Long-term survival in soil of seed of the invasive herbaceous plant *Heracleum mantegazzianum*

Dlouhodobé přežívání semen invazního druhu *Heracleum mantegazzianum* v půdě

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Seed persistence in soil is an important ecological trait enabling a species to survive at a particular site. How long the seed persists depends on its physical and physiological characteristics as well as on biotic and abiotic environmental conditions. In alien species, the ability to develop a persistent seed bank is associated with their ability to naturalize and become invasive. We carried out an experiment to find out how long the seeds of *Heracleum mantegazzianum*, one of the most invasive monocarpic species in Europe, are able to persist in soil and explore the effect of environmental conditions on seed depletion over a long period of time. The seeds were buried at 10 localities in different regions of the Czech Republic to cover a range of climatic, edaphic and geographic conditions. After seven years of burial, 0.1% of the seed of *H. mantegazzianum*, averaged across the localities, were viable, and none survived at five localities, at one of which the seed bank was completely depleted after five years and at one already after two years. The highest recorded survival at the end of the burial period was 0.5% of seed. In general, the average seed-bank survival was very low after five years and never exceeded 1%. We found a significant correlation between the percentage seed bank depletion and the content of total carbon and organic carbon; the effects of other soil characteristics, climatic and geographical factors were not significant. High percentages of seed persisted after the first year at localities with a low carbon content but the percentage depletion after seven years was slower at localities with a high carbon content. In addition, low carbon content and high seed survival after the first year was recorded at localities with nutrient poor soils. The course of seed bank depletion in *H. mantegazzianum* corresponds to its classification as short-term persistent. Therefore, monitoring well beyond the reported period of seed bank persistence is recommended after full eradication of this species from a site.

Keywords: Czech Republic, giant hogweed, long-term survival, plant invasion, seed bank, seed burial

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Introduction

Invasive plants represent the group of alien species with most profound negative impacts on biodiversity and ecosystem functioning (Vilà et al. 2010, Rumlerová et al. 2016, Nentwig et al. 2018) and there is a large body of research explaining the invasiveness based on their ecological and biological traits. Among these, those related to reproduction are repeatedly suggested as important determinants of the success of invasive species (see Pyšek & Richardson 2007 for review, Moravcová et al. 2010, 2015, Pyšek et al. 2015). Plant species invasiveness is frequently associated with rapid dispersal and high production of seed that can persist in the soil for a long time. Some studies addressed the role of soil seed bank in relation to invasiveness (see Gioria et al. 2012 for review) and available data from seed bank studies, based on a comparison of native/alien and invasive/non-invasive congeners or confamilials, indicate that aliens and successful invasive species often have larger and longer-persisting soil seed banks (Pyke 1990, Honig et al. 1992, Radford & Cousens 2000, Van Clef & Stiles 2001, Phillips & Murray 2012). Recently, this notion was strongly supported by analyses of large data sets comprising hundreds of species that point to the generally important role of persistent seed banks and early germination in plant invasions (Gioria & Pyšek 2017, Gioria et al. 2018).

Heracleum mantegazzianum Sommier et Levier (*Apiaceae*), which can be 4–5 m height is the tallest herbaceous plant in Europe (Jahodová et al. 2007b) and the most problematic invasive species in many countries (Jahodová et al. 2007a, b), including the Czech Republic (Pyšek 1991, Pyšek & Pyšek 1995), where it is also classified as invasive (Pyšek et al. 2012, Pergl et al. 2016). Its invasion of plant communities, including those in seminatural habitats, reduces native-species seed-bank richness and density (Gioria & Osborne 2009, Gioria et al. 2014). *Heracleum mantegazzianum* is a monocarpic species that reproduces exclusively by seed and for such species the knowledge of its seed ecology is crucial for understanding its invasiveness (Pyšek et al. 2007a, b). Previous studies focused on the germination of this species (Grime et al. 1981, Nikolaeva et al. 1985, Tiley et al. 1996, Moravcová et al. 2006) and its soil seed bank dynamics over the course of a year (Krinke et al. 2005), but there are no long-lasting experiments for this species in which seed was buried in the field under varying climatic conditions.

