
10 Seed Ecology of *Heracleum mantegazzianum* and *H. sosnowskyi*, Two Invasive Species with Different Distributions in Europe

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Waste no time! They are approaching!

(Genesis, 1971)

Introduction

Heracleum mantegazzianum Sommier & Levier and *H. sosnowskyi* Manden. (*Apiaceae*) belong to the group of 'large' or 'giant' hogweeds in the section *Pubescentia* and both species are among the worst invasive aliens in Europe. The term 'giant' reflects their size – the flowering plants of *H. mantegazzianum* grow up to 5 m and those of *H. sosnowskyi* up to 4 m (Nielsen *et al.*, 2005). Although there is another species of this group, *H. persicum* (see Jahodová *et al.*, Chapter 1, this volume), which is now invasive in Scandinavia, this chapter only compares the germination ecology of *H. mantegazzianum* and *H. sosnowskyi*.

Both species are natives of the Caucasus Mountains, where they grow in medium- to high-altitude meadows (see Jahodová *et al.*, Chapter 1, this volume; Satsyperova, 1984). The invaded distribution range of *H. mantegazzianum* is central and western Europe, while that of *H. sosnowskyi* is mainly in Poland and some countries of the former USSR (for details of the distribution in Europe see Jahodová *et al.*, Chapter 1, this volume), where it was widely used as a fodder plant.

Both species are monocarpic perennials (Tkachenko, 1989); after several years as a vegetative rosette, they flower once and die. *H. sosnowskyi* is

reported to live for up to 6 years when planted in pastures and fields for biomass and silage production (Satsyperova, 1984). However, only the life span of *H. mantegazzianum* is well studied. Under natural conditions, this species usually flowers between the third and fifth year, with a recorded maximum of 12 years, and is strictly monocarpic (see Perglová *et al.*, Chapter 4, this volume; Pergl *et al.*, 2006).

Both species reproduce exclusively by seeds and are very prolific. *H. mantegazzianum* produces on average 10,000–20,000 fruits in Europe, with maxima occasionally reaching around 50,000 fruits (see Perglová *et al.*, Chapter 4, this volume). An average plant of *H. sosnowskyi* is reported to have produced 8836 fruits in the Leningrad area, Russia (Tkachenko, 1989).

Fruits of both species are broadly winged mericarps, which are connected in pairs by a carpophore and split when mature (Holub, 1997). Each mericarp contains one seed. For simplicity the mericarp is termed a 'fruit' throughout this chapter and the term 'seed' is used when referring to germination. The fruits of *H. sosnowskyi* are oval to elliptical; fruits collected in Lithuania (from terminal umbels) and used for experiments in the present study were 10.5–16.5 mm long (mean 13.4 ± 1.3 mm, $n = 60$) and 5.3–8.7 mm wide (mean 7.2 ± 0.7 mm). Mandenova (1950) gives the ranges of the length and width of mericarps as 7–9 and 4–6 mm, respectively, without specifying to which umbel order these sizes relate. The fruits of *H. mantegazzianum* are oval-elliptical; Tiley *et al.* (1996) give the ranges of the length and width as 6–18 and 4–10 mm, respectively, also without specifying which umbel. The fruits of *H. mantegazzianum*, originating from terminal umbels, used for the experiments in the present study, were 8.8–14.6 mm long (mean 11.7 ± 1.2 mm, $n = 200$) and 5.3–9.2 mm wide (mean 7.4 ± 0.8 mm).

Seeds of both species have a morphophysiological dormancy (Nikolaeva *et al.*, 1985; Baskin and Baskin, 1998), which is broken by the cold and wet conditions of autumn and winter stratification in the field and in the laboratory by temperatures within the range of 1–6°C. Seeds of both species germinate early in spring but not during summer (see Moravcová *et al.*, Chapter 5, this volume; Z. Gudžinskis, unpublished data). Autumn germination is possible in *H. sosnowskyi* (but was not recorded). The reproductive traits of *H. mantegazzianum* are well studied (Krinke *et al.*, 2005; Moravcová *et al.*, 2005, 2006; Chapters 4 and 5, this volume), but poorly so for *H. sosnowskyi*; so far the research on this species has focused mainly on biomass production (Satsyperova, 1984), seed production (Tkachenko, 1989) and content of furanocoumarins (Tkachenko and Zenkevich, 1987). The present study, based on both field research in the invaded region of Lithuania and common garden experiments, is the first published information on its germination, stratification and dormancy requirements, and seed bank dynamics.

