4

Reproductive Ecology of *Heracleum mantegazzianum*

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> *Botanical creature stirs, seeking revenge*
>
> (Genesis, 1971)

Introduction

Reproduction is the most important event in a plant's life cycle (Crawley, 1997). This is especially true for monocarpic plants, which reproduce only once in their lifetime, as is the case of *Heracleum mantegazzianum* Sommier & Levier. This species reproduces only by seed; reproduction by vegetative means has never been observed.

As in other *Apiaceae*, *H. mantegazzianum* has unspecialized flowers, which are promiscuously pollinated by unspecialized pollinators. Many small, closely spaced flowers with exposed nectar make each insect visitor to the inflorescence a potential and probable pollinator (Bell, 1971). A list of insect taxa sampled on *H. mantegazzianum* (Grace and Nelson, 1981) shows that Coleoptera, Diptera, Hemiptera and Hymenoptera are the most frequent visitors.

Heracleum mantegazzianum has an andromonoecious sex habit, as has almost half of British *Apiaceae* (Lovett-Doust and Lovett-Doust, 1982); together with perfect (hermaphrodite) flowers, umbels bear a variable proportion of male (staminate) flowers. The species is considered to be self-compatible, which is a typical feature of *Apiaceae* (Bell, 1971), and protandrous (Grace and Nelson, 1981; Perglová *et al*., 2006). Protandry is a temporal separation of male and female flowering phases, when stigmas become receptive after the dehiscence of anthers. It is common in umbellifers. Where dichogamy is known, 40% of umbellifers are usually protandrous, compared to only about 11% of all dicotyledons (Lovett-Doust and Lovett-Doust, 1982). Although protandry has traditionally been considered to be a mechanism of avoiding or reducing selfing, it is itself unlikely to guarantee outcrossing. However, when it is strongly developed, the male and female phases of a plant may be completely separated in time so that outcrossing is assured (Webb, 1981; Snow and Grove, 1995).

*Ecology and Management of Giant Hogweed (*Heracleum mantegazzianum*).* (eds P. Pyšek, M.J.W. Cock, W. Nentwig and H.P. Ravn)

Interspecific hybrids between *H. mantegazzianum* and *H. sphondylium* L. are reported from Great Britain (McClintock, 1975) and Germany (Ochsmann, 1996). Hybrids are found in sites where both species grow together, although they are not numerous (Grace and Nelson, 1981; Stewart and Grace, 1984). This was studied and it was found that only experimental crosses in which *H. sphondylium* was the female parent were successful (Stewart and Grace, 1984).

The aim of this chapter is to summarize the knowledge about the reproductive ecology of *H. mantegazzianum*, including the results obtained during the triennial European project GIANT ALIEN. During this project, an extensive study of flowering phenology and seed production of wild populations of *H. mantegazzianum* was conducted at ten localities in the Slavkovský les Protected Landscape Area in the Czech Republic (Fig. 4.1, Table 4.1). This region is where the species was first introduced to this country in the second half of the 19th century and from where it started to spread (Pyšek, 1991; see Pyšek *et al.*, Chapter 3, this volume). The rapid spread was probably facilitated by the fact that after World War II inhabitants were displaced and part of the region became a military area until the 1960s. This led to a lack of appropriate management and a specific disturbance regime; military activities are rather specific in that they occur in 'natural' parts of the landscape, which are less affected under standard

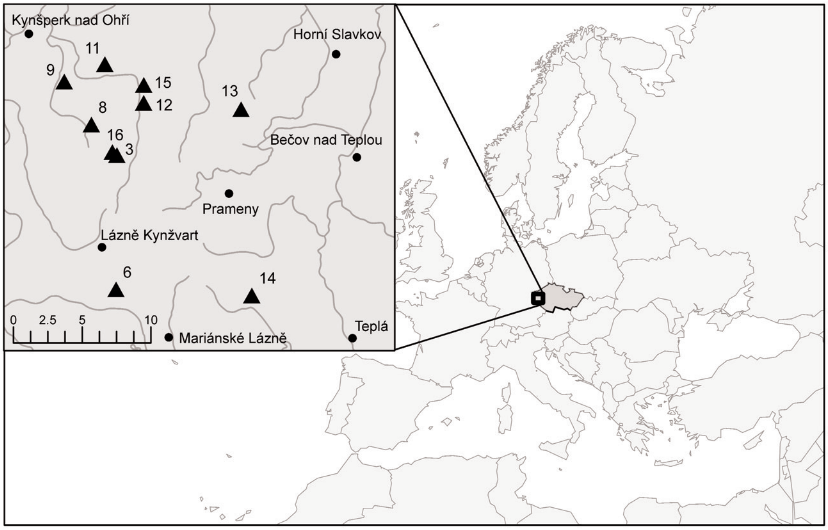

Fig. 4.1. The study area in the Slavkovský les Protected Landscape Area, which is the region where *H. mantegazzianum* was first introduced into the Czech Republic. Currently the region is still heavily infested. Most of the region is in the Ore Mountains and is formed from granite. Total size of the protected area is 617 km^2, altitudinal range is 373–983 m a.s.l. (Kos and Maršáková, 1997), January temperature ranges from –5.1°C (average mimimum) to –0.2°C (average maximum), July temperature from 10.5 to 21.5°C, respectively. Annual sum of precipitation is 1094 mm (Mariánské Lázně meteorological station, 50-year average).