Seed persistence in the soil is an important trait in plants' life history that is affected by species' physical and physiological characteristics (dormancy, germination, seed size; see e.g. Baskin & Baskin 2014 for the review) and also by biotic and abiotic environmental conditions (Pakeman et al. 2012, Abedi et al. 2014, Basto et al. 2015). Long et al. (2009) confirm that water and temperature are the main factors affecting seed longevity in the soil, which is further influenced by microbial activity (Schafer & Kotanen 2003). High temperature and water content of soil support microbial activity and turnover of organic material, leading to shorter seed persistence. Pakeman et al. (2012) report prolonged seed persistence in soils with a higher pH, low moisture content and a low soil carbon to nitrogen ratio. Basto et al. (2015), on the other hand, report that the abundance of seed in the seed bank increases in soils with decreasing pH and low concentration of nutrients. Abedi et al. (2014) also report that seed longevity varies with environmental factors, including soil moisture and its interaction with the substrate. The numerous factors that determine the ecophysiology of seed persistence in soil are thus involved and seed persistence is a complex expression of seed and species characteristics that are modified by the environment (see Long et al. 2015).

In this study we buried seed in order to identify (i) how long and what percentage of the seed of *H. mantegazzianum* is able to persist in the soil, and (ii) whether this persistence is affected by environmental conditions, such as climate and soil characteristics considered to be important for seed persistence in the soil.

Methods

Seed collection

Seeds were collected in August 2002 from extensive stands of *H. mantegazzianum* at seven sites in the Slavkovský les Protected area in the western part of the Czech Republic (see Krinke et al. 2005, Moravcová et al. 2005 for a detailed description of sites and populations). Seed was collected from the terminal umbels and a mixed sample of seed from seven localities was used in the burial experiments. The seed collected was dried for five days at room temperature and then stored in paper bags in an unheated room (~10–15 °C) until the beginning of the experiment.

Germination experiment

Before burial, a subsample of the seed mixture was tested for viability by germination and staining non-germinated seed with tetrazolium (Baskin & Baskin 2014). For germination we used a sample of seed (four replicates of 25) that visually appeared to be healthy. Seeds were first cold-stratified for two months at 3–5 °C and then germinated over one month at 20/5 °C (12h day/12h night regime). The viability of seed was between 98–100%.

Burial experiment

Only healthy seed (with estimated viability of 98–100%) was used in the burial experiment. The seeds were placed in 10 × 10 cm polyamide bags (fabric Norin) with a rectangular mesh of 266 × 162 μm, and buried at a depth of 5–10 cm in November 2002 at 10 localities in the Czech Republic. Twenty-five polyamide bags each containing 100 seeds were buried horizontally 20 cm apart at each locality. In each October, 2003, 2004, 2005, 2007 and 2009, five bags (replicates) were exhumed and the viability of the seeds tested by germination and of those that did not germinate by staining with tetrazolium. The localities for burial were selected to include the range of geographic and climatic conditions occurring in the Czech Republic (see Table 1, Electronic Appendix 1). To minimize the variation due different types of vegetation, we buried the seed in places with similar vegetation that was dominated mainly by grasses and can be characterized as mown short-grass.

Soil analyses

Soil samples were collected at each of the 10 localities (Table 1) and the content of carbon, phosphorus, nitrogen, potassium, sodium, calcium and magnesium as well as pH, dry matter, absorption capacity and soil skeleton was determined using the standard methods used in soil analysis (Tandon 2013) in the analytical laboratory of the Institute of Botany. The references to particular methods are given in Electronic Appendix 2.

Statistical analysis

Data on the long-term survival of buried seed were analysed using the percentage of viable seed (out of the 100 buried) in each bag as the dependent variable. In a linear mixed model (Crawley 2007), the year of exhumation (October 2003, 2004, 2005, 2007 and 2009) was a fixed factor and the individual localities a random factor. The simplest model was selected by backward elimination and joining of the factor levels (e.g. Crawley 2007) of the individual explanatory variables from the model. To normalize the error distribution and to homogenize the variance, all percentages were angular-transformed (e.g. Sokal & Rohlf 1995). The homogeneity of variance was checked using Cochran's test (e.g. Underwood 1997), and the fitted models by plotting standardized residuals against fitted values, and by normal probability plots (e.g. Crawley 2007).

Parameters of the depletion curves were estimated for each locality using the power function ($y = a \cdot x^b$). The rate of depletion (b) was correlated (Pearson correlation coefficient) with altitude, mean annual temperature, precipitation and soil characteristics at these localities. In addition, the correlation between the percentage of viable seed in soil after the first and last year of the experiment, and total carbon content (identified as significant factor in a previous analysis) was determined. All calculations were done in R version 3.2.1 (R Development Core Team 2015).