There are differences in germination between invasive species and their less invasive congeners (Baker, 1965; Lambrinos, 2002; Mihaluk *et al.*, 2003) or invasive species and their native congeners or related taxa (Dreyer *et al.*, 1987; Callaway and Josselyn, 1992; Vilà and D'Antonio, 1998; Radford and Cousens, 2000; Van Clef and Stiles, 2001). Similarly, some successful invasive aliens have larger (Richardson *et al.*, 1987; Honig *et al.*, 1992; Radford and Cousens,

2000) and/or longer persisting seed banks (Pyke, 1990; Van Clef and Stiles, 2001) than native or less invasive congeners. In this chapter the reproductive traits related to seed ecology of the two *Heracleum* species are compared to determine whether the differences can explain their varying success as invaders.

Differences in Soil Seed Bank of *Heracleum mantegazzianum* and *H. sosnowskyi*

Dynamics of the seed banks of both species were studied in the field by sampling three times a year and in a common garden burial experiment, where sampling was carried out repeatedly in the course of the year. Because the results for *H. mantegazzianum* have been published in detail elsewhere (Krinke *et al.*, 2005), the following account focuses on *H. sosnowskyi*, and is based on primary data and a comparison of both species.

Seed bank dynamics and composition

To obtain data on seed bank composition and dynamics comparable to those that are available for *H. mantegazzianum* (Krinke *et al.*, 2005), a similar study, using the same methods, was carried out at sites dominated by *H. sosnowskyi* in its invaded range (Table 10.1). Soil samples were taken in spring before seed germination (April), summer before seed release (July) and autumn after seed release (October). *H. mantegazzianum* was studied at seven sites in the Czech Republic (Krinke *et al.*, 2005), *H. sosnowskyi* at three sites in Lithuania. The geographical location, altitude and characteristics of the *H. sosnowskyi* populations are given in Table 10.1.

The vertical distribution of seeds in the soil seed bank is similar for both species. In the spring sample of *H. sosnowskyi*, 98.2% of the total seed, including dead seeds, are in the upper soil layer of 0–5 cm, with little in the deeper layers of 6–10 cm (1.5%) and 11–15 cm (0.3%) (Fig. 10.1). Nevertheless, no living seeds were found in the deepest soil layer (11–15 cm). The vertical distribution of living and dead seeds also varied significantly within

Table 10.1. Geographical location, altitude and characteristics of populations of *H. sosnowskyi* at three sites in Lithuania.

	Latitude N	Longitude E	Altitude	Population size (m ²)	Year of invasion	Density of flowering plants/m ² (2003)	Mean plant height (m)
Santariškės	54°44'55.7"	25°16'39.9"	191	4560	1987	1.1	3.50
Bajorai	54°45'14.6"	25°15'25.0"	182	1452	1990	0.4	3.21
Visoriai	54°45'07.9"	25°16'06.8"	183	9640	1989	0.9	2.57

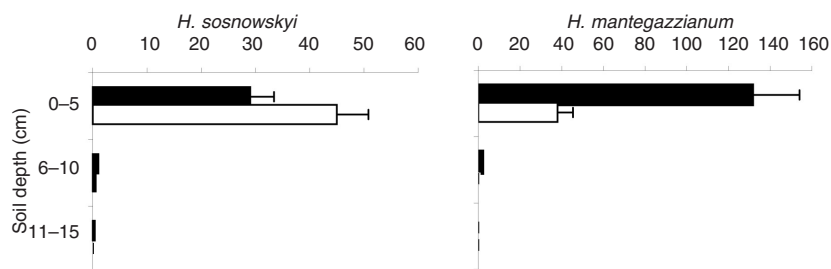


Fig. 10.1. Vertical distribution in the soil in spring of living (empty bars) and dead (black bars) seeds of *H. sosnowskyi*. Deletion tests (Crawley, 2002) on square-root + 0.5 numbers of seeds indicate that the seeds occur mainly in the upper soil layer (0–5 cm) ($P < 0.001$), and the numbers in the 6–10 cm and 11–15 cm soil layers do not differ ($P < 0.001$). Numbers of seeds per core sample (49.8 cm²) are shown; horizontal lines are standard errors of means. Corresponding figures for *H. mantegazzianum* are based on data from Krinke *et al.* (2005). Note different scales are used for the two species.

the individual sites (Table 10.2). The results for *H. mantegazzianum* show the same trend, with 95% of seeds in the upper soil layer (Fig. 10.1) and significant differences within sites (Krinke *et al.*, 2005, Table 6).

