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Seed Germination, Dispersal and Seed Bank in *Heracleum mantegazzianum*

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> *Royal beast did not forget. Soon they escaped, spreading their seed,*
> *preparing for an onslaught, threatening the human race*
>
> (Genesis, 1971)

Introduction

Since reproduction of *Heracleum mantegazzianum* Sommier & Levier is exclusively by seed (Tiley *et al.*, 1996; Moravcová *et al.*, 2005; Krinke *et al.*, 2005), a detailed knowledge of its seed ecology is crucial for understanding this species' invasive behaviour. This chapter summarizes available information on seed dormancy, pattern of germination, seed bank formation and dynamics, as well as the first solid data on the longevity of seed in the soil.

Heracleum mantegazzianum has oval-elliptical broadly winged mericarps which are connected into pairs by carpophore (Fig. 5.1A) and split when mature (Holub, 1997). The mericarps are 6–18 mm long and 4–10 mm wide, and each contains one seed. The embryo is rudimentary (Martin, 1946) and surrounded by oily endosperm. Mature fruits have a strong resinous smell (Tiley *et al.*, 1996). For simplicity the unit of generative reproduction and dispersal is termed 'fruit' throughout this chapter rather than the morphologically correct 'mericarp', and the term 'seed' is used when referring to germination.

Dormancy Breaking Mechanisms

It has long been known that seeds of *H. mantegazzianum* do not germinate after dry storage (Grime *et al.*, 1981) and cold stratification is necessary for germination (Nikolaeva *et al.*, 1985; Tiley *et al.*, 1996; Otte and Franke, 1998).

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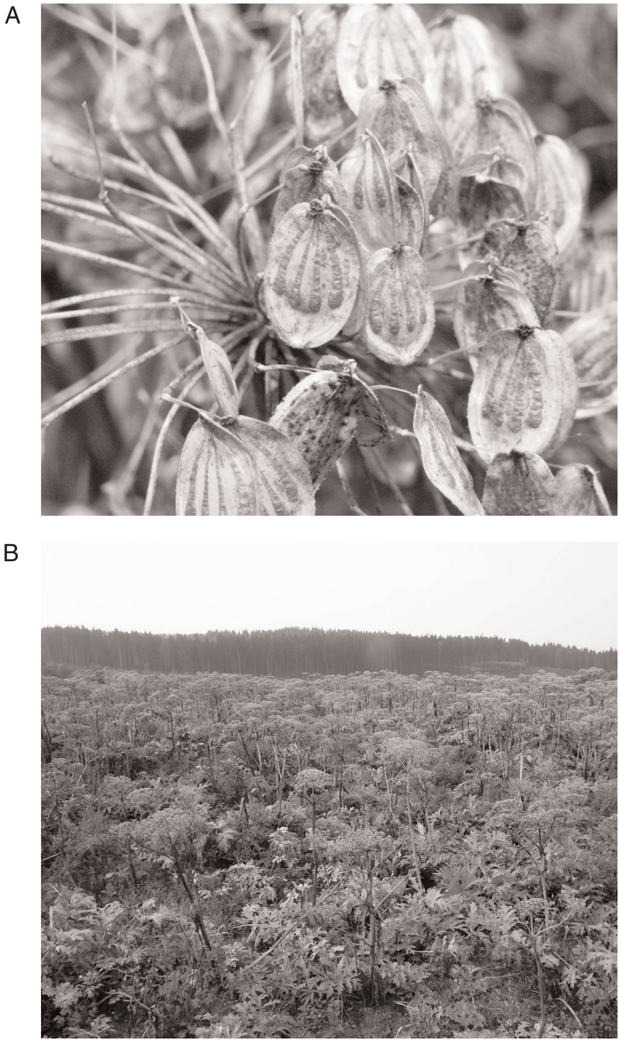

Fig. 5.1. (A) *Heracleum mantegazzianum* has oval-elliptical broadly winged mericarps which are connected into pairs by carpophore. (B) In the autumn, seeds are released from plants forming dense stands, as in the largest locality of the Slavkovký les study region, Czech Republic. Photo: P. Pyšek.

Under natural conditions in the Slavkovský les study area, Czech Republic, seeds germinate early in spring after snow melting (March to April) (see Pergl *et al*., Chapter 6, this volume; Krinke *et al*., 2005). Seeds of *H. mantegazzianum* exhibit morphophysiological dormancy in the sense of Nikolaeva *et al*. (1985) and Baskin and Baskin (2004); ripe seeds have an underdeveloped embryo which is physiologically dormant. For a seed to germinate, embryo growth needs to be completed and its physiological dormancy broken. Both these processes occur in cold and wet conditions of autumn and winter stratification in the field; corresponding laboratory conditions are temperature within the range of 1–6°C (Moravcová *et al.*, 2005). Gibberellic acid does not stimulate the germination of freshly ripe seeds (L. Moravcová, unpublished results). From all this information and according to the results of Nikolaeva *et al.* (1985), this type of morphophysiological dormancy (further MPD) in the sense of Baskin and Baskin (2004) resembles a deep complex MPD. The same type of MPD was recorded in other species of *Apiaceae*, e.g. *Heracleum sphondylium* L. (Stokes, 1952a, b; Nikolaeva, 1985) or *Anthriscus sylvestris* (L.) Hoffm. (Lhotská, 1978; Baskin *et al.*, 2000). Nevertheless, information on embryo growth is needed to prove this for *H. mantegazzianum*.