Results

Seed survival in the long-term burial experiment

Percentage of viable seed after 1, 2, 3, 5 and 7 years of burial at different localities in the Czech Republic is shown in Table 1. The differences in survival among years were significant, except that there were no differences between year 5 and 7 (AIC for model with all years –378.6 vs. model with years 5 and 7 combined –392.1; Table 2). This revealed that significant variation was attributed to different localities, and that the random effects should not be omitted (AIC: –390.1 vs –374.4; Table 1 and 2). All results are shown for the most parsimonous grouping of sites as shown in Table 1. Of the seeds buried in different regions on average 8.8% survived one year, 2.1% two years, 1.2% three years, 0.4% five years and 0.1% seven years (Fig. 1).

The effect of soil characteristics

We found a significant correlation between the rate of seed-bank depletion at a locality and total carbon ($r = 0.78$, $P = 0.008$) and organic carbon content of the soil ($r = 0.77$, $P = 0.007$), indicating that carbon-rich soils are associated with slower seed-bank depletion. There was a marginally significant negative correlation ($r = –0.59$, $P = 0.07$) between the percentage of seed persisting after the first year and carbon content in the soil, while after the seventh year the same relationship became significant and positive ($r = 0.83$, $P = 0.003$). The correlations with the other soil characteristics (see Electronic Appendix 3) and the climatic and geographic factors (Table 1) of the different localities were not significant.

Table 1. – Description of localities (with their geographic and climatic characteristics; C – central, N – northern, W – western, S – southern, E – eastern part of the Czech Republic) and the percentage of viable seed of *Heracleum mantegazzianum* surviving in the soil. Localities are arranged according to increasing altitude. Seed was buried in November 2002. Percentages of viable seed after 1, 2, 3, 5 and 7 years of burial at individual localities are shown. Seeds were exhumed in October 2003, 2004, 2005, 2007 and 2009 and tested for viability using tetrazolium. Numbers are the means and ranges (in brackets) of five replicates. Grouping of localities indicates the results of model simplification and the same letters are used for localities with the same depletion rate. The data from Černolice was not available because this locality was destroyed during in the course of this experiment. Mean values of survival of viable seed in the soil are shown.

No.	Locality	Region	Latitude (N)	Longitude (E)	Altitude (m a.s.l.)	Mean annual temperature (°C)	Precipitation (mm/yr)	% of viable seeds (1yr)	% of viable seeds (2yr)	% of viable seeds (3yr)	% of viable seeds (5yr)	% of viable seeds (7yr)	Grouping of localities
1	Kralupy	C	50°14'	14°19'	175	8.5	475	2.8 (1–5)	0.8 (0–2)	0	0.2 (0–1)	0	a
2	Koda	C	49°56'	14°7'	299	8.5	525	3.0 (1–5)	2.2 (1–5)	0.8 (0–2)	0.2 (0–1)	0.2 (0–1)	a
3	Průhonice	C	49°59'	14°34'	303	8.5	625	19.8 (6–30)	1.8 (0–6)	2.2 (0–4)	0	0	b
4	Plzeň	W	49°42'	13°19'	337	7.5	525	13.2 (2–18)	0.4 (0–1)	0.6 (0–2)	0.4 (0–2)	0.2 (0–1)	b
5	Vroutek	N	50°11'	13°23'	337	7.5	475	2.0 (1–3)	0	0	0	0	a
6	Kyjov	N	50°55'	14°28'	376	7.5	850	2.2 (0–5)	2.4 (1–4)	2.2 (1–4)	0.2 (0–1)	0	a
7	Černolice	C	49°55'	14°19'	400	7.5	525	3.0 (0–5)	1.2 (0–2)	1.2 (0–2)	0.6 (0–2)	n.a.	a
8	Lužnice	S	49°5'	14°45'	419	7.5	625	1.4 (0–6)	2.0 (1–4)	1.0 (0–2)	0.8 (0–2)	0.5 (0–1)	a
9	Broumov	E	50°38'	16°16'	520	6.5	850	34.8 (13–68)	7.8 (5–12)	2.8 (1–6)	0.6 (0–2)	0	d
10	Žitný	W	50°03'	12°37'	787	5.5	850	6.0 (2–9)	2.0 (1–3)	0.8 (0–1)	1.0 (0–2)	0.2 (0–1)	c
	Mean							8.8	2.1	1.2	0.4	0.1	

Table 2. – Results of mixed model with localities as a random factor and years as fixed effect. Number of observations was 243 with final five localities after model simplification and grouped years 5 and 7 (see Results for details). All differences between groups were significant based on deletion tests.