As the vast majority of the seeds are located in the upper soil layer, the study of the seasonal dynamics of the seed bank was based only on samples taken from the 0–5 cm layer. The variation among study sites of *H. sosnowskyi* was significant for all seed groups (dormant, living and total, i.e. their sum). For the total seed bank of *H. sosnowskyi*, averaged across spring, summer and autumn samples, 31.7% of the variation was linked to among sites and 68.3% to within sites (Table 10.3). If compared with results for *H. mantegazzianum* (77.9% of variation attributed among and 22.1% within sites; Krinke *et al.*, 2005), these figures indicate that the Lithuanian sites in which *H. sosnowskyi* was studied were less heterogeneous than the *H. mantegazzianum* sites sampled in the Slavkovský les, Czech Republic.

The composition of the *H. sosnowskyi* seed bank in the course of the season, expressed as the numbers of non-dormant, living and total seeds,

Table 10.2. Nested ANOVA of the vertical distribution of *H. sosnowskyi* seeds in the soil (layers: 0–5, 6–10, 11–15 cm) in spring. Data were transformed to square root numbers + 0.5 of living and dead seeds. Layer is evaluated as a fixed effect. *** $P < 0.001$, NS – not significant.

Source of variation	Living			Dead		
	df	MS	F	df	MS	F
Layer	2	323.12	51.402***	2	175.23	31.409***
Sites within layers	6	6.286	6.257***	6	5.579	5.788***
Replicates within sites	81	1.005		81	0.964	

Table 10.3. ANOVA of the soil seed bank of *H. sosnowskyi* among sites and within sites. Data are log transformed numbers plus 0.5 of the dormant, living and the total seeds, averaged for autumn, spring and summer samples. Sites are evaluated as random effects and variance is expressed in percentages. *** $P < 0.001$, * $P < 0.05$.

Source of variation	Dormant				Living				Total			
	df	MS	F	Variance	df	MS	F	Variance	df	MS	F	Variance
Among sites	2	2.450	9.301***	40.8	2	0.715	5.895*	30.4	2	0.783	6.263*	31.7
Within sites	27	0.263		59.2	27	0.121		69.6	27	0.125		68.3

showed significant differences among the spring, summer and autumn samples and varied significantly within individual sites (Table 10.4).

Average numbers of non-dormant, living and total seeds in the seed bank of *H. sosnowskyi* were highest in spring and lowest in summer (Fig. 10.2).

