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ORIGINAL PAPER

Timing and extent of tissue removal affect reproduction characteristics of an invasive species *Heracleum mantegazzianum*

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Abstract Response of the invasive species *Heracleum mantegazzianum* to experimental removal of tissues was studied in the Czech Republic. The study aimed at determining (i) how efficiently plants respond, in terms of quantity and quality of produced fruit, to the removal of different amounts of generative and/or vegetative tissues; and (ii) whether regeneration ability depends on the time of treatment. Total number of fruits and their mean weight were reduced by removal of leaves, but germination percentage and rate of germination did not differ from control. More vigorous individuals compensated for the loss of tissues to a higher degree, and the advantage of being larger increased with severity of the treatment. Of 40 plants with umbels completely removed, 18 (45.0%) regenerated and produced on average 103.4 ± 220.1 (mean ± SD) fruits. Total fruit numbers and total fruit weight of regenerating plants significantly differed neither among treatments nor from the control, but some treatments resulted in poorer germination compared to the control. Umbels removed from plants at the beginning of fruit development and left at the locality produced 18.6% of fruit numbers of control plants, and 24% of these seeds germinated. Control by removing umbels from plants must ensure that they are collected and destroyed. From the management viewpoint, there is a trade-off between later umbel removal, resulting in more efficient reduction in fecundity but necessity to handle more developed fruits, and early treatment, leading to a high regeneration, that produces seed of sufficient quantity and very little affected in terms of quality.

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Introduction

Reproductive traits are crucial for successful invasions by alien plants (Rejmánek and Richardson 1996; Rejmánek et al. 2005) and affect the probability of naturalization and subsequent invasion (in the sense of Richardson et al. 2000; Pyšek et al. 2004b). Although some aliens reproduce exclusively vegetatively in the adventive range and this does not limit their ability to spread (Pyšek et al. 2003; Mandák et al. 2004), majority depend on seed dispersal (Pyšek 1997). A large seed set is believed to contribute to the invasion success of alien plants and so is germination in a wide range of conditions (Baker 1965; Forcella et al. 1984; Richardson and Cowling 1992; Rejmánek 1996; Rejmánek et al. 2005).

Heracleum mantegazzianum, an alien species in the Czech Republic and many other European countries (Tiley et al. 1996; Nielsen et al. 2005), belongs to the most important invasive herbs in Europe and is regularly listed in global overviews of noxious invaders (Weber 2004). The species invades a wide range of habitats (Pyšek and Pyšek 1995; Müllerová et al. 2005; Chytrý et al. 2005) including nature reserves. This makes it a species of special conservation concern (Pyšek et al. 2004a) and subject to various control measures. Since the species' population dynamics depend entirely on reproduction by seed (Tiley et al. 1996; Moravcová et al. 2005; Krinke et al. 2005), this phase of its life history is a convenient target of mechanical control.

At present, a solid information is available on germination characteristics (Moravcová et al. 2005) and dynamics of seed bank (Krinke et al. 2005) of *H. mantegazzianum* in its invasive range in Europe and this knowledge can be used to design an appropriate control strategy aimed at reducing its reproductive output. However, since the species is known to possess a good regeneration ability (Pyšek et al. 1995; Tiley and Philp 1997; Otte and Franke 1998), information is needed on how it responds to the removal of various tissues at different times of the growing period. Because it is monocarpic and plants die after they have produced fruits, preventing them from fruit production at appropriate phenological stage is crucial for the success of control schemes. Knowledge of the timing of the treatment can therefore make the control most effective by reduction in fecundity (Pyšek et al. 1995). Also, since mechanical control of such a vigorous plants is time- and labour-demanding, it is useful to know whether whole plants need to be removed from infested localities or the same effect on reproduction is achieved by removing only part of the tissues.

Plants can compensate for the effect of removal of both vegetative and generative tissues (Belsky 1986; Verkaar 1988); the extent of such compensation varies with regards to the extent of damage, timing and conditions under which the plant is growing (Crawley 1983). The present study investigates this response in *H. mantegazzianum* and aims to answer the following questions: 1. If vegetative tissues and/or part of the flowers are removed at the flowering time, how efficiently can plants compensate for this loss in terms of quantity and quality of fruit production? 2. Does tissue removal exhibit a differential effect on fruits produced at different positions on a plant? 3. If flowering umbels are completely removed, how efficient is regeneration in terms of new fruit production, and their subsequent quality? 4. How does regenerative ability vary when tissues are removed at different times, i.e. different phenological phases?

Study area

The study area was located in the Slavkovský les Protected Landscape Area, W Bohemia, Czech Republic, where the species was first introduced into the country (Pyšek 1991). Colonization of the region by humans began at the end of the 13th century, but after World War II, German inhabitants were displaced and part of the region was military area until the 1960s. As a result, it is sparsely populated at present. Total size of the protected area is 617 km^2, altitudinal range is

373–983 m a.s.l., January temperature ranges from – 5.1°C (average minimum) to – 0.2°C (average maximum), July temperature from 10.5 to 21.5°C, respectively. Annual precipitation is 1094 mm (Mariánské Lázně meteorological station, 50-year average). Natural vegetation consisted mainly of beech and spruce forests, extensive peat bogs and pine forests on serpentine soil. Only remnants of this vegetation remain today, and have been replaced by extensive wetlands with a high diversity of flora, pastures and spruce forest plantations. The area is heavily infested by *H. mantegazzianum* and the study sites were evenly distributed to cover the range of variation in environmental conditions (see Krinke et al. 2005; Moravcová et al. 2005; Müllerová et al. 2005 for details).

