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Flowering phenology and reproductive effort of the invasive alien plant *Heracleum mantegazzianum*

Fenologie kvetení a plodnost invazního druhu *Heracleum mantegazzianum*

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Heracleum mantegazzianum is one of the most invasive species in the Czech flora. The present study describes its flowering phenology and assess the effectiveness of protandry in preventing selfing in this self-compatible species, describes the timing of flowering in a heavily invaded area of Slavkovský les (Czech Republic) and estimates fruit set in a large sample of plants, which provides reliable data on the often exaggerated fecundity of this species. The study of flowering phenology revealed that protandry is always effective only within individual flowers, where male and female flowering phases are completely separated. In contrast, anther dehiscence in some flowers can occasionally overlap with stigma receptivity in other flowers in the same umbel, providing an opportunity for geitonogamous (i.e. between-flower) selfing. Nevertheless, the potential for selfing in *H. mantegazzianum* is determined mainly by an overlap in the male and female flowering phases between umbels on the same plant; at least a short overlap between some umbels was observed in 99% of the plants at the Slavkovský les. Although the degree of protandry in *H. mantegazzianum* favours outcrossing, the opportunity to self may be of crucial importance for an invasive plant, especially if a single plant colonizes a new location. At Slavkovský les, flowering started within one week (from 20 to 27 June 2002) at all 10 sites. The duration of flowering of an individual plant was on average 36 days, with maximum of 60 days, and increased significantly with the number of umbels on a plant. In the second half of August, the majority of the fruits were ripe and had started to be shed. The beginning of flowering of a plant was significantly negatively correlated with the number of umbels it had – the earlier a plant started to flower the more umbels it had produced. A significant negative relationship was also found between basal diameter and beginning of flowering; plants with large basal diameters started to flower earlier. An average plant at Slavkovský les produced 20,671 fruits. Of these, 44.6% were produced by the terminal umbel, 29.3% by secondary umbels on satellites, 22.6% by secondary umbels on branches and only 3.5% by tertiary umbels. The estimated fruit number of the most fecund plant was 46,470 – compared to an average plant, the proportional contribution of tertiary umbels increased relative to the primary umbel. This study revealed a significant positive relationship between fecundity and plant basal diameter. Although the results of this study indicate that the fecundity of this species is often overestimated in the literature, the number of fruits produced by *H. mantegazzianum* provides this invasive species with an enormous reproductive capacity.

Keywords: alien plant, andromonoecy, *Apiaceae*, Czech Republic, fecundity, flowering, fruit production, invasive plant, phenology, protandry, self-pollination

Introduction

Attempts to explain the ability of alien plants to occur in a wide range of habitats (Chytrý et al. 2005) and exhibit remarkable invasion dynamics (Mandák et al. 2004, Pyšek & Hulme 2005) are often linked to detailed studies of biological traits. The effort to identify the characteristics of successful invasive species started with the classical study of Baker (1965). In his list of characteristics of an ideal weed, eleven out of fourteen are associated with reproduction. The recent literature documents that traits related to reproduction, such as breeding system, timing of flowering or fecundity, can affect the success of naturalization and invasion (Pyšek & Richardson 2007).

Comparative studies using large species sets repeatedly showed that it is advantageous for an alien to flower earlier or over a longer period compared to native species (e.g. Crawley et al. 1996, Cadotte & Lovett-Doust 2001, Pyšek et al. 2003, Lake & Leishman 2004, Lloret et al. 2005, Cadotte et al. 2006). Congeneric studies that address flowering phenology support these conclusions; early flowering and extended flowering period compared to natives/non-invasives provides invaders with an advantage (Baker 1965, Gerlach & Rice 2003, Radford & Cousens 2000). There is also good evidence that high fecundity and efficient dispersal of seeds promote invasiveness (e.g. Richardson et al. 1987, Pyke 1990, Callaway & Josselyn 1992, Vila & D'Antonio 1998, Radford & Cousens 2000; see Pyšek & Richardson 2007 for review and quantitative assessment).

In comparative studies, breeding system and sex habit have been evaluated with ambiguous results. Alien species are less often monoecious (Williamson & Fitter 1996) and more likely to be hermaphroditic than natives (Cadotte & Lovett-Doust 2001), but Sutherland (2004) found no significant difference in breeding system. He concluded that invasive species were more likely to be monoecious than non-invasives, and aliens more likely to be self-incompatible than natives. Some support for the importance of being able to reproduce sexually in a new region comes from case studies comparing congeners (Nadel et al. 1992, Daehler & Strong 1996). Studies comparing self-compatibility vs. self-incompatibility in alien vs. native and invasive vs. less invasive congeners, respectively, found self-compatibility to be associated with invasiveness in *Amsinckia* (*Boraginaceae*; Pantone et al. 1995), *Eupatorium* and *Ageratum* (*Compositae*; Baker 1965) but not *Centaurea* (Gerlach & Rice 2003).

That the empirical evidence for the importance of self-compatibility for invasiveness is not strong, can be attributed to the lack of data and their limitation (Pyšek & Richardson 2007). Self-pollination, nonetheless, is considered to be a suitable mating strategy for colonizing species. The ability to self is particularly advantageous when one or a very limited number of diaspores reach a new area. Nevertheless, not all sexually reproducing successful invaders are selfers. Pannel & Barrett (1998) examined the benefits of reproductive assurance in selfers versus outcrossers in model metapopulations. Their results suggest that an optimal mating system for a sexually reproducing invader in a heterogeneous landscape should include an ability to modify selfing rates according to local conditions. In early stages of invasions, when populations are small, plants should self to maximize fertility. However, later, when populations are large and pollinators and/or mates are not limiting, outcrossing will be more beneficial, mainly due to increasing genetic polymorphism.

Heracleum mantegazzianum, an invasive species and subject of the present paper, is considered to be self-compatible, which is typical of *Umbelliferae* (Bell 1971), and protandrous (Grace & Nelson 1981). Protandry has traditionally been considered to be a mechanism for avoiding or reducing selfing. When it is strongly developed, male and female phases on a plant may be completely separated in time so that outcrossing is assured (Webb 1981, Snow & Grove 1995). However, in many cases, protandry itself is unlikely to guarantee outcrossing (Bell 1971, de Jong 1993). Consequently, a detailed study of phenology on flower, inflorescence, as well as plant level is needed to assess the effectiveness of protandry in preventing selfing in *H. mantegazzianum*.

Therefore, this study was aimed at (i) describing the flowering phenology of *H. mantegazzianum* on all the above-mentioned levels, (ii) describing the timing of flowering in a heavily invaded area, its variability and underlying factors, (iii) estimating fruit set of a large sample of plants, which provides reliable data on the often exaggerated fecundity of *Heracleum mantegazzianum*, and the factors that influence reproductive output.