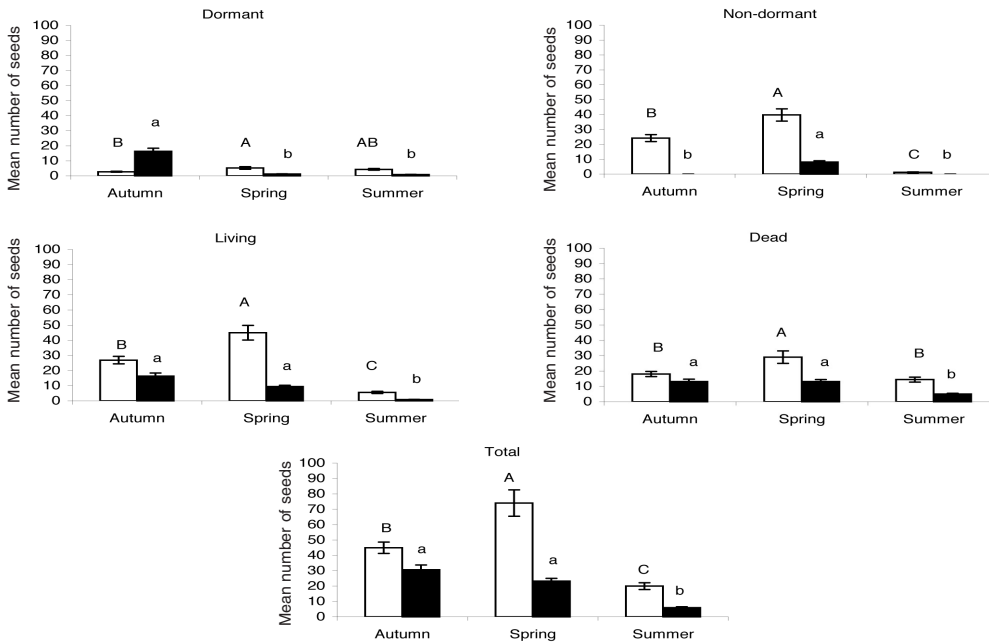


Fig. 10.2. Seasonal dynamics of the *H. sosnowskyi* seed bank (empty bars), inferred from autumn, spring and summer samples. Bars are mean numbers of dormant, non-dormant, living, dead and total seeds. Each value is pooled across three localities and ten replicates within each locality. Vertical lines are standard errors of the means. Bars with the same letters did not differ significantly ($P < 0.05$) in deletion tests (Crawley, 2002); capital letters refer to *H. sosnowskyi* and lower case letters to *H. mantegazzianum*. Corresponding values for *H. mantegazzianum* (black bars) are from Krinke *et al.* (2005). Germinated seeds were considered as non-dormant; non-germinated seeds were tested for viability by staining with tetrazolium; viable seeds were considered as dormant.

Table 10.4. Nested ANOVAs of the variation of the soil seed bank of *H. sosnowskyi* among seasons. Data are square rooted numbers + 0.5 of the dormant, non-dormant, living, dead and the total of seeds. Season is evaluated as a fixed effect. *** $P < 0.001$, * $P < 0.05$.

Source of variation	Dormant			Non-dormant			Living			Dead			Total		
	df	MS	F	df	MS	F	df	MS	F	df	MS	F	df	MS	F
Season	2	1.163	0.269 n.s.	2	193.50	33.292***	2	134.92	15.213*	2	16.045	2.135 n.s.	2	12.610	7.481*
Sites within season	6	4.317	7.796***	6	5.812	4.274***	6	8.869	5.245***	6	7.515	4.192***	6	1.133	
Replicates within sites	81	0.554		81	1.360		81	1.691		81	1.792		81	0.265	

Table 10.5. Number of seeds of *H. sosnowskyi* per m² in the soil seed bank at the three localities studied. Each value is the mean ± SD of ten replicates. Values per m² were extrapolated from the original data, which were used in statistical analyses.

Locality	Spring			Summer			Autumn			Total		
	Non-dormant	Dormant	Dead	Non-dormant	Dormant	Dead	Non-dormant	Dormant	Dead			
1	11,477 ± 6,744	2,312 ± 1,663	9,407 ± 5,937	23,195 ± 13,859	462 ± 403	1,286 ± 753	3,055 ± 2,175	4,804 ± 2,835	4,502 ± 1,254	704 ± 437	4,040 ± 2,241	9,246 ± 3,501
2	6,512 ± 3,532	503 ± 977	4,201 ± 3,543	11,216 ± 7,032	161 ± 208	643 ± 388	1,809 ± 957	2,613 ± 1,180	3,437 ± 1,771	402 ± 268	2,854 ± 2,348	6,693 ± 4,120
3	5,970 ± 1,700	362 ± 247	3,899 ± 1,283	10,231 ± 2,702	141 ± 269	663 ± 519	3,819 ± 2,127	4,623 ± 2,720	6,613 ± 4,582	543 ± 391	3,980 ± 1,805	11,135 ± 6,363
Total	7,986 ± 3,035	1,059 ± 1,087	5,836 ± 3,097	14,881 ± 7,217	255 ± 180	864 ± 366	2,894 ± 1,014	4,013 ± 1,216	4,851 ± 1,616	550 ± 151	3,625 ± 668	9,025 ± 2,229

This seemingly contradicts the pattern found for *H. mantegazzianum*, where most are found in autumn, and then the number of dormant, living, dead and total seeds decreases (Fig. 10.2). This discrepancy seems to be a result of differences in the sampling regime. The seed bank in Lithuania was sampled over a single season (from spring to autumn), while in the Czech Republic it was over two subsequent seasons (from autumn to summer the following year). Thus, the pattern in total numbers of *H. sosnowskyi* seeds reflects between-year fluctuations in the number and density of flowering plants. This explains why more seeds were found in spring than after seed set in autumn (Fig. 10.2); the seeds present in spring and summer were produced in the previous year.