Germination Characteristics Related to the Position on the Plant

Heracleum mantegazzianum bears umbels at various positions and orders (for a scheme of the plant architecture see Moravcová *et al.*, 2005: Fig. 1; and Perglová *et al.*, Chapter 4, this volume) and characteristics of seeds are affected by where on the plant they are produced. The position of a seed or fruit on a mother plant has been shown to affect seed mass, morphology, germination and dormancy characteristics (for a survey see Baskin and Baskin, 1998; Gutterman, 2000). For *Apiaceae*, seed mass and/or germination has been shown to depend on umbel position in many species (e.g. Ojala, 1985; Thomas *et al.*, 1978, 1979; Hendrix, 1984a; Hendrix and Trapp, 1992). Compared to the other members of its family, *H. mantegazzianum* is not unusual with respect to seed position on the mother plant. Moravcová *et al.* (2005) studied the influence of fruit position on the mother plant on fruit mass, germination percentage and rate of germination in *H. mantegazzianum*. The data were collected in the Slavkovský les Protected Area in the west of the Czech Republic (for details on this region, see Perglová *et al.*, Chapter 4, this volume). Seeds were collected from the terminal (i.e. primary) umbel, secondary umbels in satellite positions and secondary umbels in branch positions, separately from the centre and margin of each sampled umbel (see Fig. 4.1). The overall mean mass of a single fruit was 13.1 mg (Table 5.1) and corresponded to the range 4.6–23.2 mg given by Tiley *et al.* (1996) for *H. mantegazzianum*. Fruits from terminal inflorescences were heavier than those from satellites and branches, and those produced in the centre of an umbel were heavier than those from the margin (Moravcová *et al.*, 2005). Fruits from terminals weighed on average 15.9 mg, whereas those from satellites and branches weighed 11.7 mg, and the fruits from the centre were significantly heavier than those from the margins, being 13.3 and 12.9 mg, respectively (Table 5.1). Overall, the determination of fruit mass in *H. mantegazzianum* follows the same rules as in other *Apiaceae* (Hendrix, 1984a, b; Thompson, 1984; Hendrix and Sun, 1989), but the variation is several orders of magnitude lower than in some other species.

The mean percentage germination at 8–10°C (after 2 months of cold stratification at 2–4°C) found by Moravcová *et al.* (2005) was 91%, and varied among the seven sites studied, but was not affected by fruit position on a plant.

Table 5.1. Fruit mass in *H. mantegazzianum* depends on the position of fruit on a mother plant. Data are means ± SD (mg) and *n* (sample size) for fruit sampled from combinations of umbel types on mother plant (terminal, satellite, branch) and positions within an umbel (centre or margin) from eight plants in each of seven sites in the Slavkovský les region, West Bohemia, Czech Republic. There were five replicates of each treatment. Data from Moravcová *et al.* (2005).

Fruit position within umbel	Umbel type (fruit position on the plant)							
	Terminal	*n*	Satellite	*n*	Branch	*n*	Mean	*n*
Centre	16.15 ± 2.75	270	11.93 ± 3.47	270	11.65 ± 3.12	265	13.25 ± 3.74	805
Margin	15.60 ± 2.59	265	11.52 ± 3.44	275	11.66 ± 3.3	270	12.90 ± 3.66	810
Mean	15.88 ± 2.67	535	11.73 ± 3.46	545	11.66 ± 3.12	535	13.08 ± 3.70	1615

Such a high percentage germination seems to be usual within the context of the *Apiaceae* family, where seeds usually germinate readily once dormancy is broken (Baskin and Baskin, 1990, 1991; Baskin *et al.*, 1995); a value of 94% was reported for *Anthriscus sylvestris* (Baskin *et al.*, 2000). In the study of Moravcová *et al.* (2005), cold and dark conditions mimicked closely the natural situation under the soil surface during spring. Moreover, the high percentage germination recorded in the laboratory corresponds with that obtained in a garden burial experiment, where about 90% of seed stored in the soil germinated over the first winter (Fig. 5.5 and Moravcová *et al.*, 2006). Given its fecundity (see Perglová *et al.*, Chapter 4, this volume), *H. mantegazzianum* exerts enormous pressure of highly germinable propagules in invaded sites (see Pyšek *et al.*, Chapter 19, this volume).

These results (Moravcová *et al.*, 2005) have practical implications as mechanical control often focuses on cutting terminal umbels or whole stems at flowering time (see Pyšek *et al.*, Chapter 7, this volume). Regeneration then occurs via higher-order umbels that produce fruit with the same capability to germinate as those produced on the terminal and low-order umbels. Similarly, the ability to produce a standard fruit in terms of weight, even on umbels of higher orders, contributes to successful regeneration after the loss of flowering tissues due to control efforts (see Pyšek *et al.*, Chapter 7, this volume).

The percentage of seeds of *H. mantegazzianum* which germinate does not depend on where on the plant the fruit is produced, but the rate at which they germinate does (Moravcová *et al.*, 2005). Large seeds germinated faster than small seeds; germination rate increased with increasing fruit mass and this pattern was consistent for all plants at each site (Fig. 5.2). Since seeds from terminals were heavier than those from branches, the former germinated sooner than the latter. Heavy seeds germinated faster than light seeds, but the difference was only obvious at the beginning of the experiment (Moravcová *et al.*, 2005). Faster germination of heavier seed adds to the ecological advantage resulting from their size; heavier seeds produce bigger seedlings (Harper, 1977) and this was also reported for other species within *Apiaceae* (Thomas *et al.*, 1979; Thomas, 1996).