Study species

Heracleum mantegazzianum is native to meadows, clearings and forest margins at higher altitudes in the Western Great Caucasus (Russia, Georgia) (Mandenova 1950), where it grows in species-rich tall-herb mountain meadows up to the treeline (at ca 2000 m a.s.l.; see Otte et al. 2007). Due to its size and exotic appearance it became popular as a garden ornamental and was introduced into many European countries, where it is now naturalized or invasive. *Heracleum mantegazzianum* is also naturalized in central Russia (Tiley et al. 1996, Nielsen et al. 2005), Canada and the United States (Morton 1978, Ochsmann 1996, Kartesz & Meacham 1999). It was first recorded in the Czech Republic in 1862 in the park of a chateau at Lázně Kynžvart (W Bohemia), from where it spread across the country and became invasive (Pyšek 1991, Pyšek & Pyšek 1995, Pyšek et al. 2002, Müllerová et al. 2005). The species often develops large and dominant stands (Müllerová et al. 2005) and replaces the native vegetation (Pyšek & Pyšek 1995, Tiley et al. 1996). Besides threatening biodiversity and impeding landscape management in invaded regions, the phytotoxic chemicals in its sap can injure man and livestock (Drever & Hunter 1970, Tiley et al. 1996). So far programmes to control the spread of the species have only been of limited success (Nielsen et al. 2005).

Heracleum mantegazzianum is the tallest herbaceous species in Europe; it reaches 200 to 500 cm in height, its leaves are up to 300 cm long and a flowering stem may reach up to 15 cm in diameter. The species is monocarpic, i.e. persists in a form of a vegetative rosette for several years, then flowers and dies in the same year. Plants of *H. mantegazzianum* usually live three to five years, but twelve year old individual was also found (Pergl et al. 2006).

Heracleum mantegazzianum reproduces entirely by seed. The species produces a large number of fruits; estimates range from 5000 to more than 100,000 per plant (Tiley et al. 1996). Every flower, which contains a fertilized ovule, can produce two winged mericarps (for simplicity, the morphologically correct term "mericarp" is replaced by "fruit" throughout the text below and refers to the unit of generative reproduction). Fruits released from parent plants contain morphophysiologically dormant embryos, i.e. a period of embryo growth is required and dormancy is broken by the wet and cold conditions experienced over winter. After dormancy is broken, about 90% germinate regardless of the position on the parent plant where the fruits were produced (Moravcová et al. 2005). *Heracleum mantegazzianum* forms a short-term persistent seed bank; a small proportion (about 1%) of the fruits remain viable in the soil for at least three years (Krinke et al. 2005, Moravcová et al. 2006).

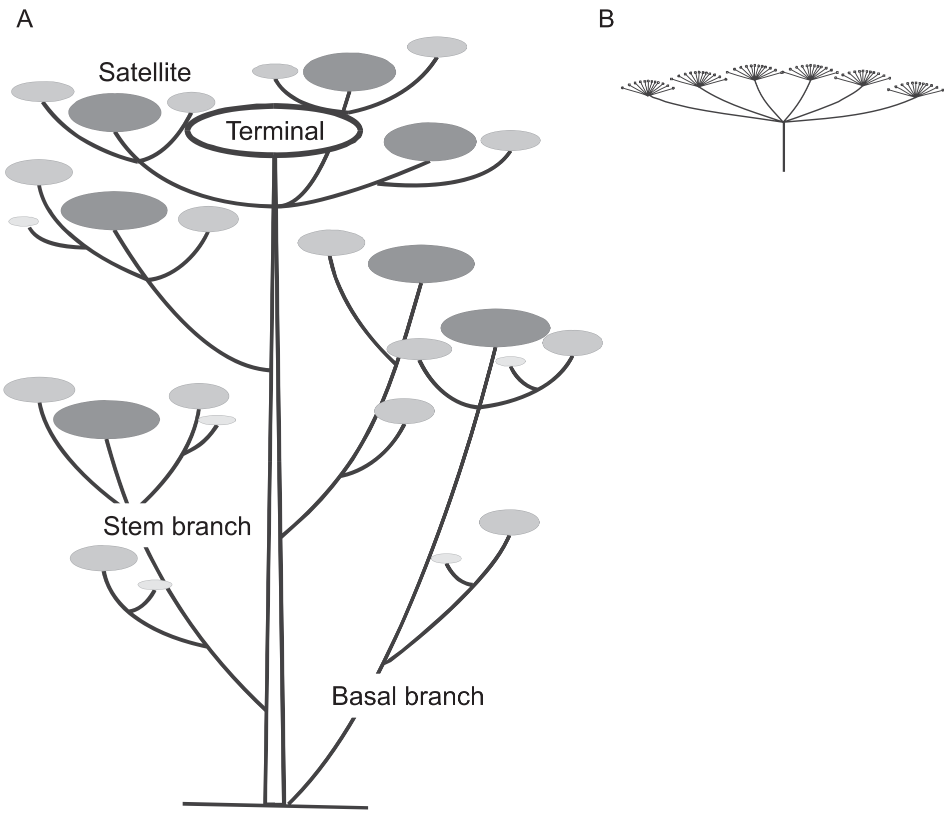

Fig. 1. – A. Schematic representation of the ordering of umbels and their position within the hierarchical inflorescence system of *Heracleum mantegazzianum*. Umbel orders: primary □, secondary ■, tertiary ▒ and quaternary ░. B. Each compound umbel consists of umbellets that bear a large number of small, closely packed flowers (see text for a detailed description).

The flowers of *H. mantegazzianum* are unspecialized and attract a variety of unspecialized pollinators, of which *Coleoptera*, *Diptera*, *Hemiptera* and *Hymenoptera* are the most frequent (Grace & Nelson 1981). Flowering plants of *H. mantegazzianum* have a distinct architecture. The inflorescences are compound umbels of four orders (umbel ordering follows the system proposed by Webb 1981). 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; these shoots are found in a satellite position, surrounding the primary umbel (hereafter also called “satellites”), or a branch position lower on the stem (hereafter also called “branches”). Tertiary umbels may arise on shoots branching from secondary shoots (in both satellite and branch position) and quaternary umbels similarly on shoots branching from tertiary shoots (Fig. 1A). Under favourable conditions, a strong plant may produce several shoots from the base of the flowering stem at ground level. The character of terminal umbels on these basal branches vary between that typical of the first- and second-order umbels in terms of umbel size, fruit size, fecundity and proportion of male flowers (I. Perglová, personal observation).

Each compound umbel consists of umbellets (umbellules), simple umbels that bear a large number of small, closely packed flowers (Fig. 1B). This species is andromonoecious; together with perfect (hermaphrodite) flowers, umbels bear a varying proportion of male (staminate) flowers. The latter usually contain a 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 (I. Perglová, personal observation), although an increasing percentage of male flowers towards the centre of an umbel is reported for some other *Umbelliferae* (Bell 1971, Lovett-Doust 1980).

How effectively protandry prevents selfing in *H. mantegazzianum*, has not so far been addressed in detail. However, a study of hybridization of *H. mantegazzianum* and *H. sphondylium* by Stewart & Grace (1984) reports complete protandry within an umbel. They also observed an overlap between female and male phases of the primary and secondary umbels in two out of the nine plants of *H. mantegazzianum*, which allowed them to transfer pollen to receptive stigmas within a plant. However, these authors did not study plants growing under natural conditions, only plants growing in a greenhouse where they had been transplanted in the spring of the same year in which they flowered. As a consequence these transplanted plants could have been smaller, with fewer umbels, which might have affected the course of flowering.

