Effects of fruit position on fruit mass and seed germination in the alien species *Heracleum mantegazzianum* (Apiaceae) and the implications for its invasion

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Abstract

The aims of this paper are to determine whether the effect of position of fruit on a plant affects the germination characteristics of seed of *Heracleum mantegazzianum* (Apiaceae), a Caucasian species invasive in Europe, and the germination potential of this species. Reproductive characteristics of *H. mantegazzianum* were studied at seven sites in the Czech Republic where this species is abundant. Fruits were collected and weighed from eight plants at each site, from three umbel types (terminal, satellite and branch) and two fruit positions within an umbel (central or marginal). Characteristics of individual umbels (duration of flowering, size) and plants (fecundity, age, height, basal diameter) were recorded. Percentage germination and germination rate (time to when 50% of the seeds had germinated) were assessed. At each site, fruit mass and percentage germination varied greatly among plants. Fruits from terminal inflorescences were heavier than those from satellites and branches, and those produced in the centre of an umbel were heavier than those from the margin. Mean percentage germination was 91%, which varied among sites but was not affected by fruit position on a plant. Germination rate increased with fruit mass. Neither umbel size nor time of flowering had a significant effect on germination characteristics. At some sites, there was a negative relationship between fruit mass and plant height. A combination of reproductive traits (high fecundity, high germination capacity, opportunistic behaviour associated with limited effect of fruit position on a plant on germination characteristics) might determine this species ability to successfully invade new habitats.
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1. Introduction

Studies of the traits of invasive plants have documented that certain reproductive characteristics are crucial for their success (Rejmánek, 1996; Grottkop et al., 2002). A minority of invaders, some of which are extremely successful (Pyšek et al., 2003; Mandák et al., 2004), rely exclusively on vegetative reproduction but the majority depend on seed dispersal (Pyšek, 1997). It is repeatedly stated that the ability to produce a large number of seeds (Baker, 1965; Noble, 1989; Ashton and Mitchell, 1989; Roy, 1990; Saxena, 1991; Richardson and Cowling, 1992; Rejmánek, 1996) is one feature of a successful invader. Successful germination in a wide range of conditions (Baker, 1965; Forcella et al., 1984; Forcella, 1985; Roy, 1990; Richardson and Cowling, 1992) increases the probability of naturalization and subsequent invasion (in the sense of Richardson et al., 2000; Pyšek et al., 2004).

The current theory of biological invasions largely relies on comparative studies of large species sets (Lonsdale, 1999). However, further progress in determining a species invasiveness is dependent on improving the quality of input data, namely the information on species traits. Case studies of invasive species can therefore contribute substantially to understanding the mechanisms underlying plant invasions.

The present paper deals with *Heracleum mantegazzianum*, an invasive species in the Czech Republic (Central

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Europe). About one-third of the flora of this country is made up of alien species (Pyšek et al., 2002), research on which is receiving considerable attention (Dančák, 2002; Mihulka et al., 2003; Šída, 2003; Petřík, 2003). *Heracleum mantegazzianum* is an important invader not only in this country but also in other parts of Europe and is regularly listed in global overviews of noxious invasive species (Cronk and Fuller, 1995; Weber, 2004). It does not reproduce vegetatively and depends on reproduction by seed (Pyšek et al., 1995; Tiley et al., 1996). Although the distribution and ecology of *H. mantegazzianum* is often studied, good information on its reproductive characteristics is lacking and comes from comparative overviews of large numbers of species (Grime et al., 1981; Thompson et al., 1997; Baskin and Baskin, 1998).

The position of a seed or fruit on a plant can affect seed mass, morphology, germination and dormancy characteristics (see Gutterman, 1992; Baskin and Baskin, 1998 for review), and such effects are reported for some species of Apiaceae. Fruit mass and seed germination are dependent on umbel position in *Angelica archangelica* subsp. *archangelica* (Ojala, 1985), *Apium graveolens* (Thomas et al., 1978; Thomas et al., 1979), *Daucus carota* (Thomas et al., 1978; Jacobsohn and Globerson, 1980; Barbedo et al., 2000) and *Pastinaca sativa* (Hendrix, 1984a; Hendrix and Trapp, 1992). Umbel position affects seed germination in *Petroselium crispum* (Thomas, 1996). Intraspecific variation in seed mass depending on the position of the umbel on the mother plant is reported for a number of species (Thompson, 1984; Hendrix and Sun, 1989).

The present study aims to answer the following questions: 1. How does the position of the fruit on *H. mantegazzianum* plants affect its mass and the germination of the seed? 2. Is fruit mass and seed germination influenced by plant characteristics? In addition, this is the first study to provide reliable information on the germination characteristics of this invasive alien species. Published germination studies for other members of the Apiaceae have not previously dealt with a highly successful invasive species.