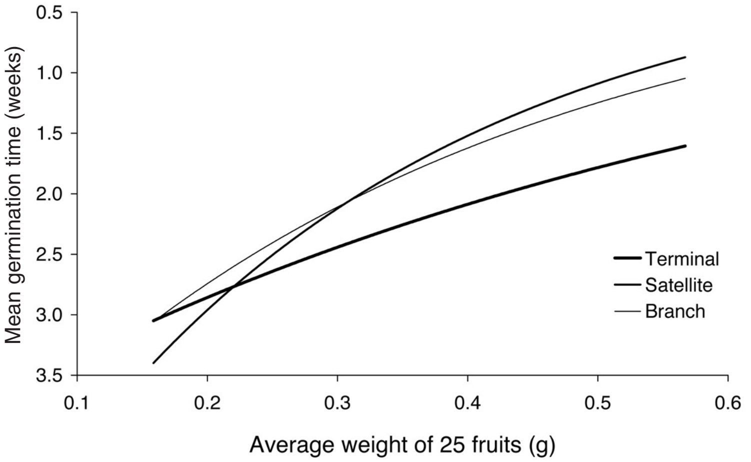

Fig. 5.2. The rate of germination of *H. mantegazzianum* seed increases with increasing fruit mass and the relationship is valid for all three umbel types (terminal, satellite, branch). Data are for a randomly chosen plant (*n* = 715 seeds). Terminal: rate = 1/exp(–3.345 + 3.852mass)$^{(1/2.45)}$; satellite: rate = 1/exp(–4.296+8.171mass)$^{(1/2.45)}$; branch = 1/exp(–3.763 + 6.441mass)$^{(1/2.45)}$. $\chi^2 = 1301.0$; $df = 5$; $P < 0.001$. The y-axis is reversed so the seeds that germinate first appear above those that germinate last for a given fruit mass. For most of the ranges in fruit mass, the germination rate of a particular fruit mass is higher for satellites and branches than terminals, but the average germination rate for terminals is higher than for satellites and branches because fruit from terminal umbels is, on average, much heavier than that from the other two umbel types. Hence seeds produced on terminals germinate faster. Seeds were stratified for 2 months at 2–4°C and then germinated at 8–10°C. Germination was recorded weekly for 6 months. From Moravcová *et al.* (2005).

Neither the characteristics of individual umbels (duration of flowering, size) nor those of whole plants (fecundity, age, height, basal diameter) had an effect on germination characteristics. The only significant relationship found was a negative one between fruit mass and plant height (Moravcová *et al.*, 2005).

Germination at Different Temperature Regimes

In the Czech Republic, seeds of *H. mantegazzianum* germinate exclusively in spring; no seedlings were found in the field in the autumn (Krinke *et al.*, 2005; Moravcová *et al.*, 2005; see Pergl *et al.*, Chapter 6, this volume). This conclusion is based on results obtained in the Slavkovský les study region, but may be considered as valid for Central European areas with similar climatic conditions. In the above region, seeds in the field germinate in March and April, when temperatures are still below 10°C (Fig. 5.6).

Preliminary results of laboratory experiments carried out at the Institute of Botany, Průhonice (Moravcová *et al.*, 2006) allow field observations to be linked with germination patterns revealed under controlled conditions.

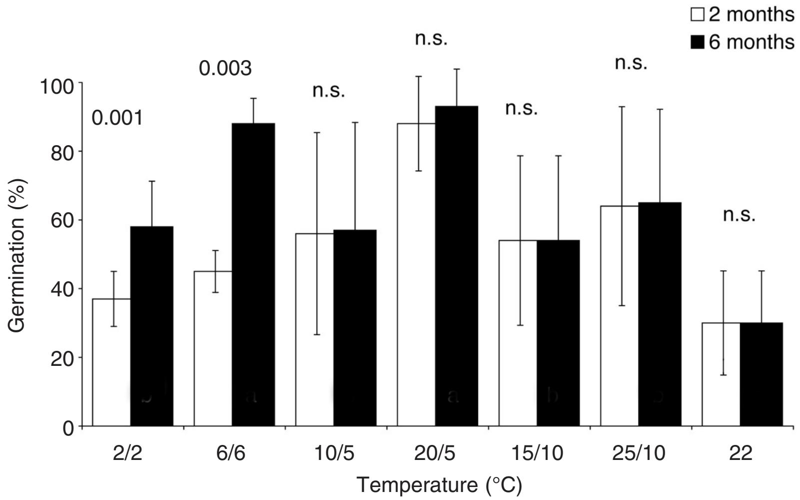

Fig. 5.3. Germination percentage of *H. mantegazzianum* seeds (mean ± SE) depends on the temperature regime and on the time provided for germination. Seeds cold-stratified for 2 months before the experiment were used for germination. Seven temperature regimes were used: 2, 6, 10/5, 20/5, 15/10, 25/10 and 22°C (in alternating day/night temperatures the day and night lasted 12 h). Percentage of seed that germinated was ascertained after 2 and 6 months. Differences between times at a particular regime are indicated on top of bars (t-test for paired comparisons). From Moravcová *et al.* (2006).