Study sites

Field site: Slavkovský les Protected Landscape Area

This area is located in W Bohemia, close to the locality where *H. mantegazzianum* was first introduced into the Czech Republic in the second half of the 19th century, and from where the species started to spread (Pyšek 1991). Heavy infestation of the region by *H. mantegazzianum* was probably promoted by the change in land-use after Word War II, when German inhabitants were displaced and part of the region became a military area until the 1960s (Müllerová et al. 2005). After that the area remained largely uninhabited, with open sites on places of demolished villages and adjacent areas, which were prone to invasion.

The size of the protected area is 617 km^2, with an altitudinal range of 373–983 m a.s.l. (Kos & Maršáková 1997), January temperature ranging from –5.1° C (average mimimum) to –0.2° C (average maximum) and July temperature from 10.5 to 21.5 ° C, respectively. Annual sum of precipitation is 1094 mm (Mariánské Lázně meteorological station, 50-year average). Orographically, most of the region belongs to the Ore Mountains, and is formed of granite. Natural vegetation of the area consisted mainly of beech and spruce forests, extensive peat bogs and pine forests on serpentine (Neuhäuslová & Moravec 1997). This vegetation is nowadays only present in remnants and was replaced by extensive wetlands with a high floral diversity, pastures and spruce forest plantations, which cover 53% of the area (Kos & Maršáková 1997).

Ten study sites with dominating stands of *H. mantegazzianum*, which were evenly distributed across an area of 20 × 30 km to cover the range of variation in environmental conditions, were selected for the study (Table 1); their altitude ranges from 506 to 800 m a.s.l.

Table 1. – Geographical location and altitude (m a.s.l.) of the 10 study sites at the Slavkovský les Protected Landscape Area, Czech Republic. The numbering corresponds to that used in other studies made in this region, where more details on the study sites can be found (e.g. Müllerová et al. 2005, Moravcová et al. 2005, Krinke et al. 2005).

Site no.	Name	Latitude (N)	Longitude (E)	Altitude
3	Žitný I	50°03.754'	12°37.569'	787
6	Lískovec	49°59.156'	12°38.721'	541
8	Potok	50°04.660'	12°35.953'	643
9	Dvorečky	50°05.982'	12°34.137'	506
11	Arnoltov	50°06.801'	12°36.147'	575
12	Krásná Lípa I	50°05.685'	12°38.546'	597
13	Litrbachy	50°06.009'	12°43.777'	800
14	Rájov	49°59.704'	12°54.933'	753
15	Krásná Lípa II	50°06.306'	12°38.393'	596
16	Žitný II	50°03.837'	12°37.304'	734

On each site, 10 plants were randomly selected and marked when the flowering stem appeared; basal diameter of the stem and plant height were recorded after plant growth ceased. As soil properties and nutrient availability affect plant performance in some species (Crawley 1997), representative soil samples were taken at each study site and analysed using standard methods for pH_{H_20}, pH_{KCl}, Mg, Ca, K and P content, and percentage of N and C (Page et al. 1982, Moore & Chapman 1986). Soil samples were collected from a depth of 10–20 cm, transported to the laboratory, air-dried, sieved (2 mm mesh sieve) and stored in paper bags.

Experimental garden: Institute of Botany Průhonice

The experiments, which required frequent regular observations, were carried out in the Experimental Garden of the Institute of Botany, Průhonice, Czech Republic (N 50°0.07', E 14°33.528'; 310 m a.s.l.). In May 2002, approx. 70 plants were transplanted at the seedling stage from the site Žitný I at Slavkovský les to a garden bed in Průhonice; the spacing between plants was sufficient to ensure that they did not compete with one another. The plants were watered regularly to compensate for the drier climate in the experimental garden (January temperature –2.4° C, July temperature 15.9 °C, annual precipitation 525 mm; Praha-Ruzyně meteorological station, 30-year average) compared to the field site. The 17 plants that flowered in 2005 were subjected to phenological observations.

Methods

Phenology of a flower

Detailed phenology of individual flowers was studied in 2005 using three of the 17 flowering plants grown at Průhonice. On each plant, the terminal umbel, one secondary and one tertiary umbel were selected. In both the central and peripheral parts of each umbel, three flowers located in peripheral part of umbellets and three flowers located in central part of umbellets were marked by threads of coloured cotton (i.e. twelve flowers per umbel); as tertiary umbels did not develop on one of the plants, the total number of flowers studied was 96.