2. Material and methods

2.1. Study species

Heracleum mantegazzianum Sommier et Levier (Apiaceae) is a perennial monocarpic herb, flowering in the third to fifth year (J. Pergl et al., unpublished data), 200–500 cm tall, with a thick tap root of up to 45–60 cm and leaves of up to 250 cm long. Flowers are arranged in compound umbels, up to 80 cm across, with the terminal umbel the largest, surrounded by satellite umbels and additional terminal umbels that may be borne on the main branches. Umbels mature in sequence. Flowers are insect-pollinated, hermaphrodite and protandrous; the anthers dehisce and pollen is shed before the stigma becomes receptive, but there is some overlap in the staminate and pistillate phase between flowers, which

makes self-fertilization possible (Steward and Grace, 1984; I. Perglová et al., unpublished data). Plants in the study area flowered from the last third of June to late July and sequential ripening of seed followed. Umbels bear oval-elliptical, broadly winged fruit, which split into two winged mericarps (Holub, 1997; for simplicity the unit of generative reproduction is termed a "fruit" throughout this paper rather than the morphologically correct "mericarp", and the term "seed" is used when referring to germination); the mericarps are 6–18 mm long and 4–10 mm wide. The embryo is rudimentary and surrounded by endosperm (Martin, 1946). The endosperm is oily and mature fruits have a strong resinous smell (Tiley et al., 1996).

A single plant is capable of producing a large quantity of fruit and estimates range from 5 000 to more than 100 000 per plant (Pyšek et al., 1995; Tiley et al., 1996). Unfortunately such estimates are for a single plant without any measure of variation; the maximum value reported is 107 984 (Caffrey, 1999). An average value for eight plants in the Czech Republic is 16 139 ± 2 617 (mean ± standard deviation, S.D.) fruit per plant (Pyšek et al., 1995).

Seeds germinate early in spring (March to April in the study area) and cold stratification is necessary for germination (Nikolaeva et al., 1985; Tiley et al., 1996; Otte and Franke, 1998); they do not germinate after dry storage (Grime et al., 1981). The seeds exhibit a morphophysiological dormancy in the sense of Nikolaeva et al. (1985) and Baskin and Baskin (1998). They have underdeveloped embryos and are physiologically dormant. Embryo growth must occur and physiological dormancy must be broken before germination. Both types of dormancy are broken by cold conditions in autumn and winter.

The species is native to the western Caucasus, where it occurs in the upper forest belt on southern slopes, mainly in meadows, clearings and forest margins (Mandenova, 1950). In the Czech flora, *H. mantegazzianum* is considered invasive (Pyšek et al., 2002), following the criteria of Richardson et al. (2000) and Pyšek et al. (2004). It was introduced as a garden ornamental to a chateau in Lázně Kynžvart (Slavkovský les region), western Bohemia in 1862 and the oldest herbarium specimen documenting its occurrence outside cultivation close to the introduction site is dated 1877 (Holub, 1997). The species spread from this region, encouraged in areas with a high human population density but restricted to those with low January isotherm. It has been reported from 603 localities in the Czech Republic (P. Pyšek and K. Prach, unpublished data).

Heracleum mantegazzianum is the largest herb in Central Europe and rapidly attains dominance, with up to 40% of suitable habitats covered by stands of this species in the area of Slavkovský les (Pyšek and Pyšek, 1995). Replacement of native vegetation and injuries to human skin caused by phototoxic substances (Drever and Hunter, 1970; Tiley et al., 1996) are the main reasons for attempting to eradicate it (de Waal et al., 1994). The substantial fecundity and efficient dispersal of fruit by water, wind and human-related factors

(Pyšek and Prach, 1993) contribute to its rapid spread. Disturbed habitats with good possibilities for the fruit dispersal and establishment of seed are readily invaded, but the species also invades seminatural vegetation (Pyšek and Pyšek, 1995).

Heracleum mantegazzianum is naturalized or invasive in a number of European countries and Central Russia (see Tiley et al., 1996 for the list and references). Outside Europe, it is found naturalized in Canada and United States (Morton, 1978; Ochsmann, 1996; Kartesz and Meacham, 1999).

2.2. Germination experiments

Data were collected in the Slavkovský les Protected Area in the western part of the Czech Republic. Seven sites dominated by *H. mantegazzianum* were selected; the area covered by this species at the study sites varied from 4 711 to 47 110 m^2 (Table 1). At each site, eight plants were randomly selected and their fruit collected as it ripened on several occasions during August 2002. From each plant, fruit was collected from six morphological positions: the three umbel positions (terminal, satellite and branch; termed "umbel type") and the two positions within an umbel (centre and margin; termed "fruit position") (Fig. 1). Fruit was transported to the laboratory in labelled paper bags, dried for 2 weeks at room temperature (20 °C) and stored at 15 °C for 8 months until the beginning of the germination experiment. Fruit was kept for 2 weeks at room temperature (20 °C) before stratification and weighing.