Study species

Heracleum mantegazzianum Sommier et Levier (Apiaceae) is native to the western Greater Caucasus, where it occurs in the upper forest belt on southern slopes, mainly in meadows, clearings and forest margins (Mandenova 1950). In the Czech Republic, *H. mantegazzianum* is invasive (Pyšek et al. 2002), following the criteria of Richardson et al. (2000) and Pyšek et al. (2004b). 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 a low January isotherm (Pyšek et al. 1998). *Heracleum mantegazzianum* is naturalized or invasive in a number of European countries and Central Russia (Nielsen et al. 2005). Outside Europe, it is found naturalized in Canada and United States (Morton 1978; Kartesz and Meacham 1999).

This species is a perennial monocarpic herb, flowering usually in the third to fifth year (Pergl et al. 2006), 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, complemented by satellite umbels and umbels that may be borne on the branches. Umbels mature in a terminal down sequence. Flowers are insect-pollinated, hermaphroditic and protandrous; the anthers dehisce and pollen is shed before the stigma becomes receptive, but there is some overlap in the staminate and pistillate phases, which makes self-fertilization possible (Steward and Grace 1984; Perglová et al. 2006). Plants in the study area flowered from the last third of June to late July and sequential ripening of fruit followed. Umbels bear oval-elliptical, broadly winged mericarps which are connected into pairs by carpophore and split when mature (Holub 1997; for simplicity the unit of generative reproduction and dispersal is termed ''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, with a mean mass of about 13.1 mg (average from 700 measurements; Moravcová et al. 2005) and range of 4.6–22.3 mg (Tiley et al. 1996). Fruits produced by terminal umbels are significantly heavier than those from satellite and branch umbels (Moravcová et al. 2005). The embryo is rudimentary and surrounded by an oily endosperm, and mature fruits have a strong resinous smell (Martin 1946; Tiley et al. 1996).

A single plant is capable of producing a large quantity of fruit and estimates range from 5000 to more than 100,000 per plant (Pyšek et al. 1995; Tiley et al. 1996); the maximum value reported is 107,984 fruits per plant (Caffrey 1999). From the study area of Slavkovský les, Perglová et al. (2006) found a mean (n = 100) fecundity of 20,500 fruits per plant, with almost half of them produced on the terminal umbel. Seeds germinate from early March to April in the study area (Krinke et al. 2005) and cold stratification is necessary for germination (Tiley et al. 1996; Moravcová et al. 2005). Seeds exhibit a morphophysiological dormancy in the sense of Baskin and Baskin (1998), having underdeveloped embryos that are physiologically dormant. Embryo growth must occur and physiological dormancy broken before germination. Both types of dormancy are broken by cold conditions in autumn and winter. Moravcová et al. (2005) reported a mean percentage germination under laboratory conditions of 91%, and found that seed germination rate was independent of fruit position on a plant (Moravcová et al. 2005).

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 attempts to eradicate it (Nielsen et al. 2005). This species substantial fecundity and efficient dispersal of fruit by water, wind and human-related factors (Pyšek and Prach 1993) have contributed to its rapid spread. *Heracleum mantegazzianum* invades not only disturbed habitats but also seminatural vegetation (Pyšek and Pyšek 1995).

Methods

Experiment 1: Type and magnitude of removal

Ten study sites were used for this experiment; these sites were the same as those used to study various aspects of *H. mantegazzianum* ecology in the study area (Moravcová et al. 2005; Krinke et al. 2005; Müllerová et al. 2005). To cover the variability of treatments effect at individual sites, one plant at each locality was subjected to each treatment, giving the total of 10 plants per treatment. Plants were selected randomly and marked using plastic tags. Treatments varied in terms of the proportion of generative (F: flowering umbels) and/or vegetative (L: leaves) organs that were removed. The following combinations of removal were applied; the numbers after codes for flowers and leaves indicate the percentage of organs removed:

- L50-F0 (50% of leaves and no flowers removed);
- L100-F0 (100% of leaves and no flowers removed);
- L0-F50 (no leaves and 50% of flowers removed; half of umbels of each type and half of the terminal umbel was removed);
- L0-F100 (no leaves and 100% of flowers removed);
- L50-F100 (50% of leaves and 100% of flowers removed);
- L100-F50 (100% of leaves and 50% of flowers removed);
- L50-F50 (50% of leaves and 50% of flowers removed);
- L100-F100 (100% of leaves and 100% of flowers removed);
- All (whole plant cut at ca. 5 cm above ground level, removing not only 100% of leaves and flowers but also the stem)
- Control plants, with no organs removed, were selected on the day of treatment.

Experimental treatments began in early July 2002, when plants at most localities were at the peak of flowering. Flowers were cut off below the base of the umbel and leaves were removed by cutting the petiole near the stem in order to remove the assimilation surface completely. To explore whether the effect of particular treatments was affected by vigour of individual plants, the following characteristics were recorded for each plant at the time of treatment: number of leaves, length of the largest leaf, diameter of the terminal umbel and the number of satellite umbels. The value of this experiment was, however, limited by confounding the effect of treatment with that of site; therefore, the effect of plant vigour must be interpreted with caution, bearing in mind that the possible different effect of plant vigour at different sites could not be assessed statistically.

Experiment 2: Timing of removal

To remove the site effects on treatments, this experiment was restricted to the largest infested locality Žitný I (see Müllerová et al. 2005 for details on locality and the dynamics of its invasion since the beginning in the 1950s). This decision was also justified by the results of a previous study that showed little effect of a site on germination characteristics (Moravcová et al. 2005). Based on the results of Experiment 1, conducted a year earlier, only treatments removing all flowers and leading to substantial reduction of the fruit set on regenerating plants were applied. In June 2003, 70 plants were randomly selected at the locality and marked with plastic tags. On the same day, 10 of them were designated as controls and the first treatment was applied: 10 individuals were cut at 5 cm above ground, removing the whole plant including leaf rosette (this treatment was termed All), and in another 10 plants, all organs above the leaf rosette were removed (treatment termed Rosette).