Although the stratified seeds of *H. mantegazzianum* were able to germinate under various temperature regimes (Fig. 5.3), the best germination was achieved either at a low temperature of 6°C (88% of seed germinated) or at an alternating temperature of 20/5°C (93%). At higher temperatures all germination occurred in the first 2 months, but then it virtually ceased and the percentage of germinated seeds did not increase up to the 6th month. On the other hand, seeds at low constant temperatures of 2°C and 6°C germinated gradually and for a long time; between 2 and 6 months, the percentage of germinated seeds increased by 20% and 43%, respectively (Fig. 5.3). These results suggest that higher spring and summer temperatures either induce seed dormancy or rather prevent the process of breaking dormancy which can only be completed under cold temperatures.

The Persistent Seed Bank of *Heracleum mantegazzianum*: in Pursuit of an Urban Myth

The development of opinions on the persistence of the soil seed bank in *H. mantegazzianum* is an interesting story, illustrating how dangerous it can be to accept information without checking original sources. Manchester and Bullock (2000) mention *H. mantegazzianum* among plants that have so far caused a serious problem in the UK and conclude that 'due to extensive seed banks and possible long-term viability of seeds, any control programme would need to have follow-up monitoring and control for at least 7 years after the initial control measures using herbicide or cutting'. To support this statement, they refer to Dodd *et al*. (1994) and Collingham *et al*. (2000). The paper of Dodd *et al*. (1994) is, however, a general review of the control of *H. mantegazzianum*, and bases the statement that the species produces 'an extensive seed bank in the vicinity of the parent plant' on Morton (1978), who refers explicitly to the longevity of dry seeds, and Lundström (1989). The latter paper is more ambiguous, claiming that 'seed viability of 15 years is possible' (Lundström, 1989). Collingham *et al*. (2000) make no direct reference to seed persistence, they only refer to the *Biological Flora of British Isles* for *H. mantegazzianum* (Tiley *et al*., 1996).

Tiley *et al.* (1996) are reasonably clear about seed persistence in the soil. They note that the seed biology of *H. mantegazzianum* is very similar to that of the native *H. sphondylium* – once seeds are adequately chilled, they germinate quite well at 5°C in the dark – and therefore a persistent seed bank is unlikely. They conclude that 'field observations indicate that most if not all shed seeds germinate in the following year', although only unpublished observations are cited in support of this. Once more Morton (1978) and Lundström (1989) are cited as sources of data on seed longevity, but again it is not clear whether Lundström is referring to dry seeds or to seeds in the soil.

Astute readers will have begun to detect a pattern here. Wherever the possibility of a persistent seed bank in *H. mantegazzianum* is raised, the ultimate source appears to be Lundström (1989). Lundström and Darby (1994) is a good example:

> The plant is characterised by rapid growth and the production of large numbers of viable seeds, which remain capable of germinating over 7–8 years. Because of these factors, vigorous control measures are required over a number of years in order to control and eradicate the plant (Dodd *et al*., 1994).

The circle seems to close here, because the information on seed persistence in Dodd *et al*. (1994) comes from Lundström (1989)…

So, what does Lundström (1989) have to say? Very little, in fact: 'It cannot be avoided [even after control with herbicides] that new seedlings emerge for several years when the stand has been in the same place for several decades. There are data suggesting that germinability could extend up to fifteen years.' There are at least two ambiguities here. It is hardly surprising that new seedlings emerge after an attempt to control a large stand by herbicides. Such control is rarely complete, and new seeds may always be dispersed from outside. It is also now clear why those who cite Lundström are vague about whether he is referring to dry seeds or to seeds buried in the soil – Lundström is himself vague. Even if he is referring to buried seeds, it is most likely that the 'suggestive data' come from the sporadic appearance of seedlings in the field, which could be recently dispersed.

In fact, the similarity of *H. mantegazzianum* and *H. sphondylium*, a species without a long-persistent seed bank (Thompson *et al*., 1997), might have made researchers more suspicious about the claimed longevity of

H. mantegazzianum seed in the soil. Further, indirect evidence that the period is actually much less has been around for some time – Andersen and Calov (1996) sampled the soil beneath a stand of *H. mantegazzianum* that had been eliminated by 7 years of sheep grazing and, as they found no viable seeds, concluded that longevity in the soil is certainly less than 7 years.

Seed Bank Type, its Size and Seasonal Dynamics

What is clear from the above is that no-one has previously conducted a serious study of seed bank dynamics or controlled burial experiments with *H. mantegazzianum* seeds. To clarify the behaviour of this species in terms of seed bank type and its dynamics, several studies were carried out within the framework of the GIANT ALIEN project. The amount of seeds in the seed bank, its vertical distribution and seasonal changes were studied by Krinke *et al.* (2005) at seven sites in the Slavkovský les region, Czech Republic. The study spanned two growing periods with censuses made in autumn after most seeds were released, in spring before seed germination, and in summer after spring germination and before seed release in the following autumn. The seeds were classified into three categories (dormant, non-dormant and dead) after collection (for explanation see Fig. 5.4).

The total number of seeds significantly increased with mean density of flowering plants at a site. The numbers of living, dead and total seeds were high in autumn, remained at the same level until spring, but from spring to summer, they all decreased. The number and proportion of dormant seeds was significantly higher in autumn than in spring or summer, and the number of non-dormant seeds was highest in spring (Fig. 5.4A). Proportions of dormant, non-dormant and dead seeds exhibited considerable seasonal dynamics. The percentage of dead seeds consistently increased from autumn to the following summer (Fig. 5.4A). The percentage of living seeds in the total seed bank decreased during winter from 55.9% in the autumn sample to 41.7% in spring to 14.8% in summer (Fig. 5.4B). The percentage of non-dormant seeds among living seeds was 0.3% in autumn, over winter it increased to 87.5% in the spring sample, and decreased to 3.0% in summer (Fig. 5.4B). After massive fruit release in autumn, nearly all living seeds (99.7%) were dormant. As almost no non-dormant seeds were found in autumn, this supports the observations that germination and population recruitment from seedlings in this species occur exclusively in spring (Krinke *et al.*, 2005; see Pergl *et al.*, Chapter 6, this volume).