Table 4.1. Geographical location, altitude (m a.s.l.) and population size of *H. mantegazzianum* estimated from aerial photographs taken at ten study sites in the Slavkovský les Protected Landscape Area, Czech Republic. Estimates were made for 60 ha sections of landscape (taken from Müllerová *et al*., 2005).

Site no.	Name	Latitude	Longitude	Altitude (m)	Population (m^2)
3	Žitný I	50°03.754′	12°37.569′	787	99,121
6	Lískovec	49°59.156′	12°38.721′	541	8174
8	Potok	50°04.660′	12°35.953′	643	39,774
9	Dvorečky	50°05.982′	12°34.137′	506	24,817
11	Arnoltov	50°06.801′	12°36.147′	575	47,170
12	Krásná Lípa I	50°05.685′	12°38.546′	597	–
13	Litrbachy	50°06.009′	12°43.777′	800	4711
14	Rájov	49°59.704′	12°54.933′	753	5198
15	Krásná Lípa II	50°06.306′	12°38.393′	596	7945
16	Žitný II	50°03.837′	12°37.304′	734	–

land use. There are still very few people in this protected landscape, which consists mainly of extensive wetlands, pastures and spruce plantations. Nowadays, the area of the Slavkovský les is still invaded to a large extent (see Pyšek *et al*., Chapter 3, this volume; Müllerová *et al*., 2005). The field study was complemented by detailed studies of flowering phenology and selfing in the experimental garden of the Institute of Botany, Průhonice, Czech Republic (50°0.071′ N, 14°33.5281′ E; 310 m a.s.l.). Furthermore, information on the age at which *H. mantegazzianum* reproduces, gathered in both its native (Western Greater Caucasus) and invaded (Czech Republic) areas, is presented.

Description of the Pattern and Timing of Flowering

Flowering plants of *H. mantegazzianum* have a distinct architecture. The inflorescences are compound umbels of four orders. The main flowering shoot develops as a leafy stem that terminates in a primary (first-order) umbel, also called ‘terminal’. Lateral shoots, which are produced on the stem, terminate in secondary (second-order) umbels and can be found in a satellite position, surrounding the primary umbel (hereafter also called ‘satellites’), or in a branch position below them on the stem (hereafter also called ‘branches’). Third-order umbels may arise on shoots branching from secondary shoots (in both satellite and branch position) and fourth-order umbels on shoots branching from tertiary shoots (Fig. 4.2). Under favourable conditions, strong plants can produce several other shoots, which arise from the base of the flowering stem at ground level (further referred to as ‘basal branches’). The character of the terminal umbels of these basal branches varies and in terms of umbel size, fruit size, fecundity and proportion of male flowers is intermediate between typical first- and second-order umbels.

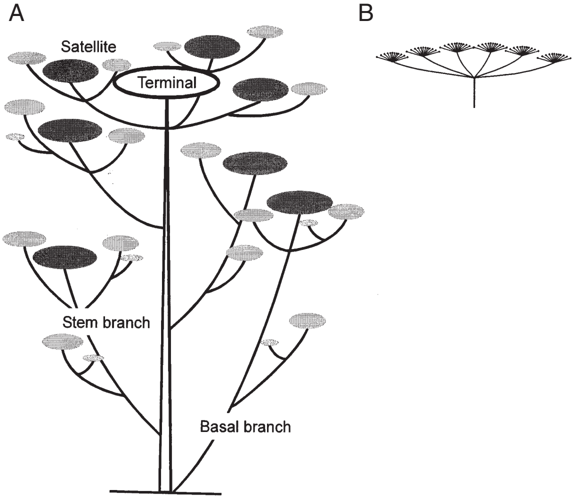

Fig. 4.2. (A) Schematic representation of the ordering of umbels and their position within the hierarchical inflorescence system of *H. mantegazzianum*. Umbel orders: primary □, secondary ■, tertiary ■ and quaternary ●. (B) Each compound umbel consists of umbellets that bear a large number of small, closely packed flowers. Taken from Perglová *et al.* (2006), published with permission from the Czech Botanical Society.

Each compound umbel consists of umbellets (umbellules), simple umbels that bear a large number of small, closely packed flowers. Flowers are either hermaphrodite or male (staminate); the latter usually contain reduced stylopodia (Bell, 1971) and no, or a shrunken, style. The proportion of male flowers increases in higher-order umbels, while the terminal umbel usually contains only hermaphrodite flowers. If present, male flowers are located in the central part of umbellets. Within the same umbel, the proportion of male flowers seems to be the same in all umbellets (Perglová *et al.*, 2006), despite the increasing percentage of male flowers towards the centre of the umbels reported for *Zizia aurea* (Michaux) Fernald and *Thaspium barbinode* (Michaux) Nutt. (Bell, 1971). Fourth-order umbels usually consist only of male flowers (Perglová *et al.*, 2006).

Male sterility was observed in the experimental garden in Průhonice. A plant transplanted from a natural stand at the seedling stage and grown in a garden bed bore only physiologically female flowers with stamens, filaments of which remained unrolled, and the anthers remained closed and did not dehisce. Pistils were fully functional and the fruits were set after fertilization. The same phenomenon is described for wild *Daucus carota* L. plants by Braak and Kho (1958).

