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Seed bank of an invasive alien, *Heracleum mantegazzianum*, and its seasonal dynamics

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Abstract

The seed bank of *Heracleum mantegazzianum*, native to the western Caucasus and invasive in Europe, was studied in the Slavkovský les Protected Landscape Area, the Czech Republic, during the course of two growing seasons. In each of seven study sites with dominating stands of the species, soil samples were taken in October (after the fruit release), April (before germination) and June–July (before the fruit release). Ten samples were taken from each site using a soil hand bore, 4.6 cm in diameter. Seeds elutriated from the samples were immediately germinated in laboratory conditions (10°C, 12 h light/12 h dark); those that germinated during 1 month were considered as non-dormant. Non-germinated but viable seeds, tested for viability by tetrazolium, were considered as dormant. The number of dead seeds was also recorded. The total number of seeds significantly increased with mean density of flowering plants at a site. Of the total variation in seed-bank size, about four-fifths were attributed to that among sites, and one-fifth to that within sites. The number and proportion of living seeds differed significantly between years in summer, but not in autumn and spring. Total number and the numbers of dormant, non-dormant, living and dead seeds significantly differed among the autumn, spring and summer samples. The percentage of living seeds in the total seed bank decreased from 56% in autumn to 42% in spring to 15% in summer. The percentage of non-dormant seeds among those living was 0.3% in autumn, it increased to 87.5% in the spring sample, and decreased to 3% in summer. Pooled across all sites, the average seed numbers (expressed per m^2) were 6719 ± 4119 (mean ± SD) in autumn, 4907 ± 2278 in spring and 1301 ± 1036 in summer for the total number of seeds, and 3759 ± 2906, 2044 ± 1198 and 192 ± 165, respectively, for living seeds. The majority of seeds (95%) were concentrated in the upper 5 cm soil layer. However, some seeds were present in lower soil layers, which indicates a short-term persistent seed bank. The present data are the first quantitative estimate of the seed bank in *H. mantegazzianum*, and show that the reproductive potential of the species is enormous, which seems to be a crucial feature of its invasion success.

Keywords: *Apiaceae*, dormancy, germination, *Heracleum mantegazzianum*, plant invasions, seasonal dynamics, seed bank

Introduction

The study of biological invasions has become one of the most dynamic, developing fields of ecology in recent decades (Richardson *et al.*, 2000; McNeely *et al.*, 2001) because invasive species represent a threat to native biota and contribute to the decrease of native biological diversity (McNeely *et al.*, 2001), and because of scientific attractiveness. Species introduced to the region where they have not been present before provide a unique opportunity for the study of ecological processes (Williamson, 1996), such as competition with native taxa unbiased by a common evolutionary history (Connell, 1980), relationships with biota on other trophic levels (Keane and Crawley, 2002) and patterns of colonization of new sites that occur with unprecedented dynamics (Williamson, 1996; Liška and Soldán, 2004; Mandák *et al.*, 2004).

Reproductive characteristics are crucial for the invasive success of any alien plant. A minority of invaders, some of them extremely successful, rely

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exclusively on vegetative reproduction, but the majority of species depend on seed dispersal. It has been stated repeatedly that the ability to produce a large number of seeds increases invasion success and that easy germination in a wide range of conditions is another necessary condition for successful invasion (Baker, 1965; Forcella *et al.*, 1986; Roy, 1990; Rejmánek, 1996). However, much less is known about formation of the seed bank for alien plants, which is an important aspect of seed plant strategies that may favour invasiveness (Baker, 1965; Roy, 1990). Spreading germination over time to await favourable conditions or major disturbance is an efficient mechanism to reduce the hazardous effect of severe environmental conditions (Kalamees and Zobel, 2002).

An extensive theory has been built around the issue of seed banks in the past decades (Thompson, 1986, 1992; Leck *et al.*, 1989), and there is also a solid amount of quantitative data on seed banks in particular species (Thompson *et al.*, 1997; Baskin and Baskin, 1998). Specific knowledge of soil seed-bank characteristics of vascular plants is a crucial element in understanding life cycles (Matus *et al.*, 2001), which is particularly relevant in studies of invasive aliens that exhibit high population dynamics. However, detailed accounts of seed-bank characteristics are missing for many species, and methodological issues associated with seed bank estimation and germination characteristics often complicate the reliability of published data (Baskin and Baskin, 1998). Moreover, information about the role of the soil seed bank in plant communities is generally very scarce (Kalamees and Zobel, 2002).