Of the total variation in seed bank size, about four-fifths was attributed to variation among sites, and one-fifth to that within sites. 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 number of seeds, and 3759 ± 2906, 2044 ± 1198 and 192 ± 165, respectively, for living seeds (Krinke *et al.*, 2005 and their Table 5). These data (Krinke *et al.*, 2005) represent the first quantitative estimate of a seed bank in *H. mantegazzianum*, because numbers reported previously were based on

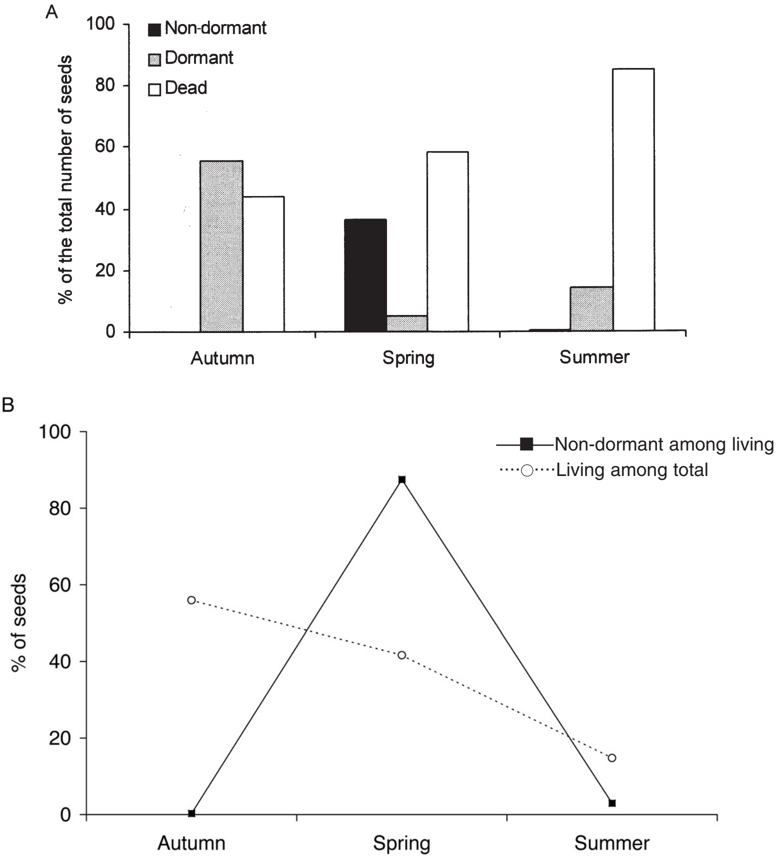

Fig. 5.4. (A) Changes in representation of dormant, non-dormant and dead seeds in the seed bank of *H. mantegazzianum* from autumn (after seed release) through spring (before germination) to the following summer (before new seeds are shed). Mean values shown are pooled across nine localities in the Slavkovský les region, Czech Republic. (B) The proportion of non-dormant among living seed is close to zero in autumn, reaches a peak in spring after dormancy has been broken by cold and wet stratification over winter, and decreases to very low values in summer, after the vast majority of non-dormant seed germinated in spring. The proportion of living seed among the total number of seed steadily decreases in the course of the 'seed-cycle year', as part of the seed population gradually decays. Based on data from Krinke *et al.* (2005). Seeds germinated up to 1 month were considered as non-dormant, non-germinated living seeds were considered as dormant and decayed seeds found in the soil sample or seeds found dead after germination were considered as dead.

estimates from seedlings germinating in the field (Andersen and Calov, 1996) or on multi-species seed bank studies (Thompson *et al.*, 1997). Such numbers of seeds found per m^2 of the soil exceed the average value in the family *Apiaceae* by an order. Only two species of *Apiaceae* (*Ammi majus* L. and *Torilis japonica* (Houtt.) DC.) exhibit seed density values comparable with

H. mantegazzianum (Thompson *et al.*, 1997). The reproductive potential of *H. mantegazzianum* is enormous and seems to be a crucial feature making invasion possible to the extent observed in the region (Krinke *et al.*, 2005) and elsewhere in Europe (Ochsmann, 1996; Tiley *et al.*, 1996).

Quantitative data of Krinke *et al.* (2005) allow some extrapolations to the landscape level. From knowledge of *H. mantegazzianum* population size in the largest study site (99,000 m^2) and the average number of non-dormant seeds present in the spring, it can be calculated that each year in spring there are 386 million seeds, ready to germinate, in a single site.

So which seed bank type best fits what we now know about *H. mantegazzianum*? The species was 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). However, Krinke *et al.* (2005) classified the soil seed bank of *H. mantegazzianum* as a short-term persistent soil seed bank *sensu* Thompson *et al.* (1997) as in their samples 95% of seeds were concentrated in the upper soil layer and some living seeds were also present in lower soil layers. Moreover, the data reported in the following sections clearly indicate that seeds of *H. mantegazzianum* do persist in the soil for some years and that a short-term persistent seed bank is the case here.