Within-flower and within-umbel phenology

A study of flowering phenology conducted on plants growing in the experimental garden in Průhonice, Czech Republic (Perglová *et al.*, 2006) revealed that in an individual flower, flowering starts by the sequential expansion and dehiscence of the five stamens, which takes usually 1 and sometimes 2 days. Anthers are ready to shed pollen almost immediately after expansion is completed. Within an umbellet, the outer flowers are first to flower and flowering continues to the centre, where pollen is shed 3 (in the case of the terminal umbels) to 6 (secondary umbels) days later (Fig. 4.3A). In umbellets located in the centre of an umbel, the onset of flowering can be 1 day later than in peripheral umbellets.

In contrast, stigma receptivity is well synchronized throughout the whole umbel and lasts 1–2, maximum 3 days. Receptivity can be recognized visually – the stigmas are fully elongated with a fresh glistening appearance at the tip of the initially dome-shape style, which spreads and becomes bulbous

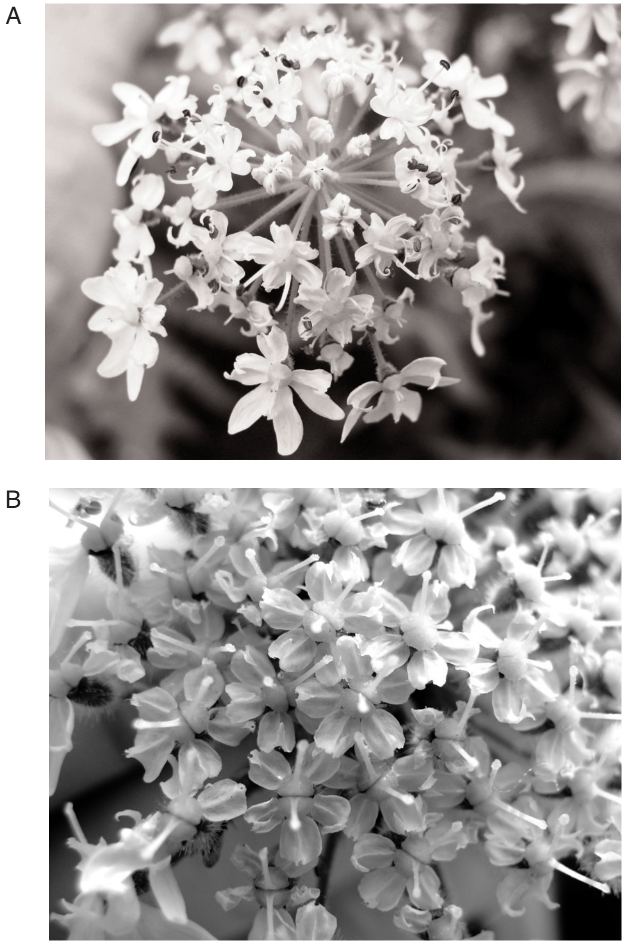

Fig. 4.3. (A) The flowers of an umbellet open centripetally over a period of several days. (B) When the stigmas are receptive the styles are fully elongated, separate and with a fresh glistening appearance at the tip. Photo: I. Perglová.

Fig. 4.4. The overlap in anther dehiscence and stigma receptivity in flowers of the same umbellet. Photo: P. Pyšek.

(Fig. 4.3B). Flowers in the centre of umbellets can be male and do not have a female phase.

Between anther dehiscence and stigma receptivity, there is a neutral phase of variable length, depending on the position of a flower in an umbellet and position of an umbellet in the umbel. In the outer flowers of peripheral umbellets, the neutral phase may last up to 6 days because they are the first flowers within an umbel to shed pollen. The neutral phase of the outer flowers of central umbellets is usually 1 day shorter. Neutral phase of central flowers, both in peripheral and central umbellets, lasts 2 days at most or there is no neutral phase or even an overlap in anther dehiscence of these flowers, which are often male, with the receptivity of other flowers in the same umbel (Fig. 4.4).

Such overlaps only occur in some umbels and only a small proportion of the late dehiscing anthers are usually involved (Perglová *et al.*, 2006). Consequently, stigmas are not covered by a mass of pollen from the same umbel but geitonogamous selfing can occur.

Within-plant phenology

Umbels of different orders flower in sequence. The terminal (primary) umbel is the first to flower, followed by secondary, and later tertiary and quaternary umbels on satellites and branches. By way of an example, Fig. 4.5 shows the course of flowering of different umbels and the flowering phases of one plant growing in the experimental garden. In some umbels of higher orders (mainly quaternary), the female phase and fruit development do not occur after the male phase, because those umbels contain only male flowers and thus wither after anther dehiscence. At the umbel level, male phase is defined as a phase in which at least some flowers dehisce anthers while other flowers can be

