 2005, Pergl *et al.* 2006, Hüls *et al.* 2007).

Abandonment of anthropogenic herb stand habitats and mesic herb meadow habitats promoted the formation of dense stands of *H. sosnowskyi*, with a moderate equilibrium between all development groups, whereas extensive management reduced recruitment and increased the fraction of mature vegetative and generative individuals. These results lead us to infer that even extensive or occasional management of habitats invaded by *H. sosnowskyi* may slow down its expansion.

Seedling survival

The seedling survival rate in our study was 4.15% (Table 4), which was higher than in the Czech Republic and in Germany, where seedling survival rates were below 1% (Pergl *et al.* 2007). However, the mean density of immature individuals (6.31 indiv. m^{-2}) in our study is similar to the seedling survival rate until the following year in the Czech Republic (Pergl *et al.* 2007) and Germany (Hüls 2005). Higher seedling survival rates in our study could have resulted from plot selection. Plots in our study were outside the stand with mature vegetative and generative individuals of *H. sosnowskyi*; thus, seedlings were not affected by infraspecific competition, which affects survival rates and development of individuals, especially during the early stages of their life cycle (e.g. Meekins & McCarthy 2002, Pergl *et al.* 2006, 2007).

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