Factor	Value	t-value	P
Year 1	0.28	7.97	< 0.001
Year 2	0.14	–6.96	< 0.001
Year 3	0.11	–8.56	< 0.001
Years 5+7	0.04	–13.04	< 0.001

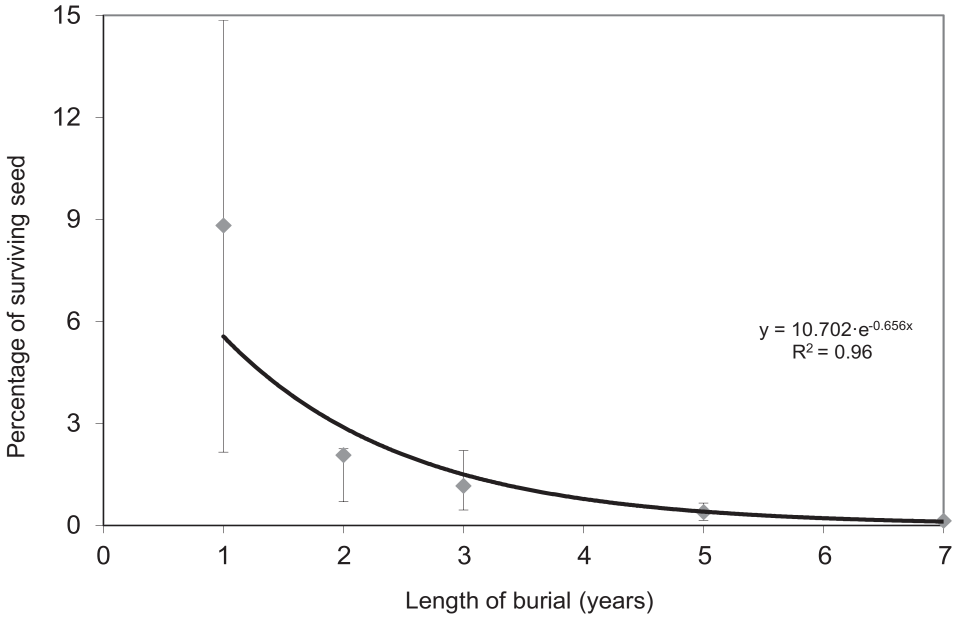

Fig. 1. – Mean percentage of viable seed of *Heracleum mantegazzianum* after 1, 2, 3, 5 and 7 years of burial. The data are year averages across localities and replicate samples (see Table 1 for data). Error bars indicate the range between the 25 and 75% of the means per site.

Discussion

After seven years of burial, 0.1% of the seed of *Heracleum mantegazzianum*, averaged across various soil and climatic conditions in the Czech Republic, still persisted in the soil. At five localities there were no surviving seeds – at one of them already after two years and at another after five years. The highest recorded value at the end of the monitoring period was 0.5% surviving seed. In general seed-bank survival was already very low after five years and never exceeded 1% (Table 1).

These results are in accordance with those of Andersen & Calow (1996) who sampled soil beneath stands of *H. mantegazzianum* in Denmark where these plants were controlled by sheep grazing. These authors did not find any viable seeds after seven years of grazing. Our results are also consistent with the results of Krinke et al. (2005) who studied the natural soil seed bank dynamics of *H. mantegazzianum* in heavily infested areas in the Czech Republic and conclude that the soil seed bank of this species is short-term persistent (i.e. persisting for 1–5 years sensu Thompson et al. 1997).

Seed depletion decreased exponentially over time and most seed germinated in the first spring, reflecting that this species has a morphophysiological dormancy (Moravcová et al. 2006, Baskin & Baskin 2014) and cold stratification in winter is necessary for embryo growth and seed germination. It is evident that a small amount of seed can stay dormant (either physiologically or morphologically) in the soil or do not germinate for some reason for several years. The survival time appears to be influenced by specific environmental and soil conditions. The seed bank at one locality was depleted as early as in the second year; this locality was characterized by a high mean temperature, a high nutrient content and the lowest precipitation of all the sites.

The only environmental factor significantly related to seed bank depletion was the content of organic and total carbon. Although the seed bank was depleted faster at sites with a low carbon content, even in soils with a high carbon content that were less acidic and nutrient-rich (N, P), the majority of seed had germinated by the end of the first year. Moreover, the seed depletion process varied at the different localities (Fig. 1, Table 1). The fastest depletion was recorded at localities where more seed survived the first year (Broumov, Plzeň, Průhonice), and slowest where the percentage of seed surviving the first year was low, but a small amount of seed persisted at the end of the seventh year (Koda, Lužnice, Žitný). The highest percentage of surviving seed after the first, second and third year was recorded at Broumov, where the soil had the lowest C, N, P, K content, lowest pH and highest absorption capacity, and was located in the region with the overall highest precipitation and a low mean annual temperature.