The experimental design consisted of six treatments (three umbel types/two fruit positions) performed on eight plants from seven sites. There were five replicates of each treatment/plant/site combination, giving a total of 1680 (= 3 × 2 × 7 × 8 × 5) samples of fruit. Samples consisting of 25 randomly selected healthy fruit were weighed and placed in Petri dishes with sterilised moist sand for stratification. Tap water was used and the fruit was not treated with disinfectant. Fruit was stratified for 2 months at 2–4 °C and then germinated in the dark at 8–10 °C. This temperature mimics the conditions the fruit is exposed to during germination in spring. In the study area, March and April temperatures are
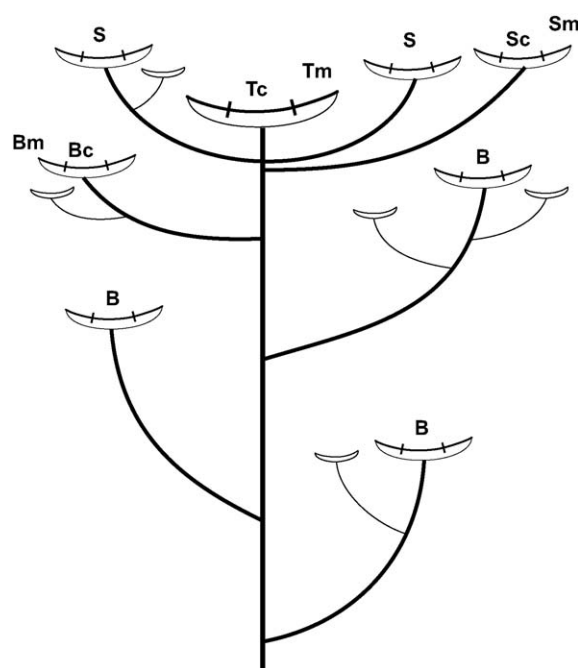

Fig. 1. Diagram of the umbel types and positions of the fruit on a plant of *H. mantegazzianum*. This is relevant to the terminology used in the germination experiments. Umbel position: T – terminal, S – satellite, B – branch; fruit position: c – centre, m – margin.

rather low and rarely exceed 10 °C. Pilot experiments using fruit from the study area showed that germination is not affected by light and that seeds germinate at up to 10 cm below the soil surface (L. Moravcová et al., unpublished data).

Germination was recorded weekly starting on 24 July 2003. Since the aim was to determine the germination potential of this species (as a crucial feature of its invasion potential), the experiment was run for 6 months. Fruit that decayed during the experiment was considered dead, viable seeds that did not germinate were considered to be dormant. The viability of dormant seeds was tested by squeezing the fruit using forceps. Prior to the experiment, the results obtained using the tetrazolium test were compared with those obtained by squeezing the fruit; the proportion of dead fruit was very low (4.8%) and not considered in the statistical analyses.

Table 1

Geographical location, altitude (m a.s.l.) and population size of *Heracleum mantegazzianum* estimated from aerial photographs taken in 1996, except as indicated (J. Müllerová et al., Institute of Botany Průhonice, unpublished). Percentage germination (mean ± the central 50% of the data) is shown for particular treatments, i.e. umbel types (terminal, satellites, branches; pooled across fruit positions) and fruit positions (central, marginal; pooled across umbel types). Values are based on 8 plants and 5 replicates, giving the sample sizes n = 80 and 120 for umbel type and fruit position, respectively. For localities pooled across treatments n = 240 and for the grand total n = 1680.

Site characteristics					Final germination					
Locality	Latitude	Longitude	Altitude (m a.s.l.)	Population (m²)	Terminal	Satellite	Branches	Central	Marginal	Total
Arnoltov	50°06.801	12°36.147	575	47 170[a]	90.9(86–96)	91.1(88–9 6)	90.5(80–96)	90.9(84–96)	91.0(84–96)	90.9(84–96)
Dvorečky	50°05.982	12°34.137	506	24 817	90.0(80–92)	90.6(84 –96)	91.3(84 –100)	91.1(84–96)	91.1(80–96)	91.1(80–96)
Krásná Lípa 1	50°05.692	12°38.544	597	n. a.	91.4(89–100)	90.6(87–100)	91.1(87 –96)	91.2(88–9 6)	91.2(88–100)	91.1(87–9 8)
Krásná Lípa 2	50°06.306	12°38.393	596	7945[a]	91.(88–100)	90.9 (88–100)	91 .0(88–96)	91.2(88–100)	91.1 (88–96)	91.0(88–100)
Litrbachy	50°06.009	12°43.777	800	4711	90.2(8 0–94)	90.6(80–96)	90.8 (90–100)	90.9(84–96)	90.7(84–9 6)	90.9(84–96)
Žitný I	50°03.754	12°37.569	787	99 121	91.4(90–100)	91.0(88–100)	91.6(88–100)	91.3 (88–100)	91.2(90 –100)	91.2(90–100)
Žitný II	50°03.837	12°37.304	734	65 273	91.2 (88–100)	91.7(90–100)	91.4(89–100)	91.2(90–100)	91.3(90–100)	91.2(90–100)
Total					90.9(8 8–97)	91.2 (86–98)	91.2(86–98)	91.2(8 7–98)	91.1(86 –98)	91.1(88 –100)

[a] from 2000.

Phenological characteristics of individual umbels ('start', opening of the first flower in the inflorescence; 'end', withering of the last flower; 'flowering', period between start and end; 'umbel diameter') were recorded and plant characteristics (fecundity, height and basal diameter, recorded when the fruit was ripe; age) measured on the same plants as fruit was collected from for germination experiments. Fecundity of each umbel was estimated using a regression model based on the relationship between umbel diameter, proportion of developed fruit and position on the plant (I. Perglová, unpublished data). Plant age was determined using the method of herbchronology (Dietz and Ullmann, 1997).