Seasonal and Long-term Survival of Buried Seed and Timing of Germination

In another experiment, Moravcová *et al.* (2006) monitored the survival of buried seeds and seasonal timing of germination in *H. mantegazzianum* over 2 years. They found that the depletion of the seed bank during the first winter following burial was very fast; of seeds buried in September 2002 at the experimental garden of the Institute of Botany in Průhonice, Czech Republic, 91.4% germinated (or decayed) by May and 91.8% by October of the following year. During the second winter, the proportion of germinated (or decayed) seeds increased to 97.4% in May 2004 (Fig. 5.5). Only a small proportion of seeds survived in a viable state in the soil over the first winter following burial. In May and October 2003, dormant seeds made up 8.4% and 8.2%, respectively, of the total. A year later, the proportions recorded were 2.6% in May 2004 and 3.3% in October 2004 (Fig. 5.5).

These results perfectly correspond with those of Krinke *et al.* (2005) and with results of long-term survival experiments of buried seeds in the Czech Republic (Fig. 5.7). Of seeds (of the same seed batch) buried at ten different localities in the Czech Republic (five replications of 100 seeds), selected in order to represent a range of climates and soil types, on average 8.8% survived 1 year, 2.7% 2 years and 1.2% remained viable and dormant after 3 years of burial. These preliminary results provide evidence that *H. mantegazzianum* forms a seed bank, with some proportion of seeds surviving longer than 1 year. From the results of seed longevity mentioned above (Moravcová *et al.*, 2006), it can be supposed that the seeds of *H. mantegazzianum* will not persist in soil for a long time. Such species with seeds

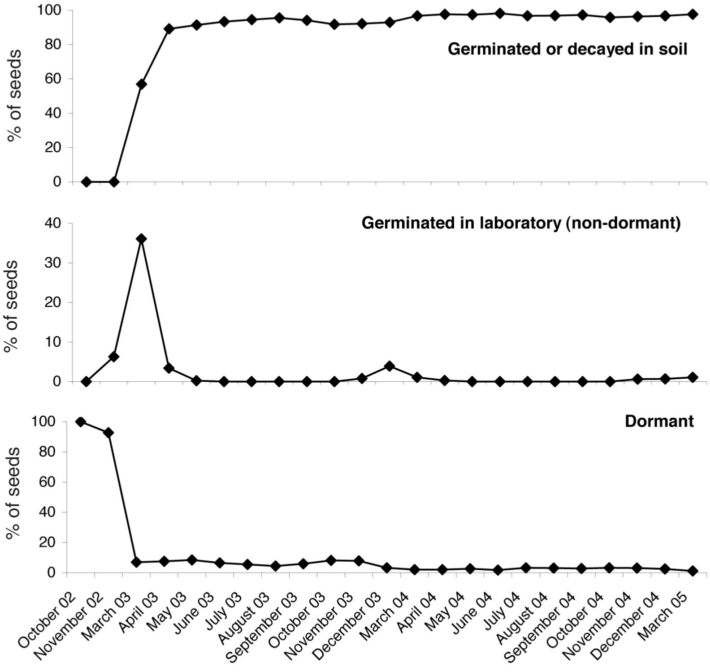

Fig. 5.5. Seasonal pattern of seed bank depletion in the course of two vegetation seasons. Percentage of dormant and non-dormant seeds among the total buried at the experimental garden of the Institute of Botany, Průhonice, Czech Republic. Each number is a mean of ten replicates. Seeds collected earlier in the same year were buried at a depth of 5–8 cm at the beginning of October 2002 and followed for two subsequent vegetation seasons, until March 2005. They were taken from the soil every month, except when the soil was frozen, and those that germinated or decayed were recorded; those that did not were tested for dormancy by germination in the laboratory at 10/5°C and for viability by tetrazolium. Based on data from Moravcová *et al.* (2006).

persisting in soil for at least 1 year, but less than 5 years, form in the sense of Thompson *et al*. (1997) a short-term persistent seed bank. The experiment continues in order to determine the maximum persistence of seeds of *H. mantegazzianum* in the soil, which can only be reliably determined by this kind of experiment.

Breaking of Dormancy: Towards a Threshold or Dormancy/Non-dormancy Cycle?

Combined together, the results of the experiments reported above make it possible to outline the pattern of seed germination and survival in the soil in *H. mantegazzianum*. Seeds in the field start to germinate early in spring (March in the study area in the western part of the Czech Republic) and most