The timing of treatments was based on the phenological stage. The first treatment (Time 1) was initiated when terminal umbels were at the bud stage (7 June 2003). Time 2 (20 June 2003) corresponded to the beginning of flowering of the terminal umbel, and the final treatment, Time 3 (2 July 2003) the beginning of fruit development on the terminal umbel while other umbels were still flowering. At Time 2 and 3, another 10 plants of those marked at the beginning of the experiment were subjected to the All and Rosette treatments, respectively. Terminal umbels cut at Time 3 were marked and left at the locality, to determine whether fruits separated from maternal plants would ripen. This information is of considerable practical value when designing control strategy.

To explore whether or not the effect of treatments was related to plant vigour, basal diameter of the stem and plant height were recorded for each plant at Time 1, when the plants were selected.

Response variables analyzed

During both experiments sites were repeatedly visited in August and September of the respective year and ripe fruits were harvested. Fruits harvested from plants with none or half of the flowers removed (F0 and F50 treatments) were categorized according to the position on a plant into those from the terminal (primary) umbel, and secondary umbels from satellites and/or branches. Fruits from plants subjected to removal of all flowers (treatments F100 in Experiment 1 and all plants in Experiment 2) were collected without reference to their position on a plant. The resulting total number of fruit samples was somewhat lower than expected (2002: 6 treatments × 3 positions × 10 plants + 4 treatments × 10 plants = 220 samples; 2003: 7 treatments × 10 plants + 20 cut-off terminal umbels = 90 samples), because not all plants have regenerated due to mortality. Fruits were transported to the laboratory and kept in paper bags at room temperature until the germination experiments began.

Four sets of 25 fruits were taken from each fruit sample, weighed to the nearest 0.001 g and placed on Petri dishes with 0.5 cm of wet sand sterilized for 48 h at 120°C. Seeds were cold-stratified at refrigerator at 2–6°C, and germinated at the same temperature (Moravcová et al. 2005) and monitored at three-week intervals. The germination experiments ran until majority of viable seeds germinated; both experiments were terminated after approximately 1 year ensuring that all viable seeds had an opportunity to germinate (Moravcová et al. 2005).

The following characteristics were recorded for each plant: (i) mean fruit weight (calculated from the weight of 25 fruits and recorded separately for the three positions where appropriate); (ii) total fruit weight (total weight of all fruits collected from a plant); (iii) total number of fruits (estimated from the mean fruit weight and total fruit weight, or counted where low numbers of fruits were produced); (iv) germination time of each seed; and (v) final germination percentage.

Statistical analysis

The two different situations imposed by the treatments in Experiment 1 were analyzed differently: (i) Plants with none or half of the flowers removed (F0 and F50 treatments) and only subjected to the removal of different levels of vegetative organs exhibited compensatory growth in the remaining part of the growing season. The fruits analyzed here started to develop before the application of treatments, and at the end of the growing period, they were compared with those produced on control plants and analyzed separately for terminal, satellite and branch umbels (Table 1). This group of treatments is further referred to as ‘‘Compensation‘‘ and relates to a part of the Experiment 1. (ii) In plants subjected to treatments with all the flowers removed, fruits collected at the end of the growing season were

Table 1 Overview of the models analyzed

Model	Response variable	Explanatory variables	Remark
Compensation (Experiment 1)	Mean fruit weight	Control, L100-F0, L50-F0, L0-F50, L100-F50, L50-F50 + Umbel type + Covariates[a]	
	Total fruit number	$\frac{1}{2}$ Control, $\frac{1}{2}$ L100-F0, $\frac{1}{2}$ L50-F0,[b] L0-F50, L100-F50, L50-F50 + Umbel type + Covariates[a]	
	Final germination %	Control, L100-F0, L50-F0, L0-F50, L100-F50, L50-F50 + Umbel type + Covariates[a]	
	Germination rate	Control, L100-F0, L50-F0, L0-F50, L100-F50, L50-F50 + Umbel type + Covariates[a]	
Regeneration (Experiment 1)	Total fruit number	L0-F100, L50-F100, L100-F100, All + Covariates[a]	Control and umbel type irrelevant
	Mean fruit weight	Control,[c] L0-F100, L50-F100, L100-F100, All + Covariates[a]	Umbel type irrelevant
	Final germination %	Control,[c] L0-F100, L50-F100, L100-F100, All + Covariates[a]	Umbel type irrelevant
	Germination rate	Control,[c] L0-F100, L50-F100, L100-F100, All + Covariates[a]	Umbel type irrelevant
Regeneration (Experiment 2)	Total fruit number	All, Rosette + Covariates[d]	Control and umbel type irrelevant
	Total fruit weight	All, Rosette + Covariates[d]	Control and umbel type irrelevant
	Mean fruit weight	Control, All, Rosette + Covariates[d]	Umbel type irrelevant
	Final germination %	Control, All, Rosette + Covariates[d]	Umbel type irrelevant

Compensation treatments relate to those with flowering umbels not or only partly removed, where flowers/fruits were initiated before the treatment. Regeneration relates to treatments where new fruits were produced as a response to complete fruit removal by the treatment. Note that control is irrelevant for regeneration treatments related to the total fruit production and umbel type is always irrelevant because regenerating fruits are not produced on normal types of umbels produced on unaffected plants (terminal, satellite, branches). Note that total fruit weight in Experiment 1 and germination rate in Experiment 2 were not analyzed. Total fruit weight in Experiment 1 was used to estimate fruit numbers. Since germination rate in regeneration treatments of Experiment 1 varied without a consistent pattern, it was not analyzed in Experiment 2. Treatment codes: L: leaves, F: flowers; numbers indicate percentage of organs removed (see text for details)

[a] Length of the largest leaf; number of leaves; diameter of the terminal umbel; number of satellite umbels at the time of treatment

[b] Only half of the fruits produced on control plants was used for comparison because half of the flowers were removed by these treatments

[c] Average value obtained from fruits produced on terminal, satellite and branch umbels of control plants was used as a control

[d] Basal diameter of the stem and plant height at the time of treatment

all produced after the treatment. Their characteristics were neither related to control nor analyzed with regards to the position (Table 1). This group of treatments is further referred to as ‘‘Regeneration‘‘ and relates to F100 treatments in the Experiment 1 to the results of Experiment 2.