2.3. Statistical analysis

The effect of umbel type and fruit position on fruit mass (total mass of 25 fruits) and percentage germination (% of seeds that germinated up to the end of the experiment) was analysed using ANOVA. At each site, four plants of the eight sampled were randomly selected and replicates were averaged for fruit position (central and marginal). In the remaining four plants, replicates were averaged for umbel type. Either the umbel type (with three levels: terminal, satellite and branch) or fruit position (with two levels: central and marginal) was an orthogonal fixed factor, whereas site was an orthogonal random factor. Plants were nested in the combination of these two orthogonal factors. The construction of linear models and calculations of the degrees of freedom, mean square estimates and *F*-ratios in these analyses follow Underwood (1997, p. 358–369). Differences among fruit positions were tested using *a posteriori* Student–Newman–Keuls (SNK) sequential tests (Underwood, 1997). To normalize the error distribution, the proportions of germinated seeds were angular transformed (Sokal and Rohlf, 1995). Homogeneity of variance was checked by Cochran's test.

Germination rate was analysed separately for each plant and site by survival analysis, following Crawley (1993, p. 325–330). The time to germination (in weeks) of each seed in each replicate of 25 seeds, summed for the fruit position or umbel type, was the response variable. Dormant seeds were censored. Seeds from the same four plants as in the analyses of the effects of umbel type and fruit position on final germination percentages were analysed. Umbel types and fruit positions were factors as in previous analyses, while fruit mass was added as a covariate. Differences in germination rate were fitted by likelihood functions, described by two parameters, mean time to germination, μ, and a shape parameter, α. The mean time to germination was the time at which 50% of the seed had germinated. The shape parameter indicated the appearance of germination curves. The curves, in which P is a proportion of the seeds that germinated as a function of time, t, were $P(t) = \exp(-\lambda t^{\alpha})$, where $\lambda = \mu^{-\alpha}$.

To evaluate the effect of individual umbels charateristics (umbel diameter, flowering start, flowering end and flowering duration) on fruit mass, percentage germination and germination rate, i.e. response variables representative of whole umbels, were obtained by averaging data for each fruit position. All eight plants at a site were included in the model. Fruit mass, percentage germination and germination rate were response variables, umbel type was a factor (with three levels: terminal, satellite and branch), and umbel diameter, flowering start, flowering end, and flowering duration were covariates. Analyses were made separately for each site, using general linear models.

The intention of each general linear model was to determine the minimal adequate model. In this model, all parameters were significantly ($p < 0.05$) different from zero and from one another. This was achieved by a step-wise process of model simplification, beginning with the maximal model, which contained all three levels of the factor umbel type (terminal, satellite and branch), and all interactions among its levels and covariates. This model was simplified by the elimination of non-significant terms, using deletion tests, and retention of significant terms, until the minimal adequate model, which contained only significant terms, was determined (Crawley, 1993, p. 188–210). All covariates were standardized (zero mean, variance one) to achieve, in absolute terms, a comparable influence of their effects. The strength of their effects is not directly comparable without this standardization, because each covariate was measured on a different scale. The adequacy of fitted statistics was confirmed by plotting standardized residuals against fitted values and by the normal probability plots of the fitted values (Crawley, 1993). All calculations were made in the commercial statistical package GLIM® v. 4 (Francis et al., 1994).

The effects of plant characteristics (fecundity, basal diameter and height) on fruit mass, final germination percentage and germination rate were analysed by general linear models, using the same procedures as in the case of the variation among umbels. Response variables representative of whole plants were obtained by averaging data over the umbel type and fruit position. All eight plants in a site were included in the model. Fruit mass, final germination percentage and germination rate were response variables, site was a factor, and plant fecundity, basal diameter and height were covariates.

3. Results

3.1. Effect of umbel type, fruit position, plant identity and site on fruit mass and germination

Percentage germination in *H. mantegazzianum* is very high, with an average of 91.1% pooled across variables. At particular sites, germination varied between 90.9 and 91.2% (Table 1). The most striking effect in the analyses of umbel type and fruit position on both fruit mass and percentage germination was highly significant variation among individual plants at each site (Tables 2 and 3). This idiosyncratic effect was larger than the general effect of umbel type, fruit position or site.

Mean mass of 25 fruit, pooled across treatments, plants and sites, was 327 ± 92 mg (mean ± S.D., $n = 700$), giving

Table 2

The effect of umbel type (terminal, satellite, branch), sites, plants, and their mutual interactions, on fruit mass and percentage germination in *H. mantegazzianum*

Source of variation	df	Fruit mass		Final germination percentage	
		MS	F_s	MS	F_s
Among umbel types	2	0.58	48.79 ***	0.058	0.974 ns
Among sites	6	0.10	3.04 *	0.31	3.54 **
(Umbel type) × (site)	12	0.012	0.347 ns	0.057	0.657 ns
Among plants within (umbel type) × (site)	63	0.035	134.8 ***	0.087	6.33 ***
Residual	336	0.0003		0.014	

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns = not significant.