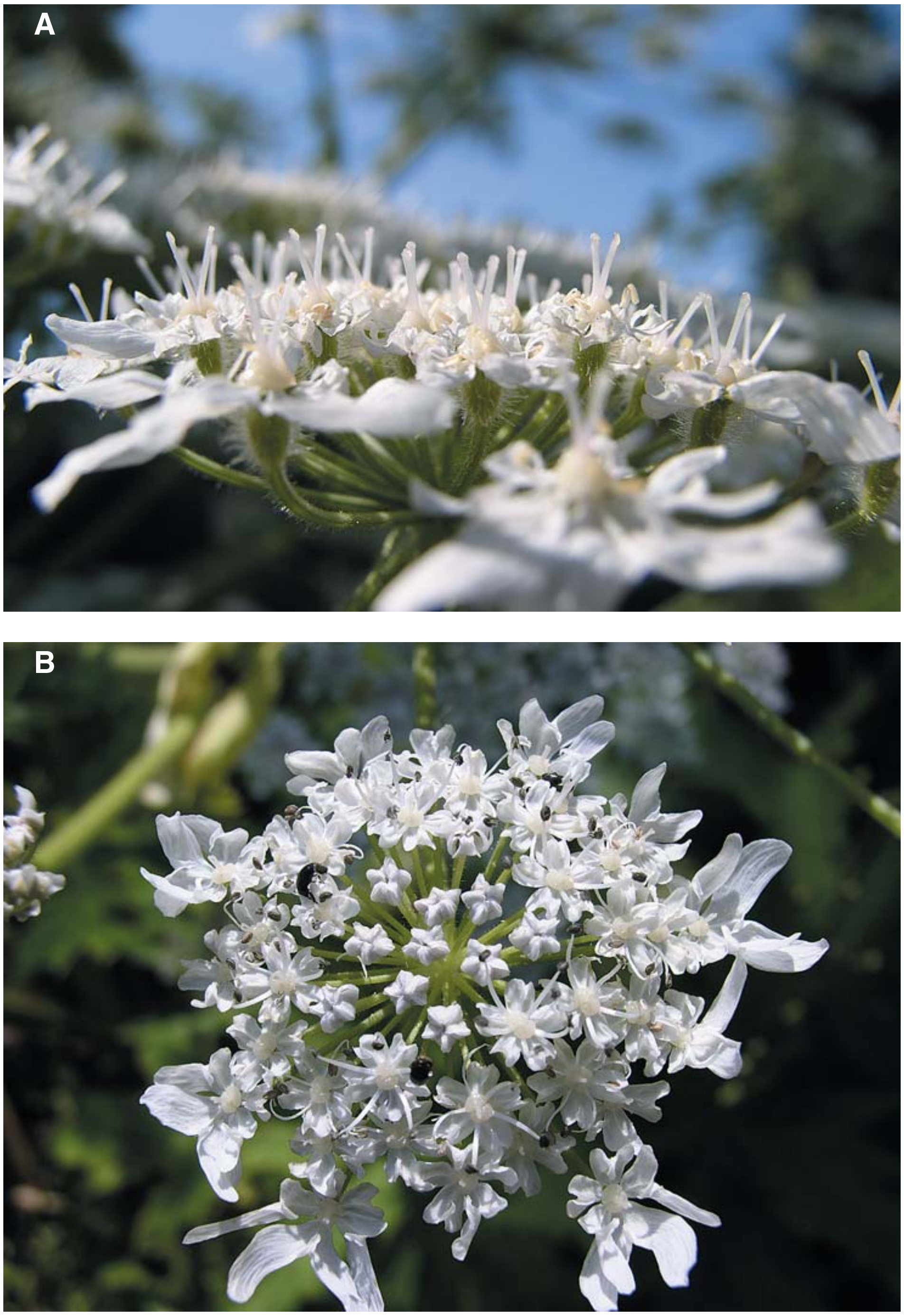

Fig. 2. – A. Flowers of *Heracleum mantegazzianum* with receptive stigmas, which at this stage have fully elongated and separated styles with a fresh glistening appearance at the tip of the style. Photo I. Perglová. B. The flowers of an umbellet open centripetally over a period of several days. Photo J. Pergl.

Fig. 3. – An overlap of anther dehiscence and stigma receptivity in flowers of the same umbellet. Photo J. Pergl.

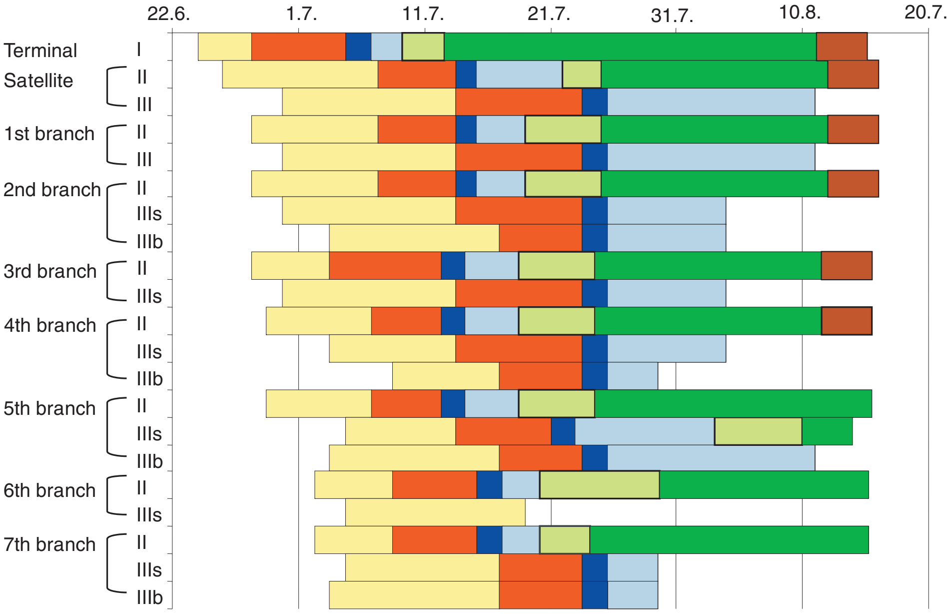

Fig. 4. – Phenological sequence from umbel opening to fruit maturation for all the umbels on a single plant of *Heracleum mantegazzianum* (one of the 100 analyzed in the present study): 🟨 umbel opening, 🟧 male phase, 🟦 female phase, ⬜ post-receptive phase, 🟩 fruit development, 🟩 final-sized fruits and 🟫 ripe fruits. See text for a detailed description of the phases.

The development of each flower was followed daily from opening to the beginning of fruit development and the occurrence of a male/neutral/female phase was recorded. The male phase was defined as that when at least one of the five stamens was dehiscent and neutral phase when stamens withered and stigmas were non-receptive. Stigma receptivity was recognized visually – when receptive, the styles are fully elongated with a fresh glistening appearance at the tip of the style; their initially dome shape spreads and they become bulbous (Fig. 2A). Correctness of this visual determination of stigma receptivity was confirmed by enzymatic activity determined by immersing the stigma into hydrogen peroxide (Dafni 1992). After the flower withered, monitoring continued to determine whether or not it developed into a fruit.

Phenology of umbels

Phenological development of umbels was studied in 2002 at Slavkovský les (100 plants) and in 2005 in the experimental garden at Průhonice (17 plants). On each plant, the phenological phases of each umbel were recorded daily at Průhonice and at 3–7 day intervals at Slavkovský les, from umbel opening to fruit development (the intervals were shorter at the beginning due to intensive flowering and lengthened after the majority of the umbels had finished flowering).

Seven phenological stages were recognized. Observation of an umbel started after the umbel bud split. An umbel with at least one dehiscent anther was designated male. Once any of the stigmas became receptive, the whole umbel was designated as female. Post-receptive phase was determined by the loss of petals. Fruit development was when the ovary swelled up to the final fruit size, seed maturity the browning of fruits. As it was not feasible to observe all plants at Slavkovský les on a daily basis, the data were linearly interpolated to determine the duration of individual phases. Dividing the male phase, which was considerably longer than the female phase, to finer categories (up to 25%, 25–75% and more than 75% of the flowers in an umbel that entered the male phase) allowed a more precise interpolation.

The detailed study of the overlap of male and female phases within the same umbel was done only at Průhonice, as it required daily observations.

Timing of flowering at the plant and population level

The timing of flowering at the plant and population levels was evaluated using data collected from the 100 marked plants at Slavkovský les in 2002. In addition, to compare the difference in phenology between the sites, 30 plants were selected randomly at each site at each sampling date and their phenological phase was recorded (the stages distinguished were: terminal and secondary umbels on satellites at the budding stage; terminal umbel flowering and secondary umbels on satellites in the budding stage; both terminal and secondary umbels on satellites flowering). The peak of flowering at a locality was the average date on which the primary and secondary umbels on satellites of the randomly selected plants flowered.

Floral architecture and reproductive effort

The proportional fecundity of each umbel of the plants studied at Slavkovský les was estimated using four fecundity classes: (i) no fruits; (ii) up to 25%, (iii) 25–75% or (iv) more than 75% of flowers in an umbel set fruits, and the diameter of each umbel was measured.

The fruit set of individual umbels was estimated by using regression equations derived from 100 umbels from the locality Žitný I. These umbels were collected from randomly selected plants to cover the range of umbel orders (terminal umbels, secondary umbels and tertiary umbels), sizes and fecundity classes; fruit production by quaternary umbels was ignored due to negligible number of fruits produced by these umbels. If the fecundity of an umbel was low (less then 1500 fruits), individual fruits were counted; otherwise it was inferred from the total number of rays and number of fruits per five inner and five outer umbellets (weighted by the ratio 4:9; based on data from a preliminary analysis). Based on these values, regression equations for each category/umbel order were developed with number of fruits as the dependent and umbel diameter as the independent variable.