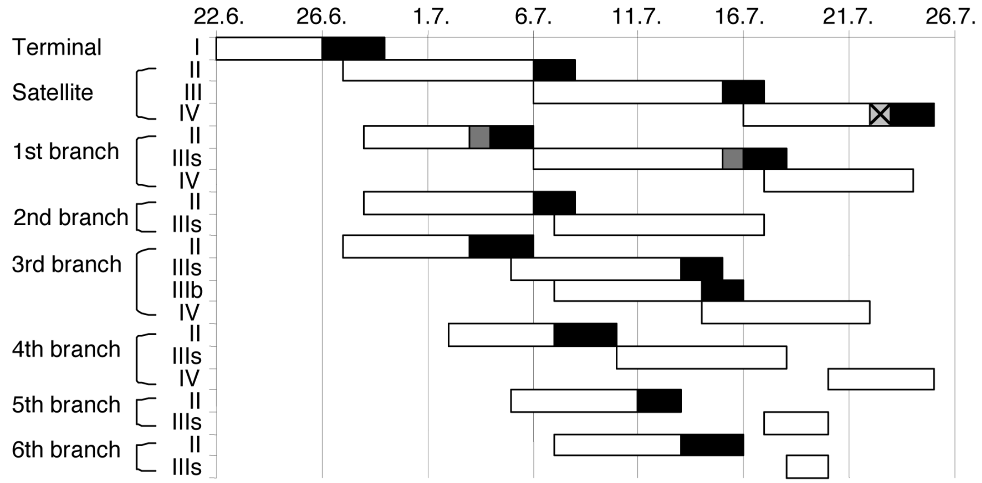

Fig. 4.5. Phenological pattern of a single plant. The sequence of □ male, ☒ neutral and ■ female phases throughout the vegetation period is shown for each umbel. Overlap in anther dehiscence and female receptivity within an umbel is indicated by ▨. Numbers I, II, III, IV refer to umbel order, letters s, b to the location of tertiary umbels on branches (satellite or branch position).

already in the neutral phase. The neutral phase of an umbel is thus defined as the stage before stigma receptivity when none of the flowers contain dehiscing anthers. However, neutral phases are uncommon. Male and female phases of umbels on the same plant can overlap and a study of the flowering phenology of 100 plants at ten localities in the Slavkovský les area revealed that such overlaps are common; at least a short overlap between some umbels was observed in 99% of plants (Perglová *et al.*, 2006).

Evidence for overlaps is also provided by Stewart and Grace's (1984) study of hybridization between *H. mantegazzianum* and *H. sphondylium*. They report complete protandry within an umbel and an overlap between female and male phases of primary and secondary umbels in only two plants out of the nine studied. However, the plants were transplanted to a greenhouse in the spring of the same year in which they flowered. The results therefore might have been affected by the plants being smaller and possibly not producing tertiary umbels, which reduce the possibilities of overlaps between male and female phases. Stewart and Grace (1984) did not include plants growing under natural conditions in their study.

An opportunity for geitonogamous selfing usually increases if a plant produces basal branches, because these often exhibit asynchronous flowering (umbels do not flower at the same time as other umbels of the same order). Basal branches are usually vigorous and branched, bearing umbels of higher orders. However, several plants observed at the Slavkovský les study sites produced late umbels on short basal shoots (shoot length up to about 20 cm, umbel diameter 10–25 cm), which consisted of physiologically female flowers with shrunken anthers (I. Perglová, Průhonice, 2003, personal observation). At that time, pollen from quaternary umbels (usually containing only male flowers) was still available; such plants exploited the last opportunity and resources to produce fruit and did not invest in the production of pollen, which would have been wasted, as there were no or very few receptive stigmas.

Timing of flowering at the plant and population level

In plants destined to flower, the first signs of the development of a flowering stem become visible in early June in the Slavkovský les (Perglová *et al.*, 2006), late May in Giessen in Germany (Otte and Franke, 1998) and approximately 1 month earlier in the UK (Tiley *et al.*, 1996). A rapid stem elongation culminates in the opening of a terminal bud, which contains terminal and satellite umbels. Then the terminal umbel expands, opens its flowers and starts to flower.

In the Slavkovský les protected area in 2002, flowering began within a period of 1 week (from 20 to 27 June) at all ten localities, despite differences in exposure and altitude (Table 4.1). The peak of flowering, expressed as the average date on which the primary and secondary umbels of 30 randomly selected plants at each locality flowered, was between 27 June and 6 July. The duration of flowering of an individual plant (time from beginning of male phase in the terminal umbel to end of female phase in the last umbel on the plant) in the Slavkovský les was on average 36 days (range of averages for individual localities: 31–41 days). The maximum observed duration of flowering was 60 days and duration increased with the number of umbels on a plant. The terminal umbel flowered on average for 10 days and its fruits were ripe on average 44 days after the beginning of flowering (Perglová *et al.*, 2006). In the second half of August, the majority of all fruits were ripe and started to be released.

Potential for Selfing

The complete separation of male and female phases in many *Apiaceae* is effective in promoting outcrossing. In contrast, a weak protandry does not appear to be an effective outcrossing mechanism and is more easily understood in terms of sexual selection and optimal allocation of resources to maternal and paternal functions (Lovett-Doust, 1980; Webb, 1981). Although species of *Apiaceae* are considered to be fully self-compatible (Bell, 1971), the potential for selfing need not be determined only by the degree of protandry. In some *Apiaceae*, selfing seems to be limited by a genetic mechanism: maternal control before fertilization (i.e. partial self-incompatibility), late-acting self-incompatibility or inbreeding depression very shortly after fertilization. These mechanisms are probably responsible for the low selfed seed set in the endangered species *Eryngium alpinum* L. (Gaudeul and Till-Bottraud, 2003) and in *Trachymene incisa* Rudge subsp. *incisa* (Davila and Wardle, 2002).