Table 3

The effect of fruit position (centre, margin), sites, plants, and their mutual interactions, on fruit mass and percentage germination in *H. mantegazzianum*

Source of variation	df	Fruit mass		Final germination percentage	
		MS	F_s	MS	F_s
Between fruit positions	1	0.00736	19.75 **	0.00170	0.057 ns
Among sites	6	0.027	1.37 ns	0.103	1.51 ns
(Fruit position) × (site)	6	0.000372	0.019 ns	0.0300	0.442 ns
Among plants within (fruit position) × (site)	42	0.020	92.90 ***	0.0680	2.08 ***
Residual	224	0.000216		0.03270	

*** $p < 0.001$, ** $p < 0.01$, ns = not significant.

the mean mass of a single fruit of 13.1 mg. Fruit mass was significantly different among umbel types and sites (Table 2). Fruit produced by terminal umbels was significantly heavier (405 ± 71 mg, $n = 25$; range 239–567 mg) than that from satellites (293 ± 92; 92–592) or branches (293 ± 91; 141–594) (Fig. 2). The effect of fruit position on fruit mass was also highly significant (Table 3) with those from the centres of

umbels (328 ± 63 mg, 25 fruits) being heavier than those from the margins (318 ± 60) (Fig. 2).

Percentage germination was significantly different among sites (Table 2), but was affected by neither umbel type (Table 2) nor fruit position (Table 3). However, the umbel type and fruit position significantly affected germination rate. Large seeds germinated faster than small seeds; germination rate increased with increasing fruit mass and this pattern was consistent for all plants at each site (Fig. 3). Since fruit from terminals were heavier than those from branches (Fig. 2), the former germinated sooner than the latter (Fig. 4).
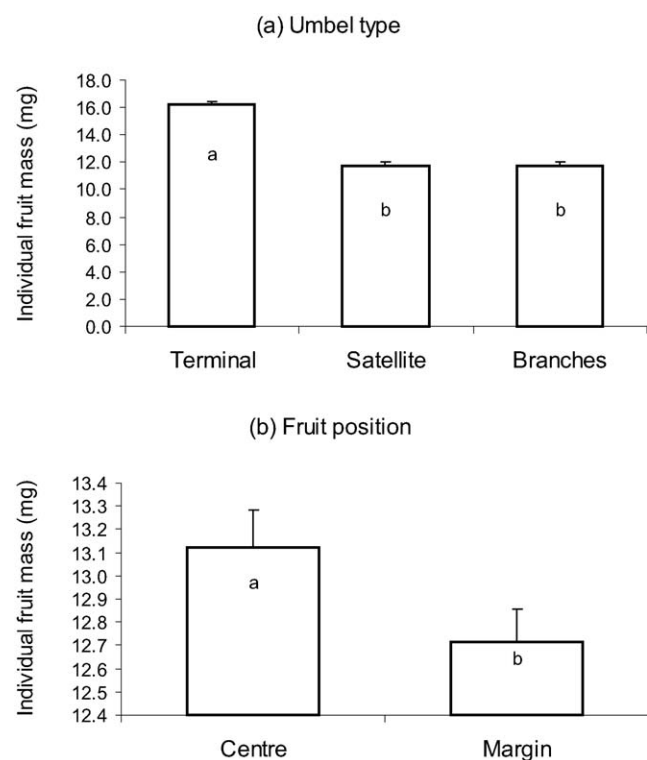

Fig. 2. Differences in mean fruit mass (with variance) among (a) umbel types and (b) between fruit positions in *H. mantegazzianum*. Different letters inside the bars indicate significant ($p < 0.05$) differences among umbel types (SNK test) and between fruit positions (ANOVA). All sample sizes are $n = 140$.
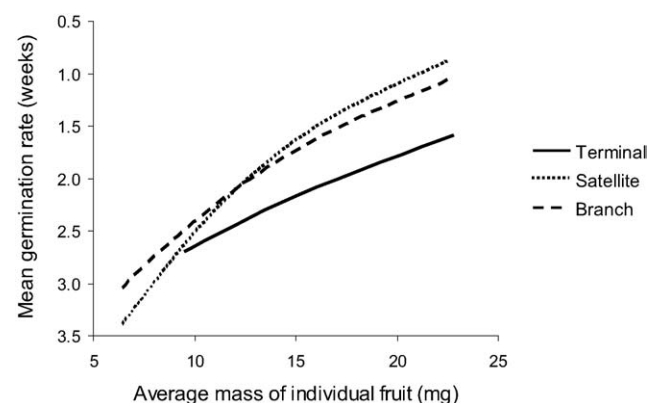

Fig. 3. Relationship between mean germination rate and fruit mass for umbel types (terminal, satellite, branch) of a randomly chosen plant of *H. mantegazzianum* ($n = 715$ seeds). Terminal: rate = $1/\exp(-3.345+3.852\text{mass})^{(1/2.45)}$; satellite: rate = $1/\exp(-4.296+8.171\text{mass})^{(1/2.45)}$; branch = $1/\exp(-3.763+6.441\text{mass})^{(1/2.45)}$. $\chi^2 = 1301.0$; $df = 5$; $p < 0.001$. The y-axis is reversed so the seeds that germinate first appear above those that germinate last for a given fruit mass. (Note that although, for most of the ranges in fruit mass, the germination rate of a particular fruit mass is higher for satellites and branches than terminals, the average germination rate for terminals is higher than for satellites and branches because fruit from terminal umbels is, on average, much heavier than that from the other two umbel types).
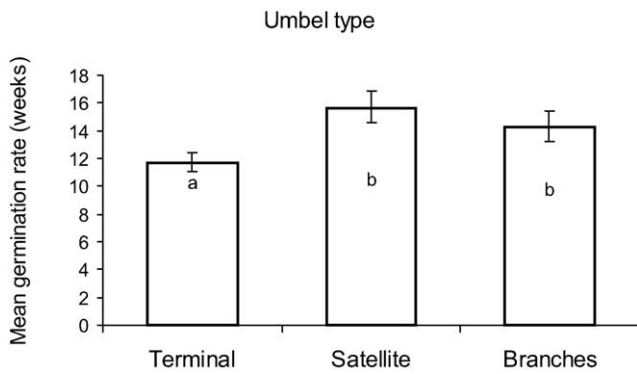
Umbel type