The fruit set of individual plants was then calculated by summing the fruit set of all the umbels produced by the plant.

Statistical analysis

The differences between the characteristics of individual plants were tested by factorial ANOVA with interactions or ANCOVA where appropriate. Deletion tests (Crawley 2002) were used to simplify the model to obtain minimal adequate models. If significant differences between individual sites were found, averaging of site averages was used to obtain a generalization for the whole study area. All analyses were performed using S-PLUS (2001). Aptness of models was checked by normal probability plots of the fitted values and distribution of residuals. If multiple comparisons were applied, a SNK test (Underwood 1997) was used. For five plants values for some of the characteristics were missing – two were destroyed in late summer by a heavy storm before their fecundity was assessed (the Dvorečky site) and three (one from Litrbachy, two from Arnoltov) started to flower too early to be recorded from the very beginning. These plants were excluded from certain analyses, leaving 98 plants for the fecundity analyses, 97 for phenology and 95 for those combining fecundity and phenology. The relationship between the beginning of flowering, and the fecundity of plants and number of umbels, respectively, was assessed by correlation due to unclear causality; the shift in phenology among sites was standardized using the residuals from the relationship between the beginning and peak of flowering, which allowed all the plants to be used in one analysis.

Results

Phenology of a flower

In an individual flower, flowering started by sequential expansion and dehiscence of the five stamens, which took usually one and sometimes (in 5% of flowers) two days. Anthers were ready to shed pollen almost immediately after the expansion was complete. Within an umbellet, peripheral flowers were the first to flower and flowering continued towards the umbellet centre, where pollen was shed 1–3 (in the case of the terminal umbels), 3–6 (secondary umbels) or 1–7 (tertiary umbels) days later (Fig. 2B). In some umbels, the onset of flowering of central umbellets occurred one day later compared to peripheral umbellets.

In contrast, the phase of stigma receptivity was well synchronized throughout the whole umbel and lasted for 1–2 days. Some of the flowers in the centre of umbellets and all flowers of quaternary umbels were male and did not go through the female phase.

Between anther dehiscence and stigma receptivity of a flower, there was a neutral phase of varying length, depending on the position of the flower in the umbellet, position of an umbellet in the umbel and umbel type. In peripheral flowers of peripheral umbellets, the neutral phase may last up to 6 days because they were the first of all flowers within the umbel to shed pollen. The neutral phase of peripheral flowers of central umbellets was usually one day shorter. That of central flowers, both in peripheral and central umbellets, lasted two days at the longest and they could also have no neutral phase.

Of 96 flowers studied for within-flower phenology, 50 were hermaphrodite (83.3% of flowers from primary umbels, 55.6% from secondary and none from tertiary umbels) and 92% of the hermaphrodite flowers set fruits after the blossom was shed.

One plant of the 17 studied at Průhonice was completely male-sterile. This plant bore only physiologically female flowers with stamens, the filaments of which remained unrolled and the anthers closed, and did not dehisce. Pistils were fully functional and fruits were set after fertilization.

Phenology of umbels

Within umbels, an overlap of anther dehiscence in some flowers with female receptivity in other flowers of the same umbel was occasionally observed (Fig. 3). Such within-umbel overlaps occurred only in 22 umbels on five of 17 plants studied. They occurred only on secondary or tertiary umbels and lasted for one day at the longest; it typicaly involved a small proportion of late dehiscing anthers of usually male flowers located in the central parts of umbellets. Consequently, stigmas were not covered with pollen from the same umbel but the opportunity for geitonogamous selfing could rise. The opposite situation, when before stigma receptivity, a whole umbel passed through a neutral phase when there were no dehiscing anthers, occurred very rarely. This was observed only in secondary umbels on satellites of two plants.

Umbels of different orders started to flower in sequence. The terminal (primary) umbel was the first to flower, followed by secondary and later tertiary and quaternary umbels on satellites and branches (Fig. 4). The individual umbels passed through a male and than a female phases and all umbels of the same order tended to be synchronized. However, synchronization was far from complete and consequently, male and female phases of umbels on the same plant overlapped (Fig. 4). Such overlaps were very common; at least a short overlap between some umbels was observed in 99% of the plants at Slavkovský les and in all plants (except the one which was male-sterile) at Průhonice. Except for the quaternary umbels of the plants at Slavkovský les, in more than half of the umbels that contained at least some hermaphrodite flowers and thus went through a female phase, the overlap lasted for the whole female phase (Fig. 5).

In some umbels of higher orders, the female phase and fruit development did not occur after the male phase (Fig. 4), because those umbels contained only male flowers, which withered after anther dehiscence. The percentage of such umbels increased with increas-

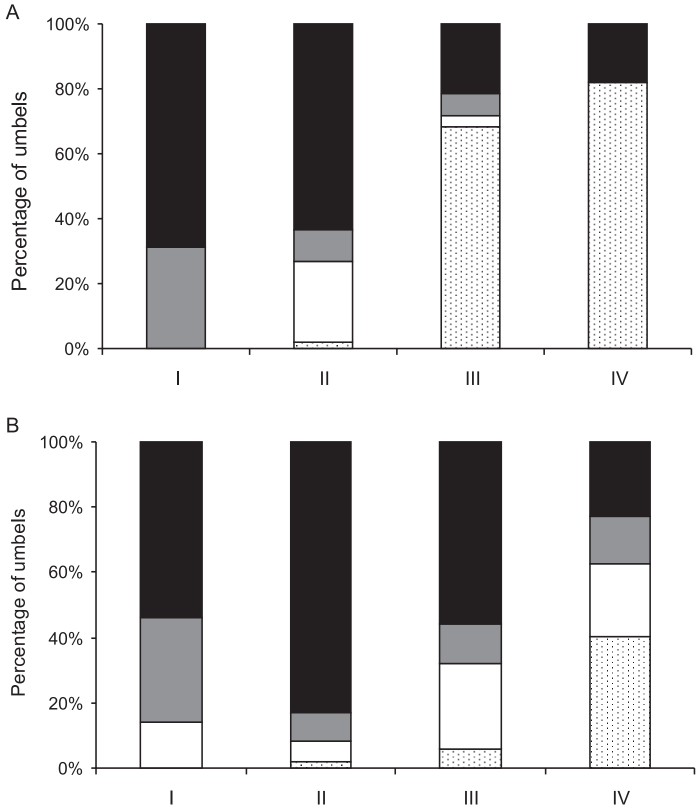

Fig. 5. – Percentage overlap of male and female phases in the four orders of umbels on a plant of *Heracleum mantegazzianum* (I–IV), based on plants grown in the garden at Průhonice (A) and a field site at the Slavkovský les Protected Landscape Area (B). The percentage of the total number of umbels is shown in which the two phases overlapped during ■ the whole female phase, ▒ part of female phase, □ did not overlap, ░ and in which no female phase occurred (the umbels contained only male flowers).

ing umbel order – at Slavkovský les, 1.7% secondary, 5.8% tertiary and 40.2% quaternary umbels were solely male; at Průhonice, the percentage was very similar in secondary umbels (1.8%), but much higher in the case of tertiary and quaternary umbels (68.2% and 82.1%, respectively) (Fig. 5).