Table 4.2. Fruit production of umbellets subjected to controlled crossing. For each plant ($n = 8$), there were four different pollination treatments, each on three umbellets of the terminal umbel: 1. manual outcrossing, 2. manual selfing, 3. autonomous selfing and 4. natural open pollination (as a control). Fruit number per umbellet (mean ± SD) for each treatment is shown, letters indicate significant differences.

Treatment	Fruit set/umbellet	
Open pollination	92.0 ± 19.5	a
Manual outcrossing	87.7 ± 21.3	a
Manual selfing	87.8 ± 24.2	a
Autonomous selfing	3.8 ± 6.3	b

To determine whether selfing is possible in *H. mantegazzianum* and whether there is a self-incompatibility mechanism and inbreeding depression, controlled crosses were made in the experimental garden in Průhonice (I. Perglová *et al.*, unpublished). There were no significant differences in fruit production among open pollinated, manually outcrossed (i.e. bagged and hand-pollinated by a mixture of pollen from other plants) and manually selfed (i.e. bagged and hand-pollinated with pollen from the same plant) umbellets (Table 4.2), indicating that artificial pollination was effective and pollen from the same and other plants was equally successful. *Heracleum mantegazzianum* is self-compatible and selfing does not seem to be limited by any genetic mechanism, such as maternal control before fertilization or inbreeding depression shortly after fertilization. There was an almost full fruit set in both hand- and open-pollinated umbellets. In contrast, fruit production of autonomously selfed umbellets (i.e. umbellets bagged to exclude pollinators and not subjected to manual pollination) was very low (Table 4.2), suggesting that pollen transfer by pollinators is needed for a standard fruit set. However, as the fruits produced by these umbellets must have arisen from near-flower fertilization, plants can reproduce even in the absence of pollinators (and successfully colonize new sites following the long-distance dispersal of a single propagule).

Experimental crosses on *H. mantegazzianum* and *H. sphondylium* were also made by Stewart and Grace (1984) in their study of interspecific hybridization of these two species. Only a negligible fruit set (1%) was obtained when pollen was transferred between flowers within the terminal umbel, which is consistent with rare overlap in anther dehiscence and female receptivity in the same umbel. However, they were able to realize high levels of selfing (68% fruit set) in two plants with incomplete separation of staminate and pistillate phases between umbels.

Implications of Self-compatibility for the Invasion

Self-pollination was identified as advantageous in some colonizing species (Brown and Burdon, 1987; Rejmánek *et al.*, 2005) and selfing may lead to acceleration of the rates of spread (Lewis, 1973; Daehler, 1998). Of the introduced species included in a study of Western Australian members of *Apiaceae* (Keighery, 1982), all the naturalized species were capable of autogamy and self-fertile. They all possessed attractive inflorescences, and were pollinated by a variety of native and introduced insects. Controlled pollination experiments on 17 invasive alien plant species in South Africa revealed that 100% of them were either self-compatible or apomictic (Rambuda and Johnson, 2004).

The ability to self is advantageous for successful colonization following long-distance dispersal of a single propagule, because there is no need to wait for a sexual partner (Baker's law; Baker, 1955). Once a plant has successfully established, selfing transmits proved genes of a plant, which was able to survive at that site. Nevertheless, theoretical models suggest that an optimal mating system for a sexually reproducing invader in a heterogeneous landscape is to be able to modify selfing rates according to local conditions. In early stages of invasions, when populations are small, plants should self to maximize fertility. Later, when populations are large and pollinators and/or mates are not limiting, outcrossing is more beneficial because it generates increased genetic polymorphism (Pannell and Barrett, 1998; Rejmánek *et al*., 2005).

Heracleum mantegazzianum is fully self-compatible, as indicated by the fact that selfed fruit set was not lower than that of naturally pollinated flowers, and it does not suffer from inbreeding depression at the germination stage (I. Perglová, unpublished results). The study of flowering phenology showed that overlaps between male and female flowering phases allow for geitonogamous (i.e. between-flowers) pollination. This indicates that plants of *H. mantegazzianum* are probably highly self-fertile if isolated or growing in very sparse populations where pollinators transport pollen within a single plant. This has very important implications for the invasion because even a single isolated plant of *H. mantegazzianum*, resulting from a long-distance dispersal event, is capable of founding a new population. However, when the species grows in abundant and dense populations, it is likely to produce predominantly outcrossed progeny because of the high incidence of pollinators moving between plants. However, natural frequencies of self-fertilization can be detected only by a genetic study of seed progeny and determination of the selfing rate in natural populations.

Fecundity

The first mention indicating the high fecundity of *H. mantegazzianum* was in the paper by Sommier and Levier (1895) in which the species was described. They mention a plant grown in Geneva, which bore no less than 10,000 flowers. Nevertheless, before evaluating what this and other reports mean in terms of the fecundity, it is useful to describe the morphology of flowers of *H. mantegazzianum*. Every flower with a fertilized ovule can produce two winged mericarps (for simplicity, the morphologically correct term 'mericarp' is replaced by 'fruit' in this chapter and refers to the unit of generative reproduction and dispersal). Thus, the number of flowers recorded by Sommier and Levier transforms into a potential fecundity of more than 20,000 fruits.

However, as some umbels (mainly those of higher orders) contain male flowers (see the section 'Description of the pattern and timing of flowering'), fruit set is most likely lower.