To avoid the bias caused by the different sequence of sampling times, the percentages of non-dormant, dormant and dead seeds were compared (Fig. 10.3A). The percentage of living seeds of *H. sosnowskyi* in the total seed bank did not change from autumn (59.8%) to spring (60.8%), but decreased to 22.8% in summer. The percentage of non-dormant seeds among living seeds was similar in autumn (89.8%) and spring (88.3%), but decreased to 27.9% in summer (Fig. 10.3B).

The main difference between the species is in the autumn seed bank, when almost all the seeds of *H. mantegazzianum* were dormant and nearly 90% of *H. sosnowskyi* seeds were non-dormant (Fig. 10.3B). It needs to be noted that due to unusual climatic conditions in Lithuania in the year of sampling, ripe seeds were covered by early snow. Thus, the autumn sample was taken after the snow had melted. This short period of wet and cold conditions might have been enough to stratify the seeds and break their dormancy. An easy breaking of seed dormancy in autumn accords well with the laboratory finding that seeds of *H. sosnowskyi* require a shorter period of cold stratification for breaking dormancy than those of *H. mantegazzianum* (see below).

The average density of *H. sosnowskyi* seeds, expressed per m² and pooled across localities, was 9025 ± 2229 (mean \pm SD) in autumn, $14,881 \pm 7217$ in spring and 4013 ± 1216 in summer for total seeds, and 5400 ± 3281 , 9045 ± 6411 and 1119 ± 889 , respectively, for living seeds (Table 10.5). For *H. mantegazzianum*, it was 6719 ± 4119 total seeds in autumn, 4907 ± 2278 in spring and 1301 ± 1036 in summer (Krinke *et al.*, 2005).

Seed bank depletion

Field data on changes in the seasonal dynamics of the seed bank provide important information on the strategy of alien species in terms of population regeneration and competition with native taxa (Van Clef and Stiles, 2001). The results, however, can be biased by factors beyond an investigator's control, such as the seasonal variation in the weather and the fact that the amount of seeds entering the soil is not known precisely. Burial of controlled numbers of seeds and the monitoring of their germination on a fine temporal scale can provide more reliable information on the temporal pattern of seed bank depletion. Moravcová *et al.* (2006) record the fate of buried seeds of