The present paper deals with *Heracleum mantegazzianum*, an invasive species in Central Europe. Although the distribution and ecology of this species have been studied thoroughly (see Tiley *et al.*, 1996 and references therein), only two studies provide information about its seed bank (Andersen and Calov, 1996; Thompson *et al.*, 1997). It has been suspected that this species does not form a persistent seed bank (Tiley *et al.*, 1996; Caffrey, 1999; K. Thompson, personal communication), and data referring to persistence come from dry seeds (Morton, 1978), or it is unclear whether they were based on burial experiments (Lundström, 1989), but a thorough study of the seed bank in *H. mantegazzianum* has not been carried out to date.

The present study was designed to obtain a deeper insight into this aspect of the ecology and population dynamics of this species, and attempts to answer the following questions: What is the size of the soil seed bank in *H. mantegazzianum* and its variation at different spatial scales? What is the vertical distribution of seeds in the soil? What are the seasonal dynamics of the seed bank and changes in the pattern of dormancy?

Materials and methods

Study species

Heracleum mantegazzianum Sommier et Levier (*Apiaceae*) is a perennial monocarpic herb, 200–500 cm tall, with a thick tap root up to length 45–60 cm, and leaves up to 250–300 cm. Flowers are arranged in compound umbels up to 80 cm across, with the terminal umbel being the largest, surrounded by satellite umbels, and additional two umbels that may be borne on the two axilliary branches. Flowers are insect pollinated, hermaphrodite and protandrous; the anthers dehisce and pollen is shed before the stigma becomes receptive, but there is some overlap in staminate and pistillate phase among flowers, which makes self-pollination possible (Tiley *et al.*, 1996; I. Perglová *et al.*, unpublished). Flowering in the study area occurs from late June to late July, and umbels bear oval-elliptical, broadly winged fruits, which split into two winged mericarps (further termed 'seed' for simplicity), 6–18 mm long and 4–10 mm wide, with a mean dry weight of 5.7 mg (range 4.6–23.2 mg). The endosperm is oily, and mature fruits have a strong resinous smell (Tiley *et al.*, 1996).

Seeds have a morphophysiological dormancy (Baskin and Baskin, 1998). When they are released, the embryo is differentiated but underdeveloped. The development of the embryo and breaking of physiological dormancy both occur during the cold and wet stratification during autumn and winter. Seed germination in the field occurs early in spring.

A single plant is capable of producing an enormous number of seeds. There is a wide range in estimated number of seeds produced, from 5000 to more than 100,000 per single plant (Pyšek *et al.*, 1995; Tiley *et al.*, 1996). Unfortunately these data often come from observation of a single plant; the maximum value reported is 107,984 (Caffrey, 1999). An average value obtained for eight plants in Central Bohemia was 16,139 ± 2617 (mean ± SD) seeds per plant (Pyšek *et al.*, 1995).

The species is native to the western Caucasus, where it occurs in the upper forest belt of the southern slopes, mainly in meadows, clearings and forest margins (Mandenova, 1950). In the Czech flora, *H. mantegazzianum* is considered invasive (Pyšek *et al.*, 2002), following the criteria of Richardson *et al.* (2000). The species was introduced to the country as a garden ornamental to a chateau in Lázně Kynžvart, the Slavkovský les area (W. Bohemia), in 1862, and the oldest herbarium specimen documenting with certainty a spontaneous occurrence in the close vicinity of the introduction site is from 1877 (Holub, 1997). The species has spread from the area of Slavkovský les, and there was a lag phase lasting until the 1940s. The beginning of the exponential phase of spread was dated 1943, based on a statistical analysis of the increase in the number of localities over time (Pyšek *et al.*, 1998). The rapid increase in the number of localities, and associated massive spread into the landscape, started in the 1970s (Pyšek, 1991; Pyšek and Prach, 1993). The spread was encouraged in regions with a high human population density and was slower in warmer areas, characterized by relatively high January temperature (Pyšek *et al.*, 1998). Up to now, there are 603 reported localities in the country (P. Pyšek and K. Prach, unpublished data).

The species is the largest central European forb and rapidly attains dominance in invaded sites; up to 40% of suitable habitats are covered by its stands in the area of Slavkovský les (Pyšek and Pyšek, 1995). Replacement of native vegetation and injuries to human skin caused by phototoxic substances (Drever and Hunter, 1970; Tiley *et al.*, 1996) are the main reasons for efforts to eradicate it from infested areas. The large seed-set with efficient dispersal by water, wind and human-related factors (Pyšek and Prach, 1993) contribute to its rapid spread. Disturbed habitats with good possibilities for seed dispersal are more easily invaded, but the species also invades semi-natural vegetation (Pyšek and Pyšek, 1995).

H. mantegazzianum is naturalized or invasive in a number of European countries and Central Russia (for a list and references, see Tiley *et al.*, 1996). Outside Europe, it is found naturalized in Canada and the United States (Morton, 1978; Ochsmann, 1996).