Fig. 4. Mean time to germination of 50% of the seed from a randomly chosen plant, for terminal, satellite and branch umbels of *H. mantegazzianum* ($n = 210$ seeds). Different letters inside the bars indicate significant ($p < 0.05$) differences among umbel types in deletion tests. Standard errors are slightly asymmetrical due to the shape of the germination curves. $\chi^2 = 14.2$; $df = 2$; $p < 0.001$. Germination rate is the time to when 50% of the seeds had germinated, hence shorter bars indicate faster germination. (Note the large difference between the mean germination rates for the two randomly chosen plants in Figs. 3 and 4, which demonstrates the large variation among plants and sites).

3.2. Effect of umbel characteristics on fruit mass, percentage germination and germination rate

Percentage germination was not affected by the measured variables relating to umbels. Neither umbel diameter nor the timing of flowering (start, end and duration) had a significant effect at any of the sites. Germination rate varied unpredictably with the measured umbel characteristics.

Fruit mass significantly increased with umbel diameter. The 95% confidence intervals of the regressions of fruit mass on umbel diameter for the different sites overlapped broadly, and these relationships were the same for each umbel type (deletion test on a different regression slope on umbel diameter for terminal, satellite and branch: $F = 0.35$; $df = 4$, 163; NS). Common regression slope of the increase in fruit mass with umbel diameter is shown in Fig. 5.

3.3. Effect of plant characteristics on fruit mass, percentage germination and germination rate

Percentage germination was not affected by plant fecundity, basal diameter or height and the germination rate varied
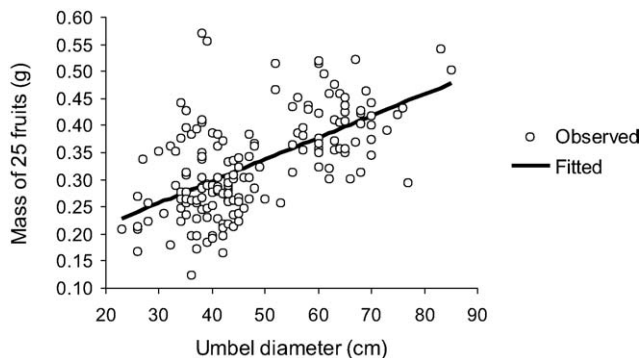

Fig. 5. Relationship between fruit mass and the size of an umbel in *H. mantegazzianum* based on data pooled across all sites. Fruit mass = 0.33 + 0.054 umbel diameter. $F = 88.73$; $df = 1$, 163; $p < 0.001$; $R^2 = 0.35$.

Table 4
Significant ($p < 0.05$) effects of plant fecundity, height and basal diameter on fruit mass in *H. mantegazzianum* at individual sites ($n = 8$ at each site)

Explanatory variable	Site	Regression slope ± standard error
Plant fecundity	Arnoltov	–0.074 ± 0.023
Plant height	Dvorečky	–0.044 ± 0.018
	Krásná Lípa I	–0.10 ± 0.038
	Žitný II	–0.11 ± 0.032
Plant basal diameter	Krásná Lípa I	0.15 ± 0.032

inconsistently. At some sites, these characteristics had a significant effect on fruit mass, which decreased with increasing fecundity at one site. A negative effect on fruit mass of plant height and fecundity and a positive effect of plant basal diameter were found at three and one site, respectively (Table 4).

4. Discussion

4.1. Percentage germination in H. mantegazzianum: higher than the family average

Percentage germination in *H. mantegazzianum* was extremely high. An extensive study of germination in 88 members of the family Apiaceae carried out at the Institute of Botany in the 1980s (M. Lhotská, unpublished data) allows the results obtained for *H. mantegazzianum* to be placed at wider phylogenetic context. Seventeen species (i.e., 19% of those tested) exhibited 90–100% germination under optimum conditions. Of the three naturalized neophytes (alien species introduced after the discovery of America; Richardson et al., 2000, Pyšek et al., 2004) on the list, only *Smyrnium perfoliatum* (92%) has a higher percentage germination, and for the other two it is lower: *Imperatoria ostruthium* (74%), *Myrrhis odorata* (72%). *Heracleum mantegazzianum* is one of 24 neophytes belonging to the Apiaceae in the flora of the Czech Republic (Pyšek et al., 2002) seven of which are classified as naturalized and four are invasive (Pyšek et al., 2004). Published data are available only for *A. archangelica* subsp. *archangelica*, another invasive species, for which the percentage germination reaches 82% and is enhanced by light (Ojala, 1985).