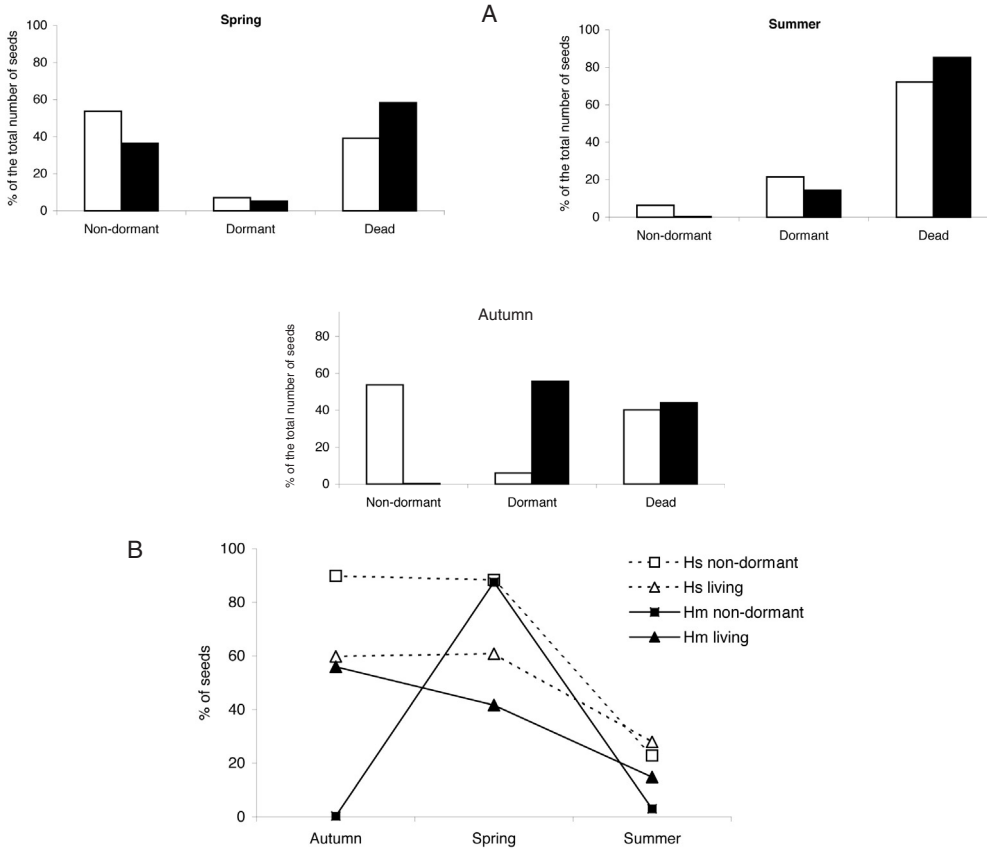


Fig. 10.3. (A) Changes in the percentage of dormant, non-dormant and dead seeds in the seed bank of *H. sosnowskyi* (empty bars) during the course of a year. Samples were taken in autumn (after seed release), spring (before germination) and summer (before new seeds are shed). Mean values shown are pooled across three localities in Lithuania. (B) Changes in the percentage of living seeds that are not dormant, and of the total seeds that are living for *H. sosnowskyi* (empty symbols). The percentage of non-dormant seeds is the same in autumn and spring, and decreases to a low value in summer, after the vast majority of non-dormant seed germinated in spring. The percentage of living seed is highest in spring and lowest in summer. Germinated seeds were considered as non-dormant; non-germinated seeds were tested for viability by staining with tetrazolium; viable seeds were considered as dormant. Corresponding data on *H. mantegazzianum* (Hm; black symbols and bars, respectively) are taken from Krinke *et al.* (2005).

both species in the experimental garden of the Institute of Botany, Průhonice, Czech Republic (50° 00' 03.9" N, 14° 33' 31.7" E). Seeds of *H. sosnowskyi* were placed in bags made of a fine mesh and buried to a depth of 5–7 cm in the autumn of 2004, those of *H. mantegazzianum* 2 years earlier, and removed at monthly intervals (except during the winter months when the soil was frozen). Living seeds were classified as non-dormant if they germinated

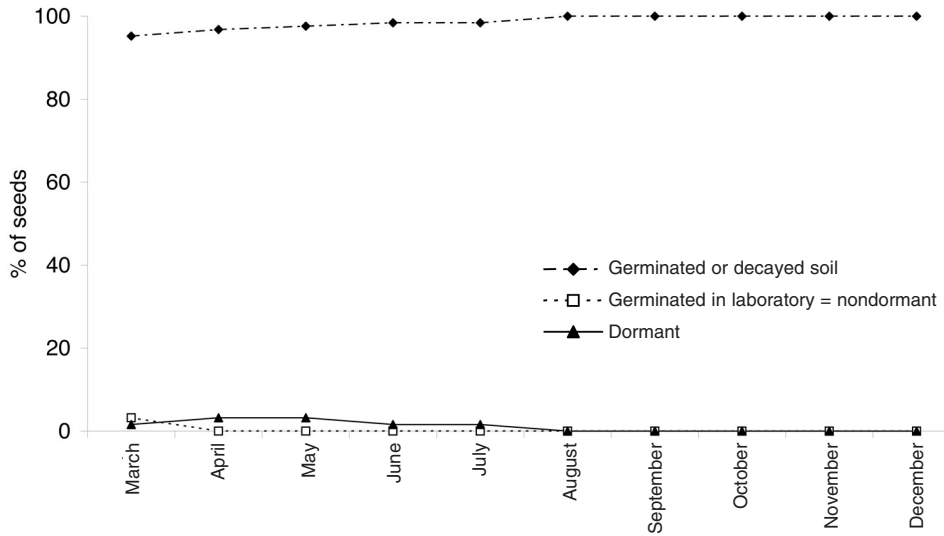


Fig. 10.4. Seasonal pattern in the depletion of the *H. sosnowskyi* seed bank during the course of one season. Percentages of the seeds buried in the experimental garden of the Institute of Botany, Průhonice, Czech Republic that were dormant and non-dormant are shown. Each percentage is based on five replicates. Seeds collected earlier in 2004 were buried at a depth of 5–8 cm at the end of October and followed until December 2005. They were taken from the soil every month, except when the soil was frozen, and those that germinated were recorded; those that did not were tested for dormancy by germinating them in the laboratory at 10/5°C and for viability using tetrazolium.