Timing of flowering at the plant and population level

At Slavkovský les, the first signs of the development of flowering stems became visible in early June. Then, a rapid elongation of the stem followed and culminated in the opening of a terminal bud, which contains terminal and satellites umbels.

Table 2. – Phenological and reproductive characteristics of *Heracleum mantegazzianum* at the Slavkovský les field site. Mean date of the beginning of flowering in 2002 (with S.D. in days), duration of flowering, date of the peak of flowering, estimated fecundity and basal diameter are shown. Based on 100 plants monitored over the season, except the peak of flowering, which is based on 30 randomly selected plants (see text for details).

Site	Beginning of flowering		Duration of flowering (days)		Peak of flowering	Fecundity (number of fruits)		Basal diameter (cm)	
	Mean	SD	Mean	SD		Mean	SD	Mean	SD
Lískovec	21.6. b	4.3	30.9 a	3.1	29.6.	9974 a	2199.4	5.3	0.95
Žitný I	22.6. b	4.2	38.4 ab	7.6	3.7.	21,573 b	8231.1	7.2	1.29
Žitný II	26.6. b	5.5	35.1 ab	5.4	6.7.	22,643 b	4778.6	7.2	1.06
Potok	25.6. b	4.8	39.0 ab	6.7	5.7.	23,966 b	1850.4	7.8	1.06
Dvorečky	25.6. b	5.6	33.8 ab	8.0	2.7.	24,930 b	9475.6	7.6	1.85
Arnoltov	20.6. ab	3.9	36.6 ab	3.2	27.6.	21,270 ab	6776.7	7.4	1.64
Krásná Lípa I	23.6. b	3.6	36.8 ab	6.1	2.7.	22,832 b	4407.4	7.2	1.09
Krásná Lípa II	27.6. bc	4.5	41.5 b	9.1	6.7.	27,633 b	6439.9	8.5	1.22
Litrbachy	24.6. b	4.1	33.2 ab	4.6	30.6.	16,258 ab	5990.3	6.9	1.25
Rájov	26.6. b	3.7	33.9 ab	4.8	2.7.	16,686 ab	5024.7	6.8	1.55

Table 3. – Summary of ANCOVAs showing the effect of plant basal diameter and site on the beginning of flowering and fecundity (number of fruits produced) of *Heracleum mantegazzianum* at the Slavkovský les field site (see text for details).

	Beginning of flowering				Fecundity			
Source of variation	DF	MS	F	P	DF	MS	F	P
Basal diameter	1	55.85	3.41	0.001	1	1175946383	56.61	<0.001
Site	9	308.32	18.85	<0.001	9	259035092	12.47	<0.001
Error	84	16.36			87	20772024		

Flowering started (e.g. the terminal umbel expanded and started to flower) within one week (from 20 to 27 June 2002; averaged over sites) at all 10 sites (Table 2); significant differences in the beginning of flowering occurred only between two extreme populations (Krásná Lípa II and Arnoltov) (ANOVA, $F_{9,87} = 2.83$, $P = 0.006$). After filtering out the effect of site by using the residuals from the regression of the beginning of flowering on peak of flowering, the correlation analysis revealed a significant negative relationship between the number of umbels on a plant and the beginning of flowering ($r = –0.33$, $P = 0.001$, df = 93). Thus, the earlier a plant started to flower, the more umbels it produced. Analysis of covariance revealed a significant negative relationship between plant diameter (independent variable) and beginning of flowering, indicating that plants with large basal diameters started to flower earlier. The interaction term was non-significant, hence the pattern was similar across all the populations studied (Table 3).

The peak of flowering, expressed as the average date on which the primary and secondary umbels on satellites of 30 randomly selected plants at the site had flowered, occurred between 27 June and 6 July 2002 (Table 2) and was not correlated with the altitude of the site ($P = 0.49$, df = 8).

The duration of flowering of an individual plant (time from the beginning of male phase in the terminal umbel to the end of female phase in the last umbel on the plant) at

Slavkovský les was on average 36 days (range of averages for individual localities: 31–41 days); with a maximum of 60 days. Significant differences in the duration of flowering were found only between the sites Lískovec and Krásná Lípa II, where plants were extremely weak and strong, respectively (Table 2). The duration of flowering increased significantly with the number of umbels on a plant, while the effect of site was non-significant (duration = 27.37 + no. of umbels × 0.27, $F_{1,93} = 89.45$; $P < 0.001$, $R^2 = 0.4903$). The terminal umbel flowered on average for 10 days and the average time from the beginning of flowering to fruit maturation was 44 days. In the second half of August, the majority of the fruits were ripe and had started to be shed.

Floral architecture and reproductive effort

Plants at Slavkovský les bore 2–8 secondary umbels on satellites, surrounding the main terminal (primary) umbel, 1–10 branches (terminated by secondary umbels), up to 43 tertiary umbels and 39 quaternary umbels. Average number of umbels of individual orders and their size are given in Table 4.

The total number of umbels formed on 98 plants is shown in Fig. 6, where tertiary and quaternary umbels are presented in detail according to their position on the plant. Of the tertiary umbels growing on branches, the majority were in the satellite position, and only 21.1% in the branch position. Regardless of their position, umbels of the same order were very similar in terms of the proportion of flowers that developed into fruits. Proportional fecundity, roughly expressed by fecundity classes, differed between umbels of individual orders. While 80.6% of the terminal umbels were in the highest fecundity class, only a few tertiary umbels set some fruits; 85% of them as well as 97.5% of the quaternary umbels did not set any fruits (Fig. 6).

An average plant at Slavkovský les produced 20,671 fruits (because of significant differences recorded among sites this was calculated as an average of site averages). Of these, 44.6% were produced by the terminal umbel, 29.3% by secondary umbels on satellites, 22.6% by secondary umbels on branches and only 3.5% by tertiary umbels (for average number of fruits produced by single umbels of individual orders see Table 4). The estimated fruit number of the most fecund plant, which was at the Dvorečky site, was 46,470. This plant bore, in addition to the terminal umbel, 6 secondary umbels on satellites, 6 secondary umbels on branches, 36 tertiary umbels and 11 quaternary umbels, which accounted for 29.9%, 26.5%, 23.1% and 20.5% of the fruit set, respectively – compared to an average plant, the contribution of tertiary umbels increased relative to the primary umbel.

The analysis of plant fecundity showed a significant role of site (ANOVA, $F_{9,88} = 7.64$, $P < 0.001$). Nevertheless, the only difference was found between Lískovec and a group of six other sites (Table 2). Population characteristics and chemical composition of soil had no significant effect on mean plant fecundity. The only pattern found was for the content of potassium and magnesium: at the site with the lowest mean fecundity per plant (Lískovec), the content of K (108.9 mg/kg) was lower than the range found at the other sites (average: 556.8, range: 387.1–917.8 mg/kg) and that of Mg (420.7 mg/kg) higher (average: 193.5, range: 88.0–330.8 mg/kg).