Surprisingly, a more precise estimate of fecundity was made no earlier than 100 years later by Pyšek *et al*. (1995). Before then, there were several reports (Williamson and Forbes, 1982; Brondegaard, 1990; Table 4.3), which were insufficiently documented in terms of where the numbers come from and how they have been obtained, yet are frequently cited. The only exception might have been the thesis of Warde (1985, cited by Caffrey, 1999), which is unfortunately not easily available. Another report of 1500–18,000 fruits, cited by Tiley *et al*. (1996) is claimed to have come from Neiland (1986), but there is no estimate of fecundity in that study. This suggests that tracing the origin of reports on *H. mantegazzianum* fecundity is as difficult as that reported for the presumed longevity of seeds in the soil (see Moravcová *et al*., Chapter 5, this volume).

Pyšek *et al*. (1995) record the first estimate of fecundity based on several plants, which provides details of the method of assessment. It reports an average fruit set of 16,140 in the Czech Republic (Table 4.3). Ochsmann (1996) records an average of 9696 fruits in Germany. Similar average values are reported from Scotland (15,729 fruits; Tiley and Philp, 2000) and again from the Czech Republic (20,671 fruits; Perglová *et al*., 2006). Caffrey (1999) reports numbers from Ireland that are markedly higher than those of previous reports: on average 41,202 fruits, and maximum 107,984 fruits! However, the method of assessment is described as 'a total count of seed numbers was recorded'. From this it is unclear how the values were derived. The number of umbels (the primary umbel, nine secondary and 14 tertiary) this author gives for that most fecund plant is by no means exceptional and is similar to that of plants studied in the Czech Republic. It is therefore likely that in Caffrey's study (Caffrey, 1999) the number of fruits was derived from the number of flowers including male flowers. Be it flowers or fruits on which the assessment was based, it is unclear how the figures were obtained; given the number, counting individual fruits is unlikely.

Tiley and Philp (1997), who 'selected the apparently largest plants' for their estimates, published a maximum number of 81,500 flowers per plant, and the fruit set of a plant with even slightly more umbels as 'only' 52,800. This is clear evidence that the number of flowers is not a good estimate of fecundity.

Probably the highest estimate of fecundity in the literature is 120,000 fruits cited by Ochsmann (1996), reportedly coming from Dodd *et al*. (1994). However, Dodd *et al*. (1994) is not the primary source as these authors refer to Tiley and Philp (1994), which is a chapter in the same book, but that gives no estimate! In any case, Ochsmann's citation is imprecise because the note in Dodd *et al*. (1994) refers to 60,000 flowers, not 120,000 fruits. As cited above (and further illustrated by Perglová *et al*., 2006), the assumption of fruit set being twice the number of flowers is unrealistic.

The most detailed study of fecundity, based on a large sample of plants, is provided by Perglová *et al*. (2006). Their study estimated the fecundity of 98

Table 4.3. Summary of published data on fecundity of *H. mantegazzianum*. The sources are arranged according to the year of publication.

Source	No. of fruits	No. of plants	No. of localities	Country	Method of assessment
Sommier and Levier (1895)	> 10,000[1]	1	1	Switzerland	n.g.
Williamson and Forbes (1982)	‘up to 5,000 or more’	n.g.	n.g.	n.g.	n.g.
Warde (1985) cited by Tiley *et al.* (1996)	14,000–29,000	n.g.	n.g.	Ireland	n.g.
Brondegaard (1990)	5000–6000; max. 27,000	n.g.	n.g.	n.g.	n.g.
Pyšek *et al.* (1995)	avg. 16,140; max. 25,894	8	1	Czech Republic	estimated from fruit mass
Ochsmann (1996)	avg. 9695; max. 28,908	33	n.g.	Germany	n.g.
Tiley and Philp (1997)[2]	81,500; 65,000[1]	2	1	Scotland	estimated from sample counts[3]
	52,800	1	1	Scotland	estimated from fruit mass
Caffrey (1999)	avg. 41,202; min. 1516; max. 107,984	80	8	Ireland	‘a total count of seed numbers was recorded’[4]
Tiley and Philp (2000)	avg. 15,729	4	1	Scotland	estimated from fruit mass
Perglová *et al.* (2006)	avg. 20,671; min. 7545; max. 46,470	98	10	Czech Republic	estimated from fecundity class and umbel diameter[5]

[1] Number of flowers.

[2] Three largest plants were sampled, two for flower and one for fruit number.

[3] Flowers in the terminal umbel were counted individually, flower counts for the remaining umbels were derived from the number of rays per umbel and the number of flowers per ray, which were counted on four rays.

[4] Formulation from the original source, see text for interpretation.

[5] See text for details.

n.g. = not given.

plants growing at ten sites in the area of Slavkovský les, Czech Republic (see Table 4.1 for characteristics of the sites). All umbels that developed on these plants were classified according to umbel order, umbel position (satellite, branch) and proportional fecundity (0, 1–25%, 26–75% and >75% of flowers set fruit; Table 4.4). For each combination of umbel order and fecundity class, fruit set was estimated based on data from an additional 100 umbels and regressions based on umbel diameter (Perglová *et al*., 2006). Nearly 81% of the terminal umbels were placed in the highest fecundity class (>75% of flowers set fruits), while tertiary umbels often set no fruits (Table 4.4). Of the quaternary umbels, 99% did not produce fruit; they did not contribute to the fruit set and their flowers only served as pollen donors. This is consistent with the increase in proportion of male flowers in higher order umbels (see 'Description of the pattern and timing of flowering'). An average plant produced 20,671 ± 5130 fruits (mean ± SD) (Table 4.5) and the maximum estimated number of fruits was 46,470. Almost half of the fruits were produced by the terminal umbel. The fecundity of individual plants significantly increased with the diameter of the flowering stem (Perglová *et al*., 2006).