within 1 month following transfer to a climate chamber, or dormant after testing for viability using tetrazolium staining (Baskin and Baskin, 1998).

Of seeds of *H. sosnowskyi* in the first spring sample (March 2005), 95.2% had already germinated or decayed in the soil. This sample contained a very small proportion of non-dormant and dormant seed, which was ascertained in the laboratory. By May and July, only 3.2% and 1.6%, respectively, of the seeds in the soil had not germinated and all were dormant. From August onwards the soil samples did not contain any living seeds (Fig. 10.4; cf. *H. mantegazzianum*, see Fig. 5.5). These results suggest that seeds of *H. sosnowskyi* are unable to survive for more than one season; the seed bank was very quickly depleted by rapid germination in spring and later on by the rapid decay of dormant seeds.

In contrast, at least a small amount of *H. mantegazzianum* seeds remained viable for considerably longer, a minimum of 3 years (1.2%, see Moravcová *et al.*, Chapter 5, this volume). This may be linked to the fact that a higher percentage of *H. mantegazzianum* seeds is located in soil layers deeper than 5 cm. The difference is rather small (5% compared to 2% in *H. sosnowskyi*), but given the fecundity of both species and the fact that the percentage of seeds that survive is generally very low, it may be important. The more seeds that occur in the lower soil layers, the higher the probability of a persistent seed bank (*sensu* Thompson *et al.*, 1997).

Further indication that the dynamics of both species' seed banks differ is the easier breaking of dormancy in *H. sosnowskyi*, which enables this species to germinate in autumn when climatic conditions are favourable; however, the survival of seedlings that emerge in autumn and their role in the population dynamics and renewal are unclear; no seedlings were found in the field in Lithuania (Z. Gudžinskas, unpublished). The seed bank of *H. mantegazzianum* is classified as 'short-term persistent' (see Moravcová *et al.*, Chapter 5, this volume; Krinke *et al.*, 2005), but that of *H. sosnowskyi*, based on the results of this study, must be considered to be 'transient' (in sense of Thompson *et al.*, 1997). This is suggested despite the relatively high percentage of dormant seeds in Lithuania in summer, which is a feature of short-term persistent seed banks. Nevertheless, other field results (very high percentage of the seeds in the upper soil layer) together with those obtained in the common garden experiment (seeds lost dormancy very rapidly and did not survive more than one season) and germination studies (seeds germinate even more readily than those of *H. mantegazzianum*) indicate that *H. sosnowskyi* has a transient soil seed bank. However, to verify this, seed bank experiments in those regions of Europe where the species is invasive (see Jahodová *et al.*, Chapter 1, this volume; Nielsen *et al.*, 2005) and the climate is different from Central Europe are needed.

Differences in the Germination Characteristics of *Heracleum mantegazzianum* and *H. sosnowskyi*

To compare the germination of both species, seeds of *H. mantegazzianum* (Moravcová *et al.*, 2006 and Chapter 5, this volume) and *H. sosnowskyi* were germinated at different temperature regimes. Seeds of both species were first stratified for 2 months at temperatures of 4–6°C to break the dormancy and then germinated at different temperatures: 2, 6, 10/5, 20/5, 15/10, 25/10 and 22°C (see Fig. 10.5).

The majority (71–94%) of the seeds of *H. sosnowskyi* germinated almost regardless of the temperature regime. The lowest germination percentages were recorded at 22°C (Fig. 10.5). However, 10% germinated during the stratification process, before setting the temperature for germination. These results suggest that the majority of the seeds of *H. sosnowskyi* break dormancy at almost the same time, following a stratification period as short as or less than 2 months, and immediately germinate, independently of the temperature. This accords with the early spring massive germination of *H. sosnowskyi* seeds, observed in the field in Lithuania as well as in the common garden burial experiment conducted in the Czech Republic. This experiment also showed that the seeds of *H. sosnowskyi* only germinated before March.