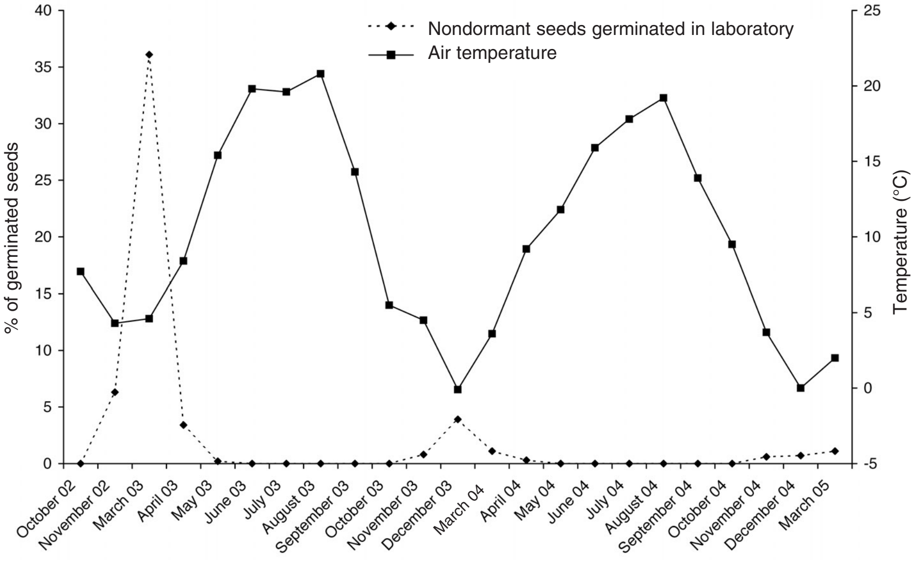

Fig. 5.6. Percentage of non-dormant seeds that germinated in the laboratory at 10/5°C, immediately after removal from the soil. Pattern recorded over two vegetation seasons is related to mean air temperature for months when seeds were tested. See Fig. 5.5 for details of data. Based on data from Moravcová *et al.* (2006).

of them do so up to the end of April or beginning of May (Figs 5.5 and 5.6). Despite considerable effort, no new seedlings were found in invaded sites later in the season and also, no buried seeds germinated in the soil after then (Moravcová *et al.*, 2006). However, the buried seeds removed from the soil started to germinate in the laboratory in November (Fig. 5.6). This corresponds to the fact that seeds need about 2 months of cold stratification below 8°C to break dormancy (Krinke *et al.*, 2005; Moravcová *et al.*, 2005); in November, this requirement is met for the seeds buried in the soil.

However, in the field seeds do not germinate in the autumn because of unsuitable conditions; in the laboratory they do. Obviously, buried seeds start to germinate in the laboratory approximately 2 months after the outside air temperature has dropped below 10°C (Fig. 5.6). But no buried seeds germinated before, i.e. in the course of the preceding late spring, summer and autumn when day temperature was above 10°C. This confirms the experimentally detected fact that although stratified seeds of *H. mantegazzianum* are able to germinate at a broad range of temperatures (Fig. 5.3), after being exposed to above 6°C for a longer time (up to 2 months) they cease germination and another cold period is needed to restart the germination process (Fig. 5.6).

It appears that seeds that have not germinated in spring (ca. 9% of seeds buried in the previous autumn) re-enter or retain dormancy during the high summer temperatures and break dormancy again during the following cold autumn and winter period (Fig. 5.5 and 5.6). It is hard to say whether the seeds in soil go through the annual dormancy/non-dormancy cycles which have been known for many annuals (Baskin and Baskin, 1998) and also for some perennials. The conditional dormancy/non-dormancy cycles are reported, for example, for a perennial *Rumex obtusifolius* L. (van Assche and Vanlerberghe, 1989), or biennials *Verbascum blattaria* L., *V. thapsus* L. (Vanlerberghe and van Assche, 1986; Baskin and Baskin, 1981) and *Oenothera biennis* L. (Baskin and Baskin, 1991) and dormancy/non-dormancy cycles are known also for perennials such as *Lychnis flos-cuculi* L. (Milberg, 1994a), *Primula veris* L. and *Trollius europaeus* L. (Milberg, 1994b), *Rhexia mariana* L. var. *interior* (Pennell) Kral & Bostick (Baskin *et al.*, 1999) or in sedges (Schütz, 1998). In *H. mantegazzianum* this question seems to be more complex. In burial experiments, the majority of seeds found dormant after 1 year in the soil had a morphologically fully developed embryo (Fig. 5.8C), which means that such seeds are only physiologically dormant; morphological dormancy must have been broken at that time. However, some seeds with an underdeveloped (Fig. 5.8A) or partially developed embryo (Fig. 5.8B) that had kept morphological (or morphophysiological) dormancy were also found (Moravcová *et al.*, 2006). Therefore, it seems more probable that dormancy in seeds of *H. mantegazzianum* is not broken completely in the first spring, but the breaking happens gradually and this process can take place only in months with sufficiently cold temperatures. This explains why the seeds staying dormant in soil have to wait until the next spring to germinate. That a small amount of seeds (about 1%) are able to survive in dormant state in the soil for at least 3 years (Fig. 5.7) suggests that the dormancy-breaking processes can take quite a long time in a small fraction of seeds and that the threshold is gradually achieved through accumulation of active temperatures during cold months.

Mechanisms of Dispersal

Fruits of *H. mantegazzianum* are elliptical, winged and dispersed mostly by wind, water and human activities. The majority of ripe fruits fall close to mother plants. For plants 2-m high, 60–90% of fruits fall within a radius of 4 m from the mother plant (Nielsen *et al.*, 2005). Clegg and Grace (1974) and Ochsmann (1996) argue that dispersal by wind could be important only over short distances. There is no direct evidence of dispersal by animals, but it can be supposed that adherence to animal skin could only play a role in short distance dispersal. Since at the landscape scale, long-distance dispersal and random events can play a crucial role in the dynamics of plant species, buoyancy can potentially affect the distance the species can reach. Clegg and Grace (1974) and Dawe and White (1979) report an ability to float up to 3 days for *H. mantegazzianum*, but L. Moravcová (unpublished results) found that 6-month-old fruits sink within 8 h. Such time, nevertheless, is likely to be sufficient for spreading a long distance, especially by fast-flowing streams. Other important dispersal vectors are humans, who spread fruit of *H. mantegazzianum* stuck to car tyres along roads, move them to new