Study area

The Czech Republic is prone to plant invasions, and new alien species are continually reported from the region (Kubát and Jehlík, 2003; Mihulka *et al.*, 2003; Petřík, 2003). The study area was located in the Slavkovský les Protected Landscape Area, W. Bohemia, where the species was first introduced into the country (Pyšek, 1991). Orographically, most of the region belongs to the Ore Mountains and is formed by granite. Its colonization by humans started at the end of the 13th century. After the Second World War, German inhabitants were displaced, and part of the region was a military area until the 1960s; it remained largely uninhabited afterwards. As a result, it is sparsely populated at present. The total size of the protected area is 617 km^2, altitudinal range is 373–983 m above sea level (Kos and Maršáková, 1997), the January temperature ranges from -5.1°C (average minimum) to -0.2°C (average maximum) and the July temperature ranges from 10.5 to 21.5°C. The annual sum of precipitation is 1094 mm (Mariánské Lázně meteorological station, 50-year average). Historically, the natural vegetation of the area consisted mainly of beech and spruce forests, extensive peat bogs and pine forests on serpentine. At the moment, this vegetation is present only in remnants, and was replaced by extensive wetlands with a high diversity of flora, pastures and mainly spruce forest plantations, which cover 53% of the area (Kos and Maršáková, 1997). The area is heavily infested by *H. mantegazzianum*, and the study sites were evenly distributed to cover the range of variation in environmental conditions. Seven study sites with dominating stands of *H. mantegazzianum* were selected (Table 1). Most represent open sites in an otherwise forested landscape, or are separated from the surroundings by scrub, water courses or roads.

Sampling

At each study site, soil samples were taken on 26 October 2002, 17 April 2003, 28 July 2003, 11 October 2003, 3 April 2004 and 20 June 2004. The

Table 1. Geographical location, altitude and characteristics of populations of *Heracleum mantegazzianum* at the study sites. Population size (area covered by *H. mantegazzianum* in a site) and year of invasion were obtained from aerial photographs (J. Müllerová *et al.*, 2005). Population density (number of plants m^{-2}) and density of flowering plants (number m^{-2}) were recorded in 10 m^2 permanent plots in the growing season preceding fruit release in autumn of the years analysed. Mean fecundity was estimated from a regression relationship (Moravcová *et al.*, 2005)

Site	Latitude	Longitude	Altitude (m asl)	Population size (m^2)	Year of invasion	Population density (2002/2003)	Density of flowering plants (2002/2003)	Mean height (m)	Mean fecundity
Žitný 1	50°03′754	12°37′569	787	99,121	1957	2.8/2.7	0.3/1.0	2.48	21,573
Potok	50°04′649	12°35′955	644	39,774	1973	3.3/2.5	0.4/0.2	2.43	23,966
Dvoreček	50°05′982	12°34′137	506	24,817	1987	3.0/3.9	0.6/0.7	2.81	24,930
Krásná Lípa 1	50°05′692	12°38′544	597	na	2000	1.4/0.6	0.6/0.3	2.58	22,832
Litrbachy	50°06′009	12°43′777	800	4711	1973	19.9/16.7	0.5/1.0	2.78	16,258
Rájov	49°59′704	12°45′933	752	5198	1991	12.2/9.9	1.3/1.8	2.65	16,686
Krásná Lípa 2	50°06′306	12°38′393	596	7454	1987	6.2/3.9	0.0/1.4	2.80	27,633

asl, above sea level; na, not available.

seed sampling patterns were selected to cover three crucial periods in the seasonal dynamics of the seed bank: (1) after fruits are shed and released into the seed bank (October, 'autumn sample'); (2) after natural cold stratification has occurred during winter, and before the beginning of spring germination (April, 'spring sample'); and (3) at the time of presumed seed bank depletion and before the current-year fruit release (June to July, 'summer sample'). This sampling covered two cycles of seed-bank dynamics: autumn 2002 to summer 2003 (termed Year 1) and autumn 2003 to summer 2004 (Year 2).

At each site, ten soil cores were taken at 2 m intervals around a 10 × 1 m permanent plot, established in a dense stand of *H. mantegazzianum* for the purpose of another experiment following population dynamics. This design, involving permanent plots, was adopted to make it possible to take consecutive samples from the same place, and relate the results from the seed-bank study to those on species population dynamics. Each core was taken from a 15 × 15 cm subplot by using a soil hand bore, 4.6 cm in diameter, to a depth of 15 cm. Three replicates were taken from each subplot. The 15 × 15 cm subplots were placed next to the previous sampling location. In total, there were 10 combined core samples × 7 localities × 3 sampling seasons, giving the total of 210 estimates of the seed bank in each year.

In addition, pilot samples were taken from ten localities, using the same design, on 22 March 2002, to estimate the vertical distribution of seeds in the soil. This sample was also taken to a depth of 15 cm, and each of the replicates was divided into the following depth sections: 0–5, 6–10 and 11–15 cm. Seeds lying on the soil surface were included in the 0–5 cm layer. In the subsequent samples, soil cores were not divided into the depth classes because the vast majority of seeds were found in the upper soil layer (0–5 cm).