This is very different from *H. mantegazzianum*, where dormancy is broken gradually and germination can extend over several years (3 years minimally; cf. Figs 5.6 and 5.7). A study of the germination requirements, using the same design as described here for *H. sosnowskyi*, provided different

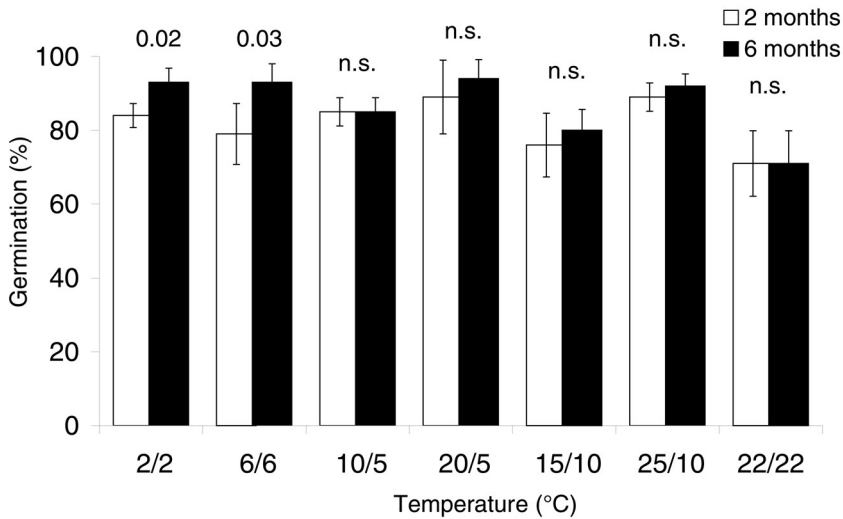


Fig. 10.5. Percentage of *H. sosnowskyi* seeds (mean \pm SE) that germinated when subjected to various temperature regimes and under two germination periods. The seeds were cold-stratified for 2 months at 4–6°C prior to the experiment. Seven temperature regimes were used: 2, 6, 10/5, 20/5, 15/10, 25/10 and 22°C (with alternating day/night temperatures; the day and night each lasted 12 hours). Percentage of seeds that germinated was ascertained after 2 and 6 months. Differences between times within the temperature regime are shown above bars (t-test for paired comparisons).

results for *H. mantegazzianum*. The stratification period for seeds of *H. mantegazzianum* needed for breaking dormancy lasts at least 2 months. The highest percentage and fastest germination occurred at alternating temperatures of 20/5°C, with slower but comparably high percentages of germination at 6°C, following stratification at the same temperature. In *H. mantegazzianum*, all germination at the higher temperatures occurred in the first 2 months and then stopped. However, germination at low temperatures of 2°C and 6°C continued (Moravcová *et al.*, 2006 and Chapter 5, this volume). This indicates that the higher temperatures represent a constraint on the breaking of dormancy in *H. mantegazzianum* and seeds remain dormant until the next cold period.

The above results can be interpreted with regard to the distribution limits of both species in Europe. The European distribution of these two *Heracleum* species is distinct, with *H. sosnowskyi* confined to the northern and eastern parts of the continent and *H. mantegazzianum* having the centre of the invaded distribution range in central and western Europe (see Jahodová *et al.*, Chapter 1, this volume). An attempt to elucidate climatic factors that might have played a role in shaping this distribution was made using *H. mantegazzianum* as a model species. Pyšek *et al.* (1998) show that the distribution of this species in the Czech Republic is significantly affected by the temperature in January; the number of reported localities decreases with increasing

temperature, but the distribution is also determined by human population density, which reflects possibilities for dispersal.

Although the transient seed bank and immediate germination not extending over a period longer than 1 year may be a disadvantage in terms of the long-term population dynamics (Pyke, 1990; Van Clef and Stiles, 2001), the germination characteristics of *H. sosnowskyi* indicate that invasion by this species is unlikely to be limited by temperature. The current distribution of *H. sosnowskyi* seems to be driven mainly by human activities and the history of introductions, namely the massive planting in eastern Europe, than by ecological constraints.

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