The analysis of covariance, with plant fecundity as a variable dependent on basal diameter and with the effect of site included in the model, revealed a significant positive relationship between fecundity and basal diameter. As in the previous analysis, the effect of

Table 4. – The number of umbels, their size, and estimated number of fruits recorded on plants of *Heracleum mantegazzianum* growing in 2002 at the Slavkovský les field site. The umbels are classified according to their order and position, in the case of secondary umbels. Based on data from the 100 plants at the Slavkovský les field site (see text for details).

Characteristic		Terminals	Secondary umbels		Tertiary umbels	Quaternary umbels	Total
			on satellites	on branches			
Number of umbels/plant:	median[1]	1	4.3	3.5	17.3	2.8	27.5
	min–max	–	2–8	1–10	2–43	1–39	5–98
Umbel size:	mean±SD[2]	61.7±3.7	36.8±3.3	36.3±4.8	17.8±2.3	7.9±1.8	–
	min–max	44–85	20–56	5–62	2–36	1–17	
Number of fruits/umbel:	mean±SD[2]	9216.0±481.7	1288.0±614.8	1157.0±429.1	32.0±30.1	n.a.	20,671.0±5129.8

[1] calculated as a median of site medians

[2] calculated as averages of site averages and among-sites standard deviations

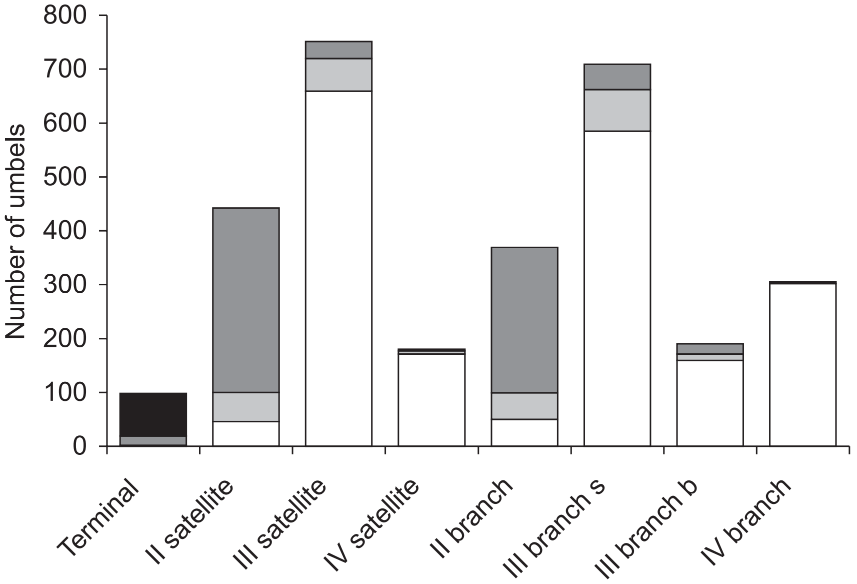

Fig. 6. – Number and fecundity of the different umbel types of *Heracleum mantegazzianum*. Fecundity defined as the percentage of flowers that produced fruits: ■ 100–76%, ▓ 75–26%, ░ 25–1%, □ 0% of flowers set fruits. Based on pooled data from 100 plants studied at Slavkovský les. Percentage of the number of umbels in each fecundity class is shown. For example, none of the terminals was completely infertile, and in 80.6% of them, more than 75% of the flowers produced fruits. Umbels are classified according to their order (terminal, II–IV), position (on satellite, branch) and in case of tertiary umbels on branches according to their position with respect to the branch axis (s – tertiary umbels on branches located in a satellite position; b – located in branch position).

site was significant (Table 3). The results thus indicate that local conditions affect plant performance, here the number of fruits produced, and similarly across all sites, as indicated by the non-significant interaction term between site and diameter (deletion test; $F_{87,78} = 0.987$, $P = 0.46$).

After the effect of site was filtered out by using the residuals from the regression of beginning of flowering on peak of flowering, the correlation analysis revealed a marginally significant negative relationship between plant fecundity and beginning of flowering ($r = –0.193$, $P = 0.0602$, $df = 93$).

Discussion

Protandry does not prevent self-pollination in Heracleum mantegazzianum

Within *Umbelliferae*, protandry has produced a mosaic of adaptations ranging from self-pollination to obligate outcrossing, which have lead to various patterns of floral composition and timing of flowering (Bell 1971). Cruden & Hermann-Parker (1977) claimed that there is no overlap between staminate and pistillate phases within umbels in protandrous *Umbelliferae* but possible overlap between umbels on an individual plant due to infrequent asynchronous flowering, which occurs most frequently in individuals with an above average number of lateral branches or stems. This accords with the findings that Molano-Flores (2001) reported for *Eryngium yuccifolium*. However, complete protandry both within flowers and umbels but frequent overlap of the two sexual phases within individuals is reported in *Daucus carota* (Koul et al. 1989) and *Trachymene incisa* subsp. *incisa* (Davila & Wardle 2002). In protogynous representatives of the genera *Thaspium* and *Zizia*, there is complete separation of the male and female phases within a single flowering stalk, but the stalks are not completely synchronized, so selfing is possible (Lindsey 1982).

The present study revealed that in *H. mantegazzianum*, protandry is effective only within individual flowers, i.e. male and female flowering phases are completely separated only at this level. In contrast, anther dehiscence in some flowers can overlap with stigma receptivity in other flowers of the same umbel. This kind of overlap is not very frequent and usually involves only a small proportion of late dehiscing anthers, but provides the opportunity for geitonogamous (i.e. between-flowers) selfing. However, the potential for selfing in *H. mantegazzianum* is determined mainly by a very common overlap of male and female flowering phases of different umbels on the same plant, documented in the present study.

Geitonogamous selfing has no genetic advantage over self-pollination, but may be of selective advantage by ensuring pollination after a period of time in which outcrossing could occur (Bell 1971). The degree of protandry in *H. mantegazzianum* favours outcrossing but does not preclude selfing, which can assure pollination in the absence of other plants. This may be of crucial importance for an invasive plant, which is likely to be dispersed to a new location where a sexual partner may not be available. However, the potential for selfing is not determined only by the degree of protandry; it may also be limited by genetic mechanisms such as maternal control before fertilization (i.e. partial self-incompatibility), late-acting self-incompatibility or inbreeding depression very shortly after fertilization, as reported for some *Umbelliferae*: *Eryngium alpinum* (Gaudeul & Till-Bottraud 2003) and *Trachymene incisa* subsp. *incisa* (Davila & Wardle 2002). Moreover, the real selfing/outcrossing rate will depend on other factors, such as population density and movement of pollinators.