Cores from Year 2 were stored at room temperature for a maximum period of 1 week preceding elutriation, which was performed using a sieve with a mesh size 2 mm. Separated seeds were placed in Petri dishes and tested for viability by germination at 10°C (day/-night:12 h light/12 h dark). Germination experiments were conducted for 1 month. Germinated seeds were considered as non-dormant. Ungerminated seeds were tested for viability by tetrazolium staining (Baskin and Baskin, 1998). Viable seeds were considered as dormant. The number of dead seeds was also recorded. Data from Year 2 were used to evaluate the dynamics of dormant seeds in the seed bank. All analyses involving dormant seed are based on this year.

In samples from Year 1 and the pilot sample from spring 2002, dormant and non-dormant seeds were not distinguished, and only living and dead seeds were recorded. Data from this year were used only for the comparison of living and total seed numbers between seasons.

To illustrate the pattern, seed densities were expressed per 1 m^2, based on the total area of the core sample ($3 \times 16.6\,cm^2$). In statistical analyses, original values (number of seeds per core) were used.

For each site, the following data were obtained during an ongoing associated research programme (Moravcová *et al.*, 2005; Müllerová *et al.*, 2005): population size (total area covered by *H. mantegazzianum*), year of invasion, population density, flowering density in 10 m^2 permanent plots, mean height, and mean fecundity of *Heracleum* plants (Table 1; J. Pergl *et al.*, unpublished).

Statistical analysis

The effect of site characteristics (Table 1) was evaluated by regressing the average numbers of dormant, living and total seeds at each site (the response variables) on altitude, population size, population density, density of flowering plants, mean height, fecundity and year of invasion (explanatory variables), using simple regressions with the Bonferroni correction for multiple testing (to keep the type I error at $\alpha = 0.05$). The variation of the soil seed bank among sites and within sites was examined for dormant, living (dormant plus non-dormant) and total (living plus dead) number of seeds averaged for the autumn, spring and summer sampling as the response variables, using ANOVA for random effects, with the proportion of variance among and within sites expressed as percentages (Sokal and Rohlf, 1995). The total number of seeds and the number and proportion of living seeds (for the evaluation of differences among years), the total number and the number of dormant, non-dormant, living and dead seeds (differences among autumn, spring and summer sampling), and the number of dormant, living and dead seeds in spring (differences among soil layers) were analysed by nested ANOVAs, using years, seasons and soil layers, respectively, as fixed effects, and sites as nested, random effects (Underwood, 1997); differences among seasons and among soil layers were further evaluated by deletion tests (Crawley, 1993).

Average values of seeds were transformed logarithmically (natural logs), while count data on seed numbers were square rooted; to avoid zeros the data were coded by adding 0.5 (Yamamura, 1999). Data on proportions were angular transformed (e.g. Sokal and Rohlf, 1995). The appropriateness of the transformations was checked by the Box–Cox method (Box and Cox, 1964, 1982), by plotting standardized residuals against fitted values, and by normal probability plots of the fitted values (Crawley, 1993).

Results

The total number of seeds significantly increased with mean density of flowering plants at a site (Fig. 1). The number of dormant and living seeds was not significantly affected by any site characteristic investigated.

Variation in the soil seed bank among sites, averaged for the autumn, spring and summer samples of Year 2, was highly significant for dormant, living and total seed number. For total seed bank, 78% of variation was attributed to that among sites, and 22% to that within sites. The partitioning of variance in numbers of dormant and living seeds exhibited a pattern similar to that in the total number of seeds, with that among sites lower by 12–13% and within sites correspondingly higher (Table 2).

In summer, the number and proportion of living seeds was significantly higher in Year 1 than in Year 2. However, neither the total number in summer, nor the numbers and proportions in autumn and spring, differed significantly between years. This was so mainly because, except for the proportion of living seeds in summer, the numbers and proportions varied significantly at individual sites within each season (Table 3).

The numbers of dormant, non-dormant, living, dead and total seeds in Year 2 differed significantly among seasons and highly significantly varied within individual sites (Table 4). Average numbers of living, dead and total seeds were high in autumn and did not significantly differ from those in spring. From spring to summer, they all decreased and were significantly lower in summer (Table 5). The number of dormant seeds was significantly higher in autumn than in spring or summer, and the number of non-dormant seeds was significantly highest in spring (Fig. 2). Proportions of dormant, non-dormant and dead seeds thus exhibited considerable seasonal dynamics. The percentage of dead seeds consistently increased over the season. The percentage of living seeds in the total seed bank decreased during winter from 56% in the autumn sample, to 42% in spring and to 15% in summer. The percentage of non-dormant seeds among the living was 0.3% in autumn; during winter it increased, to 88% in the spring sample, and decreased to 3% in summer.