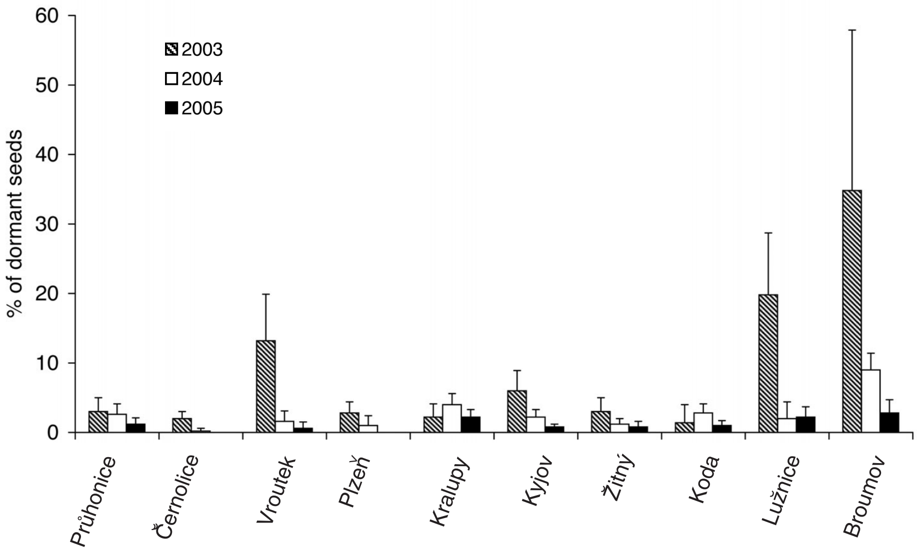

Fig. 5.7. The proportion of viable dormant seeds in the soil is rather low after the first year and rapidly decreases further. Survival over 3 years of seeds buried at ten localities in the Czech Republic in November 2002 is shown. Seeds were taken from the soil in October of the following 3 years and tested for viability by tetrazolium. Numbers are means of five replicates. Based on data from Moravcová *et al.* (2006).

locations with soil transport, or deliberately transport decorative umbels with dry fruit (Tiley *et al.*, 1996). Given that long-distance dispersal is important to the success of possible invasion (Pyšek and Hulme, 2005), dispersal by water and humans seem to be the most significant factors in this respect.

If suitable sites are available, high rate of spreading is realized at both local and regional scales. At the scale of the Czech Republic the number of localities doubled each 14 years during the exponential phase of invasion (see Pyšek *et al.*, Chapter 3, this volume). Müllerová *et al.* (2005) report an average rate of spread of about 10 m/year, and increase in the area invaded by more than 1200 m^2 each year in the Slavkovský les region, Czech Republic.

To illustrate the spreading from local populations to wider surroundings, aerial photographs can be explored (Müllerová *et al.*, 2005). Diaspore output of *H. mantegazzianum* populations can be calculated and evaluated by using additional data from experiments running in the sites analysed (Krinke *et al.*, 2005; Perglová *et al.*, Chapter 4, this volume; Pergl *et al.*, Chapter 6, this volume). Density of flowering plants as recorded from aerial photographs varied around 1.76 plants per m^2 at an average site (Müllerová *et al.*, 2005) and this value corresponds reasonably well to that recorded in permanent plots in the field (J. Pergl *et al.*, unpublished data). For the site harbouring the largest population of *H. mantegazzianum* (see Perglová *et al.*, Chapter 4, this volume, for the size of populations in individual sites), 14,164 flowering plants

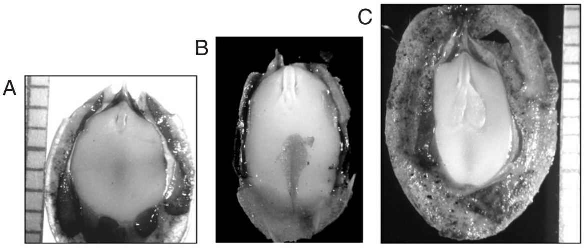

Fig. 5.8. Embryo in (A) a freshly harvested, (B) 2-months stratified and (C) 5-months stratified seed of *H. mantegazzianum.* Seeds were stratified in the soil. Photo: L. Moravcová.

were estimated to be present from aerial photographs (Fig. 3.4). Given the mean fecundity of 20,500 fruits per plant in the study area (see Perglová *et al.*, Chapter 4, this volume), the total fruit number per 60-ha area (size of the research plot used by Müllerová *et al.*, 2005) is over 290,000,000, representing an annual input of 484 fruits/m^2/year. Relating the total fruit set to the mean area actually infested at a site (31,946 m^2) gives 9089 fruits/m^2/year. These values can be compared with the number of seeds in seed banks, estimated in permanent plots: the mean value from autumn 2002, after the fruits were shed, was 3650 seeds/m^2 (Krinke *et al.*, 2005). Bearing in mind that the values derived from aerial photographs are rough estimates, they provide some idea of how large a proportion of fruits are spread outside the actual stands. The value of 484 seeds/m^2/year is a theoretical one since seeds are not dispersed evenly across the whole site. On the other hand, the amount produced by monitored populations (9089) greatly exceeds the value recorded in the field (3650); this difference indicates that a large proportion of fruits are spread into surroundings, making further population growth possible.

Conclusions

A combination of reproductive traits such as high fecundity, high germination capacity, opportunistic behaviour associated with limited effect of fruit position on a plant on germination characteristics, dormancy mechanisms together with short-term persistent soil seed bank and possibility of long-distance spread are likely to determine the ability of *H. mantegazzianum* to invade successfully new habitats in the secondary distribution range.

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