Timing of flowering

The plants growing in the garden at Průhonice had a higher proportion of umbels with exclusively male flowers compared to those in the field at the Slavkovský les Protected Area (Fig. 5). This might have been caused by the climate of the latter location, which resembles more closely the mountain conditions where *H. mantegazzianum* grow naturally in the Caucasus Mountains, hence it is likely to be more suitable for the growth of the plants. The field site is located at a higher altitude, has lower summer temperatures and is more humid than Průhonice. Such more favourable conditions might have resulted in stronger plants, which were able to produce more hermaphrodite flowers, the development of which requires more resources than male flowers. The proportion of hermaphrodite flowers is reported to be very similar in two populations of *Smyrnium olusatrum* growing at rather contrasting sites (Lovett-Doust 1980). In four of five umbelliferous species studied by Cruden (1976), the ratio of male to hermaphrodite flowers is constant. In *Heracleum lanatum*, however, the ratio varies with habitat and it is suggested that increased numbers of male flowers produced by plants growing in forest may be associated with differences in the kinds of flower visitors (Cruden 1976). That plants of *H. mantegazzianum* at Slavkovský les were stronger and their umbels were larger resulted in a longer flowering period for individual umbels: average flowering time of a terminal umbel was 10 days at Slavkovský les and 8 days at Průhonice.

In the field, plants of *H. mantegazzianum* with a large basal diameter started to flower earlier than weak plants. The accumulation of more resources and early flowering makes it possible for these strong plants to set fruits on many of their umbels. Although the plants that started to flower early produced more umbels than late-flowering plants and this difference was highly significant, it was only marginally significant if early and late flowering plants were compared in terms of fecundity. This indicates that whether or not the flowers develop into fruits depends also on factors other than plant vigour such as weather or activity of pollinators.

The sequential flowering and ripening of fruits (Fig. 4) has important implications for the management of this invasive plant. Among control methods, cutting of flowering plants to prevent fruit set is recommended (Nielsen et al. 2005). If this treatment is applied at the peak of flowering, i.e. with secondary umbels on satellites and branches in blossom, the flowers in the terminal umbel have already completed flowering and fruit development has started. Because even umbels cut at an early stage of flowering are able to produce germinable seeds (Pyšek et al. 2006), treatment at this time is unlikely to prevent population renewal by seed. The treatment should be applied earlier and a detailed knowledge of phenology and duration of individual phases provides the necessary basis for optimal timing of the most effective control (Pyšek et al. 2006).

Fecundity

Number of fruits produced by *Heracleum mantegazzianum* is very high but the results of this study, as well as thorough re-evaluation of published data (Perglová et al. 2007), indicate that the fecundity of this species is often overestimated in the literature. Unfortunately, studies reporting fruit production in *H. mantegazzianum* typically do not accurately document how the numbers were obtained and where they come from (Williamson & Forbes 1982, Brondegaard 1990), or are based on one or a few plants (see Perglová et al. 2007 for review). Some authors (Ochsmann 1996, Tiley et al. 1996) used published information on the number of flowers and multiplied it by two, assuming that every flower would produce two fruits. These reports resulted in the often cited value of over 100 000 fruits per plant. Obviously, such numbers are overestimates as a large proportion of the flowers are male and do not produce any fruits, which was confirmed by this study and also indirectly by the estimate of fecundity made by Tiley & Philp (1997). They "selected the apparently largest plants" and came to a maximum number of 81,500 flowers per plant, while the fruit set of a plant with even slightly more umbels was "only" 52,800. In the present study, an average plant produced 20,671±5130 fruits (mean±SD) and the maximum estimated number of fruits was 46,470, which accords with the results of Pyšek et al. (1995), who report an average fruit set of 16,140 in the Czech Republic, and the 9696 fruits reported in Germany (Ochsmann 1996) and 15,729 in Scotland (Tiley & Philp 2000). Only that reported by Caffrey (1999) from Ireland is markedly higher: 41,202 fruits on average, with a maximum of 107,984. However, it is likely that these values were also derived from the number of flowers (see Perglová et al. 2007 for details). All these studies were conducted in the invaded distribution range and at comparable sites, which are suitable for invasion by *H. mantegazzianum*; although geographical variation in fecundity cannot be excluded it is unlikely to account for such large differences in the number of fruits produced. The present study is based on a large sample of individuals from a number of study sites and provides a solid basis for an unbiased estimate of the real fecundity of *H. mantegazzianum*. The values found are impressive and indicate this invasive species has an enormous reproductive capacity.

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Souhrn

Bolševník velkolepý (*Heracleum mantegazzianum* Sommier et Levier) je jedním z nejobtížnějších invazních druhů české flóry. Práce přináší podrobný popis fenologie kvetení a zkoumá, nakolik protandrie účinně zabraňuje samoopylení tohoto self-kompatibilního druhu. Dále popisuje načasování a průběh kvetení v silně invadované oblasti Slavkovského lesa a poskytuje odhad plodnosti založený na velkém vzorku rostlin z řady lokalit; tato data umožnila uvést na pravou míru v literatuře často nadhodnocené údaje o plodnosti *H. mantegazzianum*. Protandrie je plně účinná pouze na úrovni květu, kde jsou samčí a samičí fáze kvetení zcela odděleny. Naproti tomu uvnitř jednoho okolíku se příležitostně může fáze uvolňování pylu v některých květech překrývat s receptivitou blizen jiných květů a poskytovat tak příležitost pro geitonogamní samoopylení. Potenciál pro takové samoopylení je nicméně dán zejména velmi častým překrýváním samčí a samičí fáze mezi okolíky téže rostliny; alespoň krátký překryv mezi některými okolíky byl pozorován u 99% sledovaných rostlin ve Slavkovském lese. Přestože stupeň protandrie u druhu *H. mantegazzianum* podporuje cizosprášení, příležitost ke geitonogamnímu samoopylení může mít pro invazní druh zásadní význam, zejména pokud jediná rostlina kolonizuje novou lokalitu, kde se nevyskytuje vhodný partner pro křížení. Na všech 10 studovaných lokalitách v oblasti Slavkovského lesa začaly rostliny kvést v rozmezí jednoho týdne (od 10. do 27. 6. 2002). Jednotlivé rostliny kvetly v průměru 36 dnů, maximálně 60 dnů; doba kvetení se průkazně prodlužovala s celkovým množstvím okolíků na rostlině. Většina plodů byla zralá v druhé polovině srpna, kdy se začínaly uvolňovat z mateřských rostlin. Začátek kvetení rostliny byl signifikantně negativně korelován s počtem okolíků – čím dříve rostlina vykvetla, tím více okolíků vytvořila. Negativní vztah byl nalezen také mezi bazálním průměrem rostliny a začátkem kvetení; statnější rostliny začaly kvést dříve. Průměrná rostlina na území Slavkovského lesa vytvořila 20 671 plodů (n = 100). Z celkového počtu plodů se 44,6 % vytvořilo v terminálním okolíku, 29,3 % v sekundárních okolících na satelitech, 22,6 % v sekundárních okolících na větvích a pouze 3,5 % v terciálních okolících. Nejplodnější rostlina vytvořila 46 470 plodů – v porovnání s průměrnou rostlinou se u nejplodnějších jedinců zvyšuje relativní význam terciálních okolíků na úkor primárního. Studie prokázala pozitivní vztah mezi bazálním průměrem rostliny a její plodností. Ačkoliv výsledky ukazují, že plodnost druhu *H. mantegazzianum* byla v literatuře často přeceňována, jeho reprodukční kapacita je enormní.

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