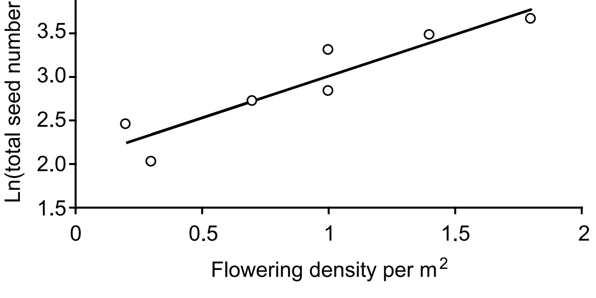

Figure 1. The relationship between the total number of seeds and mean density of flowering plants per m^2 for *Heracleum mantegazzianum*. Ln(total number of seeds) = 2.05 + 0.95 (mean density of flowering plants). $F = 31.91$; df = 1,5; $P < 0.05$ after correction for multiple testing ($P = 0.0024 < 0.00625$). $R^2 = 86.4\%$. Data from Year 2 of the study.

Expressed per m^2, the average value pooled across localities was 6719 ± 4119 (mean ± SD) in autumn, 4907 ± 2278 in spring and 1301 ± 1036 in summer for the total seed numbers, and 3759 ± 2906, 2044 ± 1198, and 192 ± 165, respectively, for living seeds.

In the spring 2002 sample, 95% of seeds were concentrated in the upper soil layer (Fig. 3). However, the vertical distribution of living and dead seeds also varied significantly within the individual sites (Table 6).

Discussion

The present study indicates that the proportional representation of dormant, non-dormant and dead seed in *H. mantegazzianum* exhibits considerable seasonal dynamics. A substantial proportion of seed (44%) are shed undeveloped or empty, and do not contain a living embryo; these were classified as dead in the present study. It should be noted that a portion of the dead seeds present in the autumn sample may have originated in previous years, i.e. that not all the dead seeds recorded are result of that year's fruit release. After the massive fruit release, nearly all living seeds (99.7%) are dormant. Because almost no non-dormant seeds are present in autumn, germination and population recruitment from seedlings in this species occurs exclusively in spring.

The total seed number in the seed bank did not change significantly over winter, but the proportion of dormant and non-dormant seeds changed due to cold stratification. Consequently, the percentage of non-dormant seeds among the living increased from 0.3% to 88% from autumn to spring. In the study area, seedling establishment starts in April and continues until the beginning of May; after that, seedling recruitment was no longer observed in the field (L. Krinke *et al.*, unpublished data). During spring and the beginning of summer, nearly all non-dormant seeds (99.7%) have germinated, and the seed bank becomes almost completely depleted; in summer, the number of living seeds decreases to 15% of the total number (and to 13% of the spring state). Living seeds present in the summer do not germinate, despite having a large, developed embryo (L. Moravcová *et al.*, unpublished); they are fully morphologically developed, but physiologically dormant. In this

Table 2. ANOVAs of the variation of the soil seed bank of *Heracleum mantegazzianum* among sites and within sites in Year 2. Data are log transformed. Numbers are coded by adding 0.5 of the dormant, living and the total of seeds, averaged for the autumn, spring and summer samples. Sites are evaluated as random effects, and variance is expressed in percentages

	Dormant				Living				Total			
Source of variation	df	MS	*F*	Variance (%)	df	MS	*F*	Variance (%)	df	MS	*F*	Variance (%)
Among sites	6	5.043	19.933***	65.4	6	5.065	19.459***	64.9	6	3.323	36.214***	77.9
Within sites	63	0.253		34.6	63	0.260		35.1	63	0.0918		22.1

***, $P < 0.001$.

Table 3. Nested ANOVAs of the variation in soil seed bank of *Heracleum mantegazzianum* between years. Data are square-rooted numbers +0.5 of living and total seeds, and the angular transformed proportions (%) of living seeds. Year is evaluated as a fixed effect

		MS								
		Autumn			Spring			Summer		
Source of variation	df	Living	% living	Total	Living	% living	Total	Living	% living	Total
Year	1	8.341 NS	1.788 NS	66.93 NS	18.72 NS	0.0565 NS	32.34 NS	34.01***	5.798***	3.221 NS
Sites within year	12	17.475***	0.386***	19.83***	5.141***	0.202***	8.458***	1.664***	0.0808 NS	5.238 ***
Replicates within sites	126	1.249	0.0523	1.450	0.686	0.0208	0.979	0.517	0.0845	0.896

***, $P < 0.001$; NS, not significant.

period, part of the dead seed fraction decays in the soil (Fig. 2), hence their proportion also decreases.