The study of Perglová *et al.* (2006) also provides detailed information on the architecture of *H. mantegazzianum* plants, based on the number of umbels of a particular order per plant and on their size (Table 4.5). In the area of Slavkovský les, a typical flowering plant bears a terminal, 4 satellites, 3–4 branches, 17 tertiary and 3 quaternary umbels. This is the first information about the architecture of *H. mantegazzianum* based on a large sample of plants; previously published estimates of fecundity did not provide information on the number of umbels (Caffrey, 1999), considered only primary and secondary umbels (Pyšek *et al*., 1995) or are based on only a few plants (Tiley *et al*., 1996; Tiley and Philp, 1997).

To summarize the issue of fecundity in *H. mantegazzianum*, it can be concluded that: (i) the hierarchical structure of flowering organs, typical of umbellifers, and varying proportions of male and female flowers made reports of the number of fruits, which did not take these factors into account, rather unreliable; (ii) in addition, values were cited without checking the original sources, which created a similar myth to the one regarding seed longevity in this species (see Moravcová *et al*., Chapter 5, this volume). *Heracleum mantegazzianum* is particularly prone to becoming the subject of exaggeration; and (iii) a detailed inspection of the literature, together with our own field estimates, indicates that the maximum reported fruit sets are overestimated. It is very doubtful whether an individual plant of *H. mantegazzianum* is able to produce over 100,000 fruits. Values of 10,000–20,000 seem to be appropriate for Europe, with the maximum occasionally reaching around 50,000 fruits.

Life Span and Age of Flowering Plants in Native and Invaded Ranges, and Under Different Management Regimes

In the above sections, the flowering pattern of *H. mantegazzianum* is described in terms of days; the timing of flowering in terms of years determines

Table 4.4. Distribution of umbel types in fecundity classes, defined as the percentage of flowers that produce fruits. Percentage of the total number of umbels in each class is presented. For example, no terminal was completely infertile, while in 80.6%, more than 75% of the flowers produced fruits. Based on 98 plants growing in the Slavkovský les Protected Landscape Area in 2002. I–IV: umbel order.

	Fecundity class				
Umbel type	0	1–25%	26–75%	76–100%	Total no. of umbels
Termina I	0	17.3	2.0	80.6	98
Satellite II	10.4	77.4	12.2	0	442
Satellite III	87.7	4.1	8.1	0	751
Satellite IV	95.0	1.7	3.3	0	180
Branch II	13.6	73.2	13.3	0	369
Branch III	82.8	7.3	9.9	0	899
Branch IV	99.0	0	1.0	0	305

its life span. Literature reports on the flowering strategy of *H. mantegazzianum* are neither consistent nor detailed. This section summarizes knowledge on the age of flowering plants and whether the species is a monocarpic (flowering only once in its lifetime) or polycarpic perennial plant (flowering repeatedly). Tiley *et al*. (1996) suggest that *H. mantegazzianum* is usually monocarpic and 2–5 years old when flowering. This conclusion is based, among others, on a study of interbreeding between *H. mantegazzianum* and *H. sphondylium*, in which Stewart and Grace (1984) found that plants of the former species flower at the age of 2–5 years. Unfortunately, their plants were grown under artificial conditions in cultivation. A possible effect of growing conditions was observed in the experimental garden at Průhonice; some of the plants grown in a garden bed, with a suitable substrate and regularly watered, flowered in the second year, which was never observed in the field, nor in a native or invaded distribution range (Pergl *et al*., 2006). Information on life span is fairly limited in literature from the native distribution range, but *H. mantegazzianum* is reported to be polycarpic in Russia (Shumova, 1972). Furthermore, the possibility of repeated flowering in the subsequent years is reported for plants damaged before they finished flowering (Tiley *et al*., 1996).

Before reporting the age of flowering plants, it is useful to clarify the position of *H. mantegazzianum* in the continuum between monocarpy to polycarpy. In field studies carried out since 2002, *H. mantegazzianum* was never observed to flower repeatedly (Pergl *et al*., 2006). Nevertheless, some species in this genus, such as the European species *H. sphondylium* (Stewart and Grace, 1984) are polycarpic, as is *H. persicum* Desf. ex Fischer, which is invasive in Scandinavia (see Jahodová *et al*., Chapter 1, this volume; Nielsen *et al*., 2005). Another invasive congener, *H. sosnowskyi* Manden, is also monocarpic (Nielsen *et al*., 2005). That both monocarpy and polycarpy exist in closely related species of the genus indicates that an occasional shift to polycarpic behaviour is not excluded and exploration of this possibility deserves attention. In addition, the majority of interspecific hybrids between

Table 4.5. The number of umbels, their size and estimate of fecundity of plants growing in the Slavkovský les Protected Landscape Area in 2002. The umbels are classified according to their order and position in the case of secondary umbels. Ten plants from each of ten sites were assessed; two plants were damaged before the fruit matured and were excluded from the analysis. Taken from Perglová *et al.* (2006), published with permission from the Czech Botanical Society.