Basto et al. (2015) report similar results for three grassland species; they found that acid soils (with less nutrients) are associated with increased seed persistence. They explain it as an indirect effect mediated by microbial pathogens that are less common in acid soils. Schafer & Kotanen (2003, 2004) evaluated the role of fungal pathogens under different moisture conditions and also conclude that soil moisture has an indirect effect on seed bank density and persistence. They found that fungi, particularly in wet soils, were a hazard for buried seeds of four species of grass. However, numerous toxic compounds (essential oils) in the seeds of *H. mantegazzianum* (Jakubska-Busse et al. 2013) may protect its seed against soil pathogens as they have antifungal and antibacterial effects (Swamy et al. 2016).

Long et al. (2009) consider water and temperature as the main factors affecting seed longevity in soil, as warmer and wetter conditions shorten persistence. Abedi et al. (2014) report that seed bank longevity varies with environmental factors, but differently for various species. The seed from dry habitats can scarcely persist in wet soils and likewise, that of species from wet habitats can hardly persist in dry soils. This could account for what happened to the seed buried at Vroutek – the seed of *H. mantegazzianum* that came from well-established plants in the region of Slavkovský les, where there is a high amount of precipitation and a low mean temperature, did not survive long under dry conditions with a high nutrient content in soil, typical of this locality.

Our results, based on the first experimentally verified quantitative data on the seed longevity of *H. mantegazzianum*, provide a basis for revisiting some older reports from the 1980s, in which seeds were claimed to persist for up to 15 years (Lundström 1984, 1989, but see Moravcová et al. 2006). We also show that seed longevity depends on specific environmental and edaphic conditions; seeds survive better at climatically colder locations with high rainfall and where the soil has a low nutrient content. Within our data set, such localities correspond well with the foci of this species distribution in the Czech Republic (Pyšek 1991, Pyšek et al. 1998) and also reflect its montane to subalpine origin.

From a management perspective, however, it needs to be borne in mind that even 0.1% of surviving seed for a plant that produces on average 20,000 seeds still represents 20 seeds that can start a new invasion (Moravcová et al. 2006, 2007). Therefore, long-term monitoring well beyond the assumed period of seed bank persistence is highly recommended.

See www.preslia.cz for Electronic Appendices 1–3.

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Souhrn

U monokarpických invazních druhů rostlin představuje persistence semen v půdě důležitou charakteristiku zodpovědnou za přetrvávání populace na lokalitě. Persistenci semen v půdě ovlivňují nejen fyzikální a fyziologické vlastnosti semen určitého druhu, ale také biotické a abiotické podmínky daného prostředí na lokalitě. Bolševník velkolepý (*Heracleum mantegazzianum*) je v Evropě řazen mezi druhy s vysokým invazním potenciálem. Abychom zjistili, jak dlouho a za jakých podmínek jsou semena tohoto druhu schopná v půdě přetrvávat, založili jsme tzv. pohřbívací experimenty, v rámci nichž byla semena pohřbena v různých klimatických, geografických a edafických podmínkách České republiky. Zjistili jsme, že po sedmi letech byla zásoba semen prakticky vyčerpána, v průměru na všech lokalitách přežívalo pouze 0,1 % semen. Na pěti ze sledovaných lokalit nebyla po sedmi letech nalezena již žádná semena, zásoba semen byla tedy vyčerpána kompletně (na jedné z nich došlo k úplnému vyčerpání již po dvou letech a na jedné po pěti letech) a nejvyšší zjištěná hodnota přežívání semen po sedmi letech experimentu byla 0,5 %. Už po pěti letech bylo přežívání semen v půdní bance obecně velmi nízké a nepřesahovalo 1 %. Byly zjištěny statisticky průkazné korelace mezi rychlostí vyčerpávání půdní banky a obsahem celkového i organického uhlíku v půdě, ale vliv klimatických, geografických a ostatních půdních charakteristik na přežívání semen v půdě prokázán nebyl. Semena však po prvním roce přetrvávala v půdě lépe na lokalitách s nižším obsahem uhlíku a půdních živin. Průběh vyčerpávání půdní banky semen, sledovaný na lokalitách České republiky v průběhu sedmi let, tak odpovídá klasifikaci krátkodobě vytrvalé půdní banky. Z tohoto důvodu doporučujeme dlouhodobé sledování lokalit, na kterých byl bolševník velkolepý již úspěšně vymýcen, neboť se může jednat o úspěch pouze zdánlivý.

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