Total seed numbers in the soil, as well as amounts of dormant and living seeds, varied both within and among localities. Nearly four-fifths of the variation in total seed numbers, and two-thirds of that in dormant and living seed, were attributed to the differences among sites. This large variation can be due to historical, geographical or ecological differences among the sites, such as the population age, climatic conditions during the winter or nutrient status of the soil. The remaining differences, among individual samples within a site, probably reflect differences in fecundity and vigour of individual plants, and variation in the genetic make-up of plants within the population. Flowering intensity within a site turned out to be the main factor affecting the amount of seeds in the seed bank, as indicated by a very close dependence (explaining 86% of variation) of seed-bank size on the number of plants that flowered in a given year (Fig. 1). Available data from both years suggest that the differences in flowering intensity can be attributed to the population dynamics within individual sites, rather than to the differences in site conditions, because the proportions of plants that flowered in particular years were not significantly correlated ($F = 0.56$; df = 1,5; $P = 0.48$).

The present data are the first quantitative estimate of the seed bank in this species. Previously published reports have not provided actual values, as the information on the seed bank in *H. mantegazzianum* was based on estimates from seedling emergence in the field (Andersen and Calov, 1996) or on multi-species seed-bank studies (Thompson *et al.*, 1997). By relating the numbers obtained in our study to the area infested by *H. mantegazzianum* in the region, an estimate of the reproductive potential of this invasive alien species can be outlined. Given the area covered by the largest *H. mantegazzianum* population in a site (99,121 m^2, Table 1), and the average number of living

Table 4. Nested ANOVAs of the variation of the soil seed bank for *Heracleum mantegazzianum* among seasons. Data are square-rooted numbers +0.5 of dormant, non-dormant, living, dead and total seeds from Year 2. Season is evaluated as a fixed effect

	Dormant			Non-dormant			Living			Dead			Total		
Source of variation	df	MS	*F*	df	MS	*F*	df	MS	*F*	df	MS	*F*	df	MS	*F*
Season	2	184.8	19.624***	2	102.25	33.328***	2	151.25	12.657***	2	44.65	3.800*	2	183.000	10.705***
Sites within season	18	9.417	18.722***	18	3.068	12.421***	18	11.95	17.677***	18	11.75	16.297***	18	17.094	18.560***
Replicates within sites	189	0.503		189	0.247		189	0.676		189	0.721		189	0.921	

***, $P < 0.001$; *, $P < 0.05$.

Table 5. Number of *Heracleum mantegazzianum* seeds in the soil seed bank per m^2 shown for the localities studied in Year 2. Each value is the mean ± SD of 10 replicates. Values per m^2 were extrapolated from original data, which were used in statistical analyses. See Table 1 for the characteristics of localities

	Autumn				Spring				Summer			
Site	Non-dormant	Dormant	Dead	Total	Non-dormant	Dormant	Dead	Total	Non-dormant	Dormant	Dead	Total
Žitný 1	0	3899 ± 2137	4844 ± 3059	8683 ± 4247	3899 ± 1589	302 ± 288	2794 ± 1699	6995 ± 3008	0	161 ± 85	603 ± 444	764 ± 551
Potok	0	844 ± 432	1970 ± 598	2814 ± 858	503 ± 288	141 ± 213	2392 ± 1463	3035 ± 1694	0	181 ± 259	985 ± 572	1166 ± 682
Dvoreček	0	3578 ± 1476	884 ± 466	4462 ± 1762	2151 ± 722	121 ± 194	1568 ± 701	3839 ± 1040	0	121 ± 169	744 ± 465	864 ± 502
Krásná Lípa 1	0	1628 ± 595	503 ± 272	2131 ± 710	1025 ± 828	181 ± 176	663 ± 285	1869 ± 758	20 ± 64	181 ± 241	362 ± 472	563 ± 662
Litrbachy	0	1226 ± 1107	3899 ± 1874	5126 ± 2076	905 ± 811	322 ± 271	2754 ± 1121	3980 ± 1729	0	121 ± 104	1045 ± 567	1166 ± 605
Rájov	60 ± 97	6613 ± 3189	5467 ± 1911	12,140 ± 3475	1407 ± 1064	563 ± 247	5809 ± 1523	7779 ± 2420	20 ± 64	523 ± 503	3055 ± 2293	3598 ± 2356
Krásná Lípa 2	20 ± 64	8502 ± 3365	3156 ± 1963	11,678 ± 4342	2633 ± 1294	161 ± 127	4060 ± 1697	6854 ± 2120	0	20 ± 64	965 ± 491	985 ± 496
Total	11 ± 23	3747 ± 2891	2960 ± 1919	6719 ± 4119	1789 ± 1188	256 ± 156	2863 ± 1677	4907 ± 2278	6 ± 10	187 ± 158	1108 ± 892	1301 ± 1036