Response variables were total fruit numbers (square root transformed + 1, Sokal and Rohlf 1995), mean fruit weights, total fruit weights (ln + 0.5 transformed, Yamamura 1999), final germination percentages (angular transformed proportions, Sokal and Rohlf 1995) and germination rates (average time to germination of each seed, see Moravcová et al. 2005). Some variables were only analyzed for some experiments (see Table 1 for an overview). Explanatory variables included categorical variables, termed factors, and continuous variables, termed covariates. Factors were control plants and treatments of the compensation and regeneration experiments. In addition, umbel positions on experimental plants (terminal, satellites and branches) were also used as factors in compensation experiments. Covariates in the Experiment 1 were the length of the largest leaf, number of leaves, size (diameter) of the terminal umbel, and number of satellite umbels at Time 1. Covariates in the Experiment 2 were basal diameter of the stem and plant height at the time of treatment. Because the covariates were measured on different scales, whenever two or more covariates appeared significant in the same model, they were standardized to zero mean and unit variance in order to achieve their comparable influence. The standardization thus enabled direct comparisons of their effects, because steeper regression slopes directly indicated larger effects. Collinearity of the covariates was checked by a matrix of correlation coefficients, and then by calculating tolerance values, using the regression of the covariate in question against all the remaining covariates in the model (Quinn and Keough 2002).

The analyses began with two-way fixed effects factorial ANOVAs for equal sample sizes for compensation models, to search for significant interactions between plant treatments and umbel positions on plants. Because no significant interactions between treatments and umbel positions were revealed, excepting germination rate, the analyses continued by ANCOVAs excluding germination rate data. The modelling of ANCOVAs started by fitting models in which each treatment, or each umbel position, was regressed on appropriate covariates with a different intercept and a different slope. The parameters of each model were inspected, and the least significant term was removed in a deletion test. If the deletion caused an insignificant increase in deviance, the term was removed. Deletion tests were repeated until minimal adequate models were established. In these minimal adequate models, all non-significant parameters were removed, and all the remaining parameters were significantly ($P < 0.05$) different from zero and from one another (Crawley 1993). If the minimal adequate models contained only plant treatments, the mean differences among treatments were evaluated by least square differences (LSD) tests (Sokal and Rohlf 1995). If the minimal adequate models contained only umbel positions, the a priori hypothesis, namely that fruit numbers, mean fruit weights and final germination percentages on terminal umbels significantly differed from average values for satellites and branch umbels, was tested by orthogonal contrasts (Crawley 1993).

Germination rate was analyzed using a survival analysis (Crawley 1993). Here, the time of germination (in weeks) of each seed was the response variable. Dormant seeds were censored. Differences in germination rate were fitted by likelihood functions, described by two parameters, mean time to germination, μ, and shape parameter, α. The mean time to germination was the time needed for germination of 50% of seed. The shape parameter indicated the appearance of germination curves. The curves, in which P is a proportion of seeds that germinated as a function of time, t, were $P(t) = \exp(-\lambda t^{\alpha})$, where $\lambda = \mu^{-\alpha}$.

All fitted models were checked for appropriateness of their structure by plotting standardized residuals against fitted values, and by normal probability plots (Crawley 1993). Calculations were made using GLIM version 4 (Francis et al. 1994).

Results

Experiment 1: Compensatory growth of plants with half or all the fruits retained

Except for treatments where half of the umbels were removed (Tables 1, 2), the total number of fruits, their mean weight and final germination percentage were always significantly affected by both the treatment and umbel position (Table 2). These effects were independent, as indicated by non-significant interactions hence they were explored separately (Table 2).

As for the effect of treatments, the total number of fruits (Fig. 1a) and their mean weight (Fig. 1b) were significantly reduced by removal of all leaves, however, the effect of treatments resulted in differential compensatory responses (Table 3). The final germination percentage also varied significantly among treatments but the pattern was not related to the magnitude of leaf and/or fruit removal and none of the treatments was significantly different from the control (Fig. 1c, Table 3).

Plant vigour played a role in individual plant response to treatments. Plants with larger leaves at the time of removal, which indicate more vigorous individuals, produced more fruits (Fig. 2a, b). The slopes of regression lines indicate that if no flowers were removed, pre-treatment leaf length had a stronger effect on the number of fruits produced in treatments with all leaves removed than in those with only half of the leaves removed (Fig. 2a). If half of the umbels were removed, the pattern was difficult to interpret: the effect of plant vigour, expressed by leaf size, on

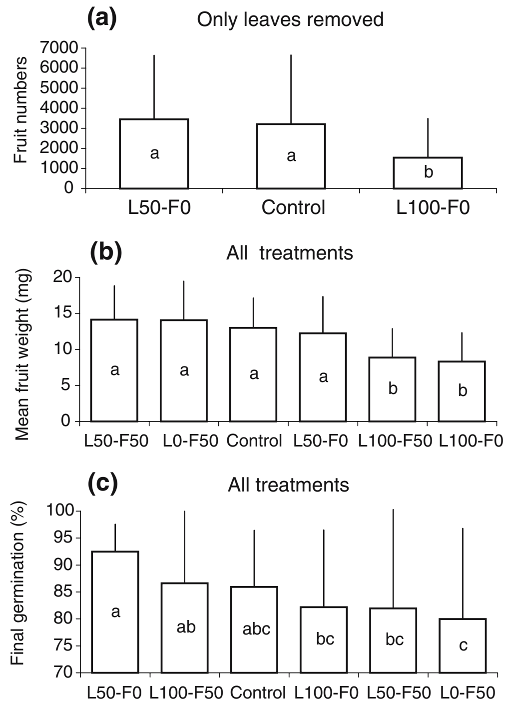

Fig. 1 Comparison by least square differences (LSD) of plants growing under the compensation treatments with control plants in Experiment 1. (**a**) Treatments with no flowering umbels removed. (**b**), (**c**) Treatments with 0, 50 and 100% of leaves (L0, L50, L100) and 0 and 50% of flowering umbels (F0, F50) removed. Bars with the same letters are not significantly ($P < 0.05$) different. Vertical lines are one standard deviation, sample sizes are $n = 30$