Good germination has also been reported for a number of other species in the Apiaceae in the literature, for example 94% in *A. graveolens* (Thomas et al., 1979) and 83% in *P. sativa* (Hendrix, 1984a). Germination exceeded 80% in 29 (33%) of the 88 species studied by M. Lhotská and the values recorded by her for *H. mantegazzianum* (80%) and in the present study (91%) are higher than the average for the family (68.7 ± 23.2%, mean ± S.D., $n = 88$). An extremely high percentage of germination is typical of this invasive alien even within the context of its family, seeds of which generally readily germinate once dormancy is broken (Baskin and Baskin, 1990,1991; Baskin et al., 1995).

Percentage germination recorded under laboratory conditions is not always realized in the wild. In our study, cold and

dark conditions mimicked closely the natural situation under the soil surface during spring. The high percentage of germination recorded in the laboratory corresponds with that obtained in a common garden burial experiment, where 90% of seeds stored in the soil germinated over the first winter (L. Moravcová et al., unpublished data).

4.2. Fruit mass and germination characteristics: the limited effect of umbel type, fruit position and intraspecific variation

The mean mass of a fruit (13.1 mg) recorded in the present study is within the range given by Tiley et al. (1996) for this species (4.6–23.2 mg) and Šerá (2003) gives a mean value of 7.43 mg for the fruit of *H. mantegazzianum* dried at 80 °C. More importantly, the present study indicates that fruit mass in Apiaceae cannot be directly compared without knowing the position of the fruit on a plant. Fruit from terminal positions weighed an average of 16.2 mg, while fruit from satellite and branch positions was smaller (11.7 mg). Fruit from the centre of umbels (13.1 mg) was significantly heavier than that from the margins (12.7 mg). Other published studies report even greater variation in the mass of fruit produced on different umbels in Apiaceae. A six-fold variation in fruit mass is reported for *P. sativa*, when fruit from the tertiary umbels of a small plant is compared with that from primary umbels of a large plant (Hendrix, 1984a; see also Thompson, 1984; Hendrix, 1984b for other species). Hendrix and Sun (1989) reported a three- to 16-fold variation in seven species, and concluded that intraspecific variation in fruit mass is the rule rather than the exception due to the effect of developmental factors such as fruit number, time of flowering and location of inflorescences. However, these factors may not affect the fruit mass in the same way, which makes it difficult to assign causality to within plant variation in fruit mass. The smaller fruit produced by the last umbels formed later in a season may suffer from a lower availability of reserves as suggested by Hendrix (1984a,1984b) for *P. sativa* and *Heracleum lanatum*. Obviously, this is less important in *H. mantegazzianum*.

Percentage germination was not affected by the position of the fruit on the *H. mantegazzianum* mother plant but germination rate was. Large seed germinated faster than small seed, but the difference was only obvious in the early weeks of the experiment. In a number of species, lower percentages of small seeds germinate than of large seeds (Ojala, 1985; Hendrix and Sun, 1989; Hendrix and Trapp, 1992), but the opposite relationship has also been reported (see Thomas et al., 1979 study on *A. graveolens*). A detailed study of Hendrix (1984a) on *P. sativa* revealed the importance of timing of seed germination. The proportion of germinating seed did not differ in autumn (i.e., without stratification), whereas in the spring a greater percentage of big seed germinate than small (Hendrix, 1984a).

There is little published information on germination rate of species of Apiaceae. A pattern opposite to that found in the present study is reported for *P. sativa*, where small seed ger-

minated more rapidly than large seed (Hendrix, 1984a). However, this was only true in autumn and there was no difference in spring. These results suggest that small seeds may have a competitive advantage over large seeds in autumn due to faster germination, but are at a disadvantage in spring because of lower percentage germination. As most germination in the field occurs in spring, population recruitment from small seeds is likely to be substantially less than that from large seeds (Hendrix, 1984a).

In our study area, *H. mantegazzianum* germinates only in spring (no seedlings were observed in study plots in the autumn). For that reason, the germination experiment was designed to mimic the temperature in spring; under such conditions large seeds germinate faster than small seeds. As large seeds also produce bigger seedlings (Harper, 1977; Thomas, 1996; Thomas et al., 1979), which provide them with a competitive advantage over seedlings produced by small seed, these results suggest that little contribution of small seeds to population recruitment can be expected in *H. mantegazzianum*.

4.3. Effect of plant characteristics on fruit mass

Plant size, expressed as height and basal diameter, had no effect on the proportion of *H. mantegazzianum* seed that germinated; only fruit mass was affected. Relationships between fruit mass and characteristics related to plant vigour, as found at some of the sites, indicate a trade-off between allocation to vegetative growth and generative reproduction (Harper, 1977). The negative effect of height on fruit mass, found at three study sites, reflects a trade-off in the allocation of resources to competition for light and reproduction. In *H. mantegazzianum*, however, small seed is not at a major disadvantage as it achieves similarly high germination percentages as large seed.

The basal diameter in *H. mantegazzianum* is closely associated with plant vigour and fruit production significantly depends on this characteristic (Pyšek et al., 1995). At one site, the most vigorous plants produced the heaviest fruit, indicating that the best performing plants are not only the most fecund (Pyšek et al., 1995) but also produce high quality fruit. That the more vigorous plants produce the heavier fruit is also indicated by the positive effect of umbel size on fruit mass.