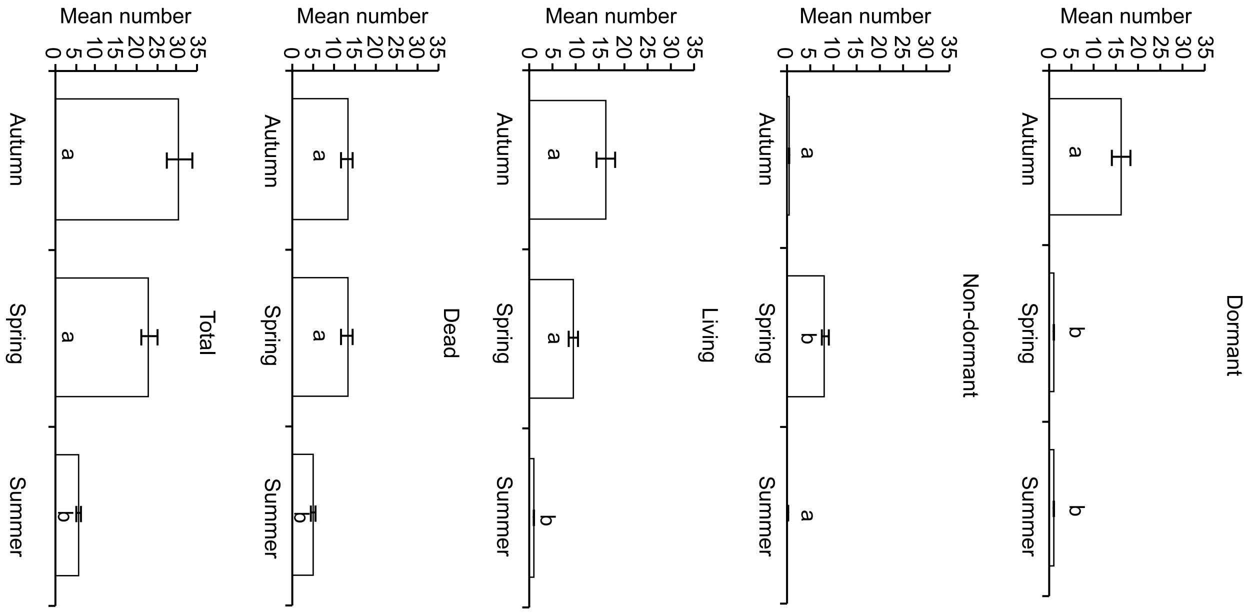

Figure 2. Seasonal dynamic of the *Heracleum mantegazzianum* seed bank among autumn, spring and summer samples of Year 2. Bars are means of dormant, non-dormant, living, dead and total numbers of seeds (per core sample) averaged over the individual sites. Vertical lines are standard errors of the means. Bars with the same letters do not differ significantly ($P < 0.05$) in deletion tests.

seeds in the seed bank at this site in the spring (4200, Table 5), it can be estimated that over 416 million seeds are present in the soil at the beginning of germination to potentially produce new plants. Using the value for non-dormant seeds (3899), immediately ready to

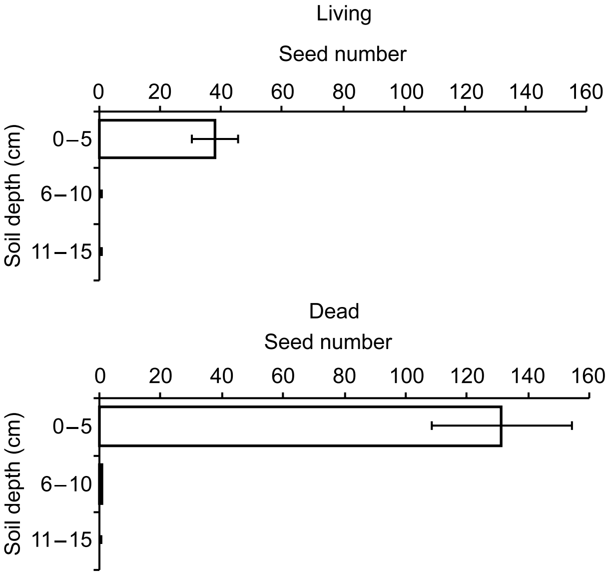

Figure 3. Vertical distribution of living and dead *Heracleum mantegazzianum* seeds in the soil. Deletion tests on square-rooted + 0.5 seed numbers indicated that the seeds significantly ($P < 0.001$) prevailed in the upper soil layer (0–5 cm), and their numbers did not differ ($P > 0.05$) between 6–10 and 11–15 cm layers. Numbers of seeds per core sample are presented; horizontal lines are standard errors of means.

germinate, yields only a slightly lower amount, of over 386 million seeds in a single site. Although this estimate is certainly biased by extrapolation of the core samples per 1 m^2, and the value may be overestimated because the average density at the site is lower than that in the surroundings of the sample plots, the reproductive potential of the species is enormous and seems to be a crucial feature, making invasion possible to the extent observed in the region and elsewhere in Europe (Ochsmann, 1996; Tiley *et al.*, 1996).