	Terminal	II. order umbel – satellite	II. order umbel – branch	III. order umbel	IV. order umbel	Total
No. of umbels/plant [median (min–max)]*	1	4.3 (2–8)	3.5 (1–10)	17.3 (2–43)	2.8 (1–39)	27.5 (5–98)
Fecundity/umbel [avg ± SD]**	9216.0 ± 481.7	1288.0 ± 614.8	1157.0 ± 429.1	32.0 ± 30.1	n.a.	20,671.0 ± 5129.8
Umbel size [cm] avg ± SD (min–max)**	61.7 ± 3.7 (44–85)	36.8 ± 3.3 (20–56)	36.3 ± 4.8 (5–62)	17.8 ± 2.3 (2–36)	7.9 ± 1.8 (1–17)	–

* Calculated as a median of site medians.

** Calculated as averages of site averages and among-sites standard deviations.

H. mantegazzianum and *H. sphondylium* are polycarpic (Stewart and Grace, 1984), which indicates a potential for polycarpy in the former species.

To clarify the reported possibility that *H. mantegazzianum* is capable of flowering the following year if damaged before it finishes flowering (Tiley *et al.*, 1996), all the umbels produced during the course of the growing season were removed from 20 flowering plants grown in the experimental garden at Průhonice. None of the plants survived and flowered the following year (see Pyšek *et al.*, Chapter 7, this volume). From field observations, a study of age structure (Pergl *et al.*, 2006) and this experiment, it can be concluded that *H. mantegazzianum* is strictly monocarpic and dies after flowering. It is possible that the reported survival of flowering plants can be attributed to plants forming rather dense clumps, which makes the identification of individual plants difficult. A new individual emerging next to a dead stem can be easily considered as resprouting from the rootstock and lead to the wrong conclusion, as was probably the case of Morton (1978).

Since the reproduction of *H. mantegazzianum* depends exclusively on fruit production, which occurs only once in its lifetime, the right timing of flowering is a crucial point in the life history of this species. Its monocarpic behaviour thus opens questions about the timing of flowering and its relation to fruit set, and whether the life span varies across distribution ranges (native/invaded) and habitat types. Monocarpic species have a single opportunity to reproduce, and need to trade-off postponing flowering until the next season, which allows the accumulation of more resources and setting more fruits in spite of the increased risk of death, or flowering as soon as possible with the resources currently available (Metcalf *et al.*, 2003).

The age at flowering of native plants in the Western Greater Caucasus and invasive plants in the Czech Republic, in managed (pastures) and unmanaged habitats, is recorded in Pergl *et al.* (2006). Unmanaged sites in the Caucasus can be considered as natural habitats of *H. mantegazzianum* (see Otte *et al.*, Chapter 2, this volume), while unmanaged sites in the Slavkovský les study area in the Czech Republic are abandoned pastures, forest clearings, meadows and abandoned former villages (for details of the history of the invasion of this region, see Müllerová *et al.*, 2005). Pergl *et al.* (2006) found that age at flowering in unmanaged habitats is significantly different between distribution ranges. Plants from the native range flowered later (median age 4 years) than those from the invaded range (3 years). Within the invaded range, plants from managed sites needed significantly more time (5 years) to flower than those from unmanaged sites. But the oldest, a 12-year-old flowering plant, was found in an unmanaged site in the Czech Republic; this can be attributed to the harsh conditions at that site. However, the general pattern is that plants from pastures flowered later than those from unmanaged sites in both distribution ranges (the mean age at flowering in pastures was 5 years), although the difference in the native range was not significant. Additional analysis by Pergl *et al.* (2006) showed that the delay in the time of flowering can be a result of higher altitude in the native distribution range, which affects the length of the growing season and consequently the time needed for accumulation of resources.

The timing of flowering in relation to the reproductive effort of plants in their native and invaded distribution ranges was also studied by Pergl *et al.* (2006), who found no relationship between the age of flowering plants and potential fecundity, based on an architecture score, calculated from the number of umbels of different orders and their importance for fruit set. This implies that once a plant accumulates a certain minimum level of resources it flowers. This strategy is the same in both distribution ranges (Pergl *et al.*, 2006). Complementary information on the age at flowering is provided by C. Nielsen *et al.* (unpublished data), who investigated the effect of the length of the management regime on the population structure of *H. mantegazzianum*. Their data are similar to those from the Czech Republic. At four study sites, grazed for 2–8 years, plants flowered from the third to fifth year. The trend in the data indicates that the proportion of older plants in the population increased with the duration of grazing, but further research is needed to confirm this.

From the overall pattern shown by *H. mantegazzianum* it is concluded that although it is able to flower in the second year, this only occurs in the favourable conditions in experimental gardens or cultivated fields (Stewart and Grace, 1984; Pergl *et al.*, 2006). The youngest flowering plant found under natural conditions was 3 years old; this is also the most common age of flowering plants in the invaded distribution range where, nevertheless, they can be as much as 12 years old (Pergl *et al.*, 2006). This suggests that *H. mantegazzianum* is remarkably plastic and when growing in unsuitable conditions can wait until the needed resources are accumulated and then reproduce.

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