Table 2 ANOVA tables for compensation treatments of Experiment 1 (L100-F0, L50-F0, L0-F50, L100-F50, L50-F50, Control), combining removal of 0, 50 and 100% of leaves (L0, L50, L100) with removal of 0 and 50% of fruits (F0, F50)

Source of variation	Fruit numbers: control, L100-F0, L50-F0			Fruit numbers: control, L0-F50, L100-F50, L50-F50			Mean fruit weights: all treatments			Final germination: all treatments			Germination rate: all treatments	
	df	MS	F	df	MS	F	df	MS	F	df	MS	F	df	χ^2
Umbel position	2	3781.5	5.78*	2	1055.0	2.57 NS	2	550.0	35.34**	2	0.3052	10.11**	2	67.00**
Treatment	2	3965.5	6.06*	3	794.7	1.93 NS	5	196.34	12.62**	5	0.12292	4.07*	5	106.00**
(Position) × (Treatment)	4	312.25	0.48 NS	6	66.33	0.16 NS	10	4.93	0.32 NS	10	0.01594	0.53 NS	10	85.00**
Error	81	654.36		108	410.97		162	15.56		162	0.03018			

Fruit numbers, fruit weights and final germination percentage are two-way fixed effect factorial ANOVAs, germination rate is survival analysis

*$P < 0.01$; **$P < 0.001$; NS = not significant

Table 3 Reproductive characteristics of plants resulting from compensation treatments in Experiment 1

	Mean fruit weight	% of control	Total fruit number	% of control	Final germination %	% of control
Control	13.0 ± 3.6	–	9613.7 ± 9183.1	–	85.9 ± 9.0	–
L100-F0	8.9 ± 1.6	68.3	4624.8 ± 4857.6	48.1	84.3 ± 9.5	98.1
L50-F0	13.0 ± 3.5	99.9	10347.1 ± 8284.7	107.6	93.1 ± 3.0	108.4
L0-F50	14.5 ± 4.1	112.0	7334.5 ± 6132.4	76.3	81.6 ± 10.1	95.0
L100-F50	9.5 ± 1.2	72.9	3844.8 ± 2936.9	40.0	89.3 ± 7.4	104.0
L50-F50	14.1 ± 3.4	108.8	5060.0 ± 2352.9	52.6	82.5 ± 13.3	96.0
Treatments pooled	12.0 ± 3.8	92.4	6242.2 ± 5667.7	64.9	86.2 ± 10.0	100.3

Percentage compensation is related to the control

Values are means ± SD, $n = 10$

fruit number was only significant if no leaves or all leaves were removed, but non-significant in treatments with half of the leaves removed (Fig. 2b). The number of fruits produced by control plants was never related to the leaf length (Fig. 2a, b). Mean fruit weight was significantly affected by length of the largest leaf and the number of leaves at the time of treatment ($F = 10.51$; df = 7, 154; $P < 0.001$), but the effect of these proxies for plant vigour varied among treatments without any consistent pattern. Final germination percentage was significantly affected by the size of the terminal umbel and by the number of satellite umbels ($F = 7.65$; df = 8, 171; $P < 0.001$), but the pattern among treatments was also inconsistent.

Analysis of the effect of umbel position on treated plants revealed that terminal umbels produced significantly more fruits that were heavier and germinated faster than fruits from satellites and branches. Fruits from satellites and branches did not differ in any of these characteristics (Table 4).

The vigour of treated plants co-determined how treatments affected reproductive characteristics on different types of umbels. Slopes of the regression lines indicate that plants with larger leaves at the time of treatment produced more fruit (Fig. 2c, d). If only leaves were removed, this effect of plant vigour was obvious on all three types of umbels but more pronounced on terminals than on satellite and branch umbels (Fig. 2c). If half of the umbels were removed, the effect of leaf length was only significant on satellite and branch umbels, but not on terminals (Fig. 2d). Mean fruit weight increased with size of the terminal umbel at the time of treatment and the rate of this increase was the same for fruits produced on all three types of umbels (Fig. 2e). Final germination percentage on particular umbel types was significantly affected by both leaf length and size of the terminal ($F = 12.94$; df = 2, 177; $P < 0.001$). The percentage of germinated seed produced on satellite and branch umbels significantly increased with leaf length (angular transformed proportion of final germination = 1.20 + 0.048 standardized leaf length; $F = 5.33$; df = 1, 178; $P < 0.05$) but at the same time, it decreased with the size of the terminal umbel (angular transformed proportion of final germination = 1.20–0.043 standardized terminal size; $F = 11.94$; df = 1, 178; $P < 0.001$). Final germination percentage of seed from terminal umbels was not affected by the size of the terminal umbel or length of the largest leaf.

Germination rate was significantly affected by both treatment and umbel position (Table 2). Because of a significant interaction between both (Table 2, last column), the germination rate was analyzed separately for all treatments within particular umbel positions and vice versa, for all umbel positions within particular treatments. In both analyses, germination rate significantly varied without any consistent pattern.

Experiment 1: Regeneration after removal of all flowering umbels

Of 40 plants with umbels completely removed, 18 (45.0%) regenerated. The number of regenerated plants from treatments L0-F100, L50-F100,

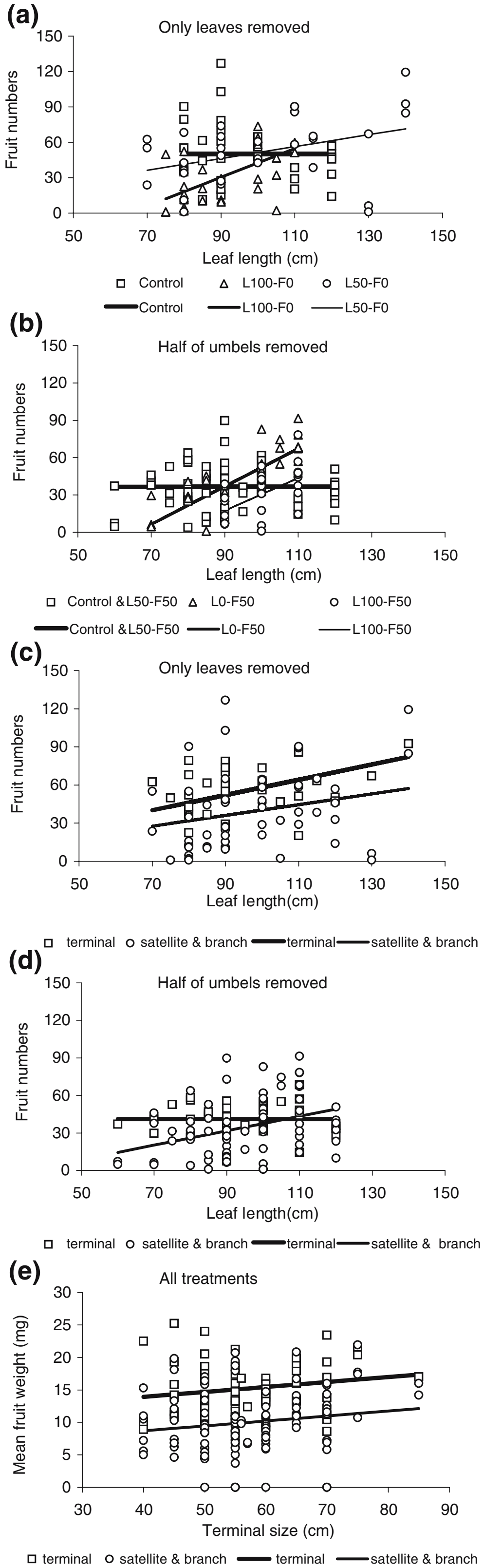

Fig. 2 Comparison by ANCOVAs of control plants with those treated by removal of 0, 50 and 100% of leaves (L0, L50, L100), and 0 and 50% of flowering umbels (F0, F50) (Experiment 1). (**a**) √Fruit numbers of control = 50.16; √Fruit numbers of L100-F0 = − 79.24 + 1.22 leaf length; √Fruit numbers of L50-F0 = 1.02 + 0.50 leaf length; $F = 7.18$; df = 4, 85; $P < 0.001$. (**b**) √Fruit numbers of control & L50-F50 = 36.56; √Fruit numbers of L0-F50 = − 99.74 + 1.52 leaf length; √Fruit numbers of L100-F50 = − 99.74 + 1.30 leaf length; $F = 19.25$; df = 3, 116; $P < 0.001$. (**c**) √Fruit numbers of terminal = − 1.79 + 0.60 leaf length; √Fruit numbers of satellite & branch = − 1.79 + 0.42 leaf length; $F = 9.07$; df = 2, 87; $P < 0.001$. (**d**) √Fruit numbers of terminal = 41.4; √Fruit numbers of satellite & branch = − 20.07 + 0.58 leaf length; $F = 8.64$; df = 2, 117; $P < 0.001$. (**e**) Mean fruit weight of terminal = 10.89 + 0.076 terminal size; √Mean fruit weight of satellite and branch umbels = 5.66 + 0.076 terminal size; $F = 30.15$; df = 2, 177; $P < 0.001$

L100-F100 and All was 6 (60%), 5 (50%), 4 (40%) and 3 (30%), respectively.

Regenerating plants produced 103.4 ± 220.1 fruits (mean ± SD, $n = 18$). Total fruit numbers and total weight of fruits produced on regenerating plants did not significantly differ among treatments (Table 5). Mean fruit weight produced on plants subjected to different treatments was 12.7 ± 6.1 mg and did not significantly differ from those produced on control plants (Table 5). The only significant differences related to germination characteristics. Seeds on plants with leaves completely removed had final germination percentage significantly lower than seeds from the control plants (Fig. 3a) and they also had the lowest germination rate (LSD test on germination rate).

Experiment 2: Effect of the timing of treatment on regeneration

Of the 60 plants treated by complete umbel removal, 53 (88.3%) regenerated until the end of growing period. They produced on average 1424.5 ± 2451.0 fruits (mean ± SD, range 3–13,229). Separated according to the time of treatment, 90, 95 and 80% of plants treated at Times 1, 2 and 3, respectively, produced some fruits. The number of fruits produced by plants treated at particular times was 3310.4 ± 3469.4 (Time 1), 461.4 ± 613.8 (Time 2) and 446.4 ± 518.5 (Time 3).

Total fruit weight produced on regenerating plants was significantly affected by both the

Table 4 One-way fixed effect ANOVA tables for compensation treatments of Experiment 1 (L100-F0, L50-F0, L0-F50, L100-F50, L50-F50, Control), combining removal of 0, 50 and 100% of leaves (L0, L50, L100) with removal of 0 and 50% of fruits (F0, F50), with orthogonal contrasts for umbel positions

Source of variation	Fruit numbers: control, L100-F0, L50-F0				Mean fruit weights: all treatments				Final germination: all treatments			
	SS	df	MS	F	SS	df	MS	F	SS	df	MS	F
Umbel position	7563	2	3781.5	5.29*	1100.22	2	550.11	27.42**	0.6104	2	0.3052	9.91**
(Terminal) vs. (mean of satellite and branch)	6875	1	6875	9.62*	1092	1	1092	54.44**	0.5687	1	0.5687	18.46**
(Satellite) vs. (branch)	688	1	688	0.96 NS	8.22	1	8.22	0.41 NS	0.0417	1	0.0417	1.35 NS
Error	62,183	87	714.7		3551.18	177	20.06		5.4528	177	0.0308	
Total	69,746	89			4651.4	179			6.0632	179		

*$P < 0.01$; **$P < 0.001$; NS = not significant

treatment and time when it was applied ($F = 9.46$; df = 6, 63; $P < 0.001$; Fig 3b). Control plants did not differ in total fruit weight from those with their rosette retained at Time 1 but differed from those plants whose rosette was removed completely at that time. Plants that retained their rosette at Time 2 did not significantly differ from individuals whose rosette was completely removed at Time 1. Not surprisingly, the most dramatic decrease in total fruit weight resulted from treatments that removed whole plants at Times 2 and 3. At Time 3, an effect of the same strength was observed if the rosette was retained. In general, the effect of treatments on the total number of fruits was weaker if applied early, at Time 1, than when conducted on plants at a more developed phenological stage. Within particular times of application, the treatments removing whole plants never significantly differed in total fruit weight from those leaving the rosette, although there was a slight tendency for plants with rosettes to produce heavier fruits (Fig. 3b).

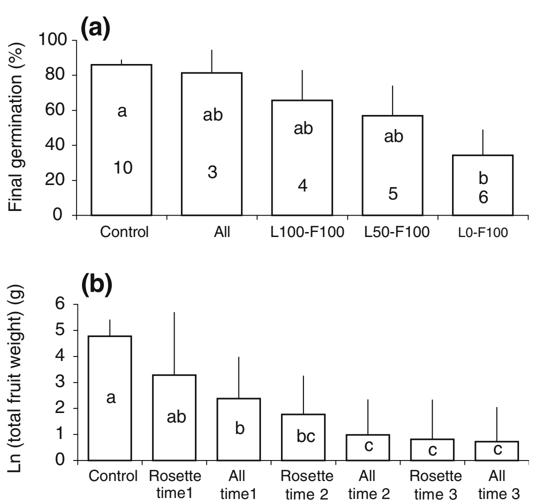

Fig. 3 Comparison by least square differences (LSD) of the final germination percentage of plants resulting from regeneration treatments with control plants. (**a**) Treatments with 100% of fruits (F100) and 0, 50 and 100% of leaves (L0, L50, L100) removed, and the whole plant completely removed (All). (**b**) Comparison of the total fruit weight of plants resulting from removal of the whole plant (All), removal of plant with rosette retained (Rosette) and control plants, with removal applied at three times (1, 2, 3). Vertical lines are one standard deviation, sample sizes not given inside the bars are $n = 10$

Mean fruit weight did not differ among treatments (full model of ANCOVA: $F = 1.31$; df = 20, 49; NS). Consequently, since fruit numbers were estimated from the total fruit weight and mean fruit weight, the effects of treatments on fruit numbers were the same as those for the total fruit weight (Fig. 3b). The effects on total fruit weight and mean fruit weight of covariates representing proxies for plant vigour, were never significant. Final germination percentage of treated plants reached 62.8 ± 29.2% (mean ± SD, $n = 53$) and did not differ significantly ($F = 2.44$; df = 1, 61; NS) from control plants (77.6 ± 15.4, $n = 10$).

Umbels from plants treated at Time 3 and left to develop at the locality produced viable fruit. Of 20 treated plants, fruits developed on the terminal umbels of 17 (85%) plants. Fruit number (1840 ± 2046, mean ± SD) and mean weight (5.74 ± 1.36 mg) were significantly (number: $F = 39.70$; df = 1, 28; $P < 0.001$; weight:

Table 5 ANOVA tables for regeneration treatments of Experiment 1 (L0-F100, L50-F100, L100-F100, All, Control), combining removal of 0, 50 and 100% of leaves (L0, L50, L100) with removal of all flowering umbels (F100), and the treatment that completely removed the whole plant, including rosette (All)

Source of variation	Fruit numbers: without control			Total fruit weights: without control			Mean fruit weights			Final germination			Germination rate	
	df	MS	*F*	df	MS	*F*	df	MS	*F*	df	MS	*F*	df	χ^2
Treatment	3	6.34	0.16 NS	3	1.20	0.32 NS	4	0.0000231	0.67 NS	4	0.47	3.19*	4	40.30**
Error	36	40.61		36	3.77		23	0.0000344		23	0.15			

Fruit numbers, total fruit weights, mean fruit weights and final germination percentage are one-way fixed effect factorial ANOVAs, germination rate is survival analysis

*$P < 0.05$; **$P < 0.001$; NS = not significant

$F = 71.59$; df = 1, 28; $P < 0.001$) lower than in control plants (9863 ± 5216 fruits and 13.09 ± 2.62 mg, respectively). The seeds from cut umbels also germinated to significantly ($F = 33.76$; df = 1, 25; $P < 0.001$) lower percentages (24.1 ± 22.3%) than those from control plants (77.6 ± 15.6%). Cut-off umbels were only terminals because satellite and branch umbels were flowering at the time of treatment and fruits were not developing yet; these umbels decayed after being detached from plants and produced no seed. For practical purpose, the fruit production of removed umbels was compared with that of whole control plants, not only with their terminal umbels. The fate of umbels that are cut and left on the ground, regardless of which type of umbel they originated from, is particularly relevant from the viewpoint of control strategies.

Discussion

Previous studies on Heracleum mantegazzianum did not consider timing and seed quality

Since reducing or eliminating fruit production is a promising control strategy for alien invaders that rely exclusively on generative reproduction, it is not surprising that *H. mantegazzianum* has been the target of such efforts. For example, Pyšek et al. (1995) followed the response of *H. mantegazzianum* plants to the removal of all leaves, all flowering umbels or only the terminal umbel. By the end of the growing period, plants had compensated for an average of 12.4% of the leaf area removed. Among plants that had tissues removed completely, fruit production was only 2.9% of observed in control plants. Fruit production doubled (5.8%), if leaves were retained at the time of treatment. Tiley and Philp (1997) applied six different treatments to plants at the peak of flowering; experimental plants were cut at different stem sections, including two below the soil surface. Cutting the root 15 cm below ground was the only treatment that killed the plants. The authors note, however, that treated plants were able to produce viable seed, albeit without any details or statistical analysis.

Otte and Franke (1998) extended the results observed in single cutting experiments by examining the effects of repeated cutting of the same plants. Plants cut at ground level during flowering time, or above the lowest stem leaf, were able to produce some new umbels and fruits. However, when the treatment was repeated on the same plants, they were again able to produce flowers for a third time but fruits were no longer produced. Caffrey (1999) also studied the role of timing in an Irish populations of *H. mantegazzianum*; plants were cut at ground level in March and May and height of regenerated plants and the number of fruit they produced was recorded. The same treatment applied at a later phenological stage resulted in the production of smaller fruits. The authors conclude that smaller fruits could be less viable, but this is not the case in this species; as shown by Moravcová et al. (2005), lighter seeds germinate more slowly but up to the same high percentages as heavier seeds.

This brief overview indicates that only one study touched the viability of seed from regenerating plants (Tiley and Philp 1997), but with insufficient experimental detail. In the same vein, only one study considered two different times of treatment applications (Caffrey 1999) but only assessed the quality of seed by measuring seed size. Since the timing of any treatment is crucial for the success of control schemes, and the quality of seed cannot be properly evaluated without recording their germination percentage and rate, the present study is the first providing solid background and guidance to efforts to eradicate *H. mantegazzianum* via constraining its generative reproduction in infested sites.

Compensation and regeneration: two sides of the same coin

The treatments applied in the present study created two qualitatively different situations. If some or all of the fruits were left on plants and only vegetative tissues (leaves) or a portion of the flowers were removed, fruits extant upon treatment were assessed at the end of the growing period. These *compensatory* treatments explore to what extent plants are able to compensate for the loss of tissues by allocating resources to reproductive structures (Crawley 1983; Belsky 1986). The second situation focused on plants with flowers completely removed by the treatment; hence fruits produced at the end of the growing season are exclusively due to the development of new floral structures initiated as a response to the treatment. Although compensatory growth (Crawley 1983) is also involved here, this situation is referred to as a *regeneration* treatment. There is also an analytical difference between both types of treatment, as for some of the characteristics studied the latter does not have a control to which results can be related, only the treatments can be compared with each other (Table 1).

The compensation treatments had highly significant effects, although some did not exhibit a consistent trend due to a high variation among individual plants (Table 3). This occurred because of treatment effects on germination characteristics: individual treatments produced seed varying to a large extent in both final germination percentage and germination rate but none of the treatments differed from the control. This indicates that the reproductive characteristics studied in the species are hardly affected by quite a severe event, which loss of a large proportion of organs certainly is. This result corresponds well with previous findings that plants of *H. mantegazzianum* are little affected by environmental conditions, which favours this species invasion in Europe (Moravcová et al. 2005; Müllerová et al. 2005).

Plants that lost all the leaves at the peak of flowering period produced fewer fruits and these fruits were lighter, but the seed germinated at the same rate as that from normally developing plants. Plants with all leaves removed produced between 40 and 50% of the fruits of the control plants and about 70% of fruit weight (Table 3). Decrease in fruit size following defoliation is a well-known phenomenon reported in the literature (Maun and Cavers 1971a; Lee and Bazzaz 1980; Bentley et al. 1980). Nevertheless, plants with half of the leaves retained were not affected in terms of fruit number or weight, and did not differ from control plants. However, plants with half of their leaves produced seed that germinated at a much higher percentage than those from plants with leaf area completely removed (Fig. 1c).

That at least some of the treatments resulted in the production of lighter seeds (92.4% of the weight of control pooled across treatments, see Table 3) but the germination rate of these seeds was unaffected (100.3% of the control; see also Moravcová et al. 2005) could have important practical implications. Lighter seeds might disperse farther, hence some control efforts may actually foster the spread of this species at the metapopulation level. Local abundance might be impacted or controlled by such treatments, but at larger spatial scales new patches could appear at larger distance from source population. This effect may not be as obvious in *H. mantegazzianum* as in wind dispersed species, where a clear effect of seed weight on dispersal distance can be assumed, but at least some means of dispersal of this species (attached to tyres, blown on frozen soil surface) could be potentially more efficient for light than heavy fruits.

Although there is a good evidence that some alien species may profit from lower levels of herbivory in their secondary distribution range (Maron and Vilà 2001; Keane and Crawley 2002), phylogenetically controlled experiments indicate that this may not be a general rule (Agrawal and Kotanen 2003). In addition, Maron and Vilà (2001) documented numerous cases of attack by native enemies on alien plants suggesting that even successful escape from some enemies may not translate into less damage, hence better performance in the novel environment. Hence the response of an alien species to tissue removal may affect its invasion success. Given the extraordinary fecundity of *H. mantegazzianum*, with an average plant producing 20,500 fruits (Perglová et