The absence of a significant relationship at most of the study sites might be partly due to small sample size ($n = 8$) and high variation. For technical reasons, it was not possible to include more plants per study site hence the resulting power of the tests was rather low. For that reason, any conclusion about the effect of plant vigour on germination in *H. mantegazzianum* must be treated with caution. While studies of the correlation between plant size and fecundity, expressed as seed number or seed mass, consistently reveal a positive relationship (Hendrix and Sun, 1989 for seven species of Apiaceae), those attempting to relate plant size and individual seed mass are less successful. In the same study, Hendrix and

Sun (1989) found heavier fruit on bigger plants in only three of seven species (see also Hendrix, 1984a). In general, it appears that while at the interspecific level seed mass is positively related to various measures of plant size (Moles et al., 2004), variation among individual plants within a population makes it more difficult to reveal the same relationships at the intraspecific level.

4.4. Implications for invasion: superior combination of reproductive traits

Interspecific comparisons show that there is a trade-off between the number and size of seed (Harper, 1977; Šerá and Šerý, 2004). High fecundity promotes invasiveness (Ewell, 1986; Roy, 1990; Richardson and Cowling, 1992; Rejmánek, 1996; Meyer, 1998), simply because more propagules are spread and the probability that some of them reach safe sites increases. Production of fewer larger seeds may be an alternative strategy. Data from field studies of populations under natural conditions showed that large-seeded species have higher survival during early seedling establishment than small-seeded species (Moles and Westoby, 2004). Compared to other species, *H. mantegazzianum* is superior both in terms of fecundity and fruit size. The reproductive potential of this species is enormous and seems to be a crucial feature of its invasion success (Pyšek et al., 1995; Tiley et al., 1996). In the study area, an average plant produced 20 500 fruit (I. Perglová et al., unpublished data). However, *H. mantegazzianum* is also remarkably large-seeded in terms of the temperate flora. Mean fruit mass of the species exceeds the average value found for 498 species in the Czech Republic (2.56 ± 7.59 mg, mean $\pm$ S.D.) by Šerá (2003); the mass of a *H. mantegazzianum* fruit in her sample was 7.4 mg. These features, together with vigorous growth and shading of resident vegetation (Tiley et al., 1996), enable this species, which does not reproduce vegetatively and relies completely on seed production, to invade new areas and achieve dominance.

In general, the determination of fruit mass in *H. mantegazzianum* follows the same pattern as in other members of the Apiaceae (Hendrix, 1984a; Hendrix, 1984b; Hendrix and Sun, 1989), but the variation is several orders of magnitude lower than in some other species. Consequently, even small seed is "big enough" and does not suffer from the negative consequences of small size. In addition, being small does not represent much of a disadvantage since size only affects germination rate. Over a period of three months (in the field, seedlings appear up until May), the difference in percentage germination of small and large seeds disappears. Under certain circumstances, delayed germination may even have positive consequences because such seedlings may avoid frosts that are common in the study area, which is located at a relatively high altitude (Table 1). In addition, population self-thinning in *H. mantegazzianum* (less than 0.5% of seedlings survive to the next year; J. Pergl, unpublished data) may enable small seed with delayed germination to contribute to population maintenance.

More importantly, over 90% of seed germinated regardless of the vigour of the mother plant or where it was produced on the plant. Many invasive species are good germinators (see for example Gleadow, 1982; Duggin and Gentle, 1998; Ernst, 1998) but this is not always the case (Grice, 1996; Meyer and Schmid, 1999). Given its fecundity, *H. mantegazzianum* exerts enormous pressure of highly germinable propagules in invaded sites. This has practical implication as mechanical control often focuses on cutting terminal umbels or stems at flowering time. Regeneration occurs via higher-order umbels (Pyšek et al., 1995) and as indicated in this study these produce good quality seed.

The most striking aspect of the effect of umbel type and fruit position on fruit mass and percentage germination was the highly significant variation in the measured characteristics among individual plants at each site. The effect of site was much less important than individual variability, suggesting that the species is able to cope with the environmental variation within the study area. It should be noted that the study was conducted in a region where *H. mantegazzianum* was first introduced to the Czech Republic (Pyšek, 1991) and that there is a good climate match between this region and its area of origin. In terms of the Czech Republic, Slavkovský les is located at a rather high altitude, and hence provides climatic conditions for *H. mantegazzianum* comparable to those in the native area of the Caucasus. This is supported by the fact that none of the parameters related to the timing of flowering were significant in the present study. Invasion throughout the Czech Republic proceeded from the study area to other parts of the country (Pyšek, 1991) and it is possible that the effect of environment would be more marked if compared across the whole range of occupied habitats.

The superior combination of reproductive traits is further enhanced by the species having a large, short-term persistent seed bank (sensu Thompson et al., 1997). In 2002, the number of viable seeds varied from 2 707 m^{-2} in autumn to 1 462 in spring to 75 in summer. In a burial experiment, 8.8% of buried seeds were dormant after the first year, and 2.7% after the second (L. Moravcová et al., unpublished data). The high fecundity and opportunistic behaviour associated with high percentages of germination of cold-stratified seed, as well as the high seed production (Pyšek et al., 1995; Tiley et al., 1996), may account for the successful invasion by *H. mantegazzianum* in Central Europe.

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