The amount of seeds in the soil seed bank of *H. mantegazzianum* is exceptional also within the family *Apiaceae*. There are 75 records of individual species of this family for which the mean seed density per 1 m^2 is available in the database of Thompson *et al.* (1997). The mean value for these records is 354 ± 707 m^{-2}. Although these data are difficult to compare with those found for *H. mantegazzianum*, because some of them come from seed-bank studies in multi-species communities and because of other limitations to their interpretation (Thompson *et al.*, 1997), they indicate that the amount of seeds in the soil found in this study exceeds the average value in the family by an order of magnitude. Only two species of *Apiaceae* (*Ammi majus* and *Torilis japonica*) exhibit seed density values comparable to those of *H. mantegazzianum* (Thompson *et al.*, 1997).

Baskin and Baskin (1998) reported that 24 species in 21 genera of *Apiaceae* form a seed bank, and suggest that morphophysiological dormancy provides a convenient explanation for formation of a persistent seed bank. The pattern of seed-bank formation in *Apiaceae* can be inferred in more detail from the database of Thompson *et al.* (1997), which contains data for 47 species of 37 genera, based on 221 seed-bank classifications of individual species published in the literature. A majority of species cannot be unequivocally attributed to particular seed-bank classes, as individual studies differ in their assessment, so that more than one type of seed bank is indicated (Thompson *et al.*, 1997). Within the family, 52% of records are of transient seed banks, 22% are short-term persistent, 12% long-term persistent, and seeds of the rest were present, but cannot be assigned to one of the three seed-bank types.

Comparison between the 2 years suggests that despite the variation in the number of seed entering the seed bank in particular localities, the overall pattern described in this study is rather robust. The only difference found between years relates to the proportion of living seeds in summer (41% in Year 1 versus 15% in Year 2) and results from different numbers of dead seed in each year. The number of dead seeds present in the soil seed bank in summer can be attributed to the seasonal course and between-year variation in weather. The summer of Year 2 was rather dry, compared to the previous year, which may have led to slower decay of dead seeds in the first half of the year. This resulted in higher numbers of dead

Table 6. Nested ANOVAs of the variation of the soil seed bank of *Heracleum mantegazzianum* among soil layers (0–5, 6–10, 11–15 cm) in the spring 2002. Data are square-rooted numbers + 0.5 of living and dead seeds. Soil layer is evaluated as a fixed effect

	Living			Dead		
Source of variation	df	MS	*F*	df	MS	*F*
Layer	2	52.45	37.952***	2	121.6	52.962***
Sites within layers	21	1.382	4.163***	21	2.296	4.276***
Replicates within sites	216	0.332		216	0.537	

***, $P < 0.001$; NS, not significant.

seeds, hence a lower contribution of living seeds to the total seed bank.

Since the present study followed a detailed seasonal dynamics of the seed bank for only 1 year, supporting studies on the longevity of *H. mantegazzianum* seeds in the soil over a longer time span are needed. Andersen and Calov (1996) found no viable seeds in the soil seed bank where flowering and fruiting had been prevented for 7 years, but no data are available to indicate whether this period cannot be substantially shorter. Our data show that, on average, only 9% of living seeds that were present in autumn can persist in the soil seed bank until the next summer. Additional support for the observed pattern can be found in an ongoing study of seed burial in *H. mantegazzianum*. Of the seeds buried in ten localities in the Czech Republic in autumn 2002, 8.8% remained viable until the autumn of the following year, and only 2.6% survived in the soil for 2 years (L. Moravcová *et al.*, unpublished). The species is considered to have a transient soil seed bank, i.e. missing from the seed bank or present only in the surface layer (Thompson *et al.*, 1997). Our results on vertical distribution of seeds in the soil and on seed survival over 2 years suggest that some seeds may be present in lower soil layers, which indicates a short-term persistent seed bank. However, the amount of these seeds is rather negligible, and they do not seem to contribute substantially to the population dynamics of the species. More data are needed to determine the persistence of the *H. mantegazzianum* seed bank on a longer time scale, because this aspect of population dynamics is a crucial determinant of success of an invasive species that relies exclusively on seed production and dispersal. This is especially relevant with respect to control; given the *H. mantegazzianum* fecundity and high percentage of germination, regardless of where on a plant the fruit is produced (Moravcová *et al.*, 2005), even a few seeds persisting in the seed bank over a longer time can potentially start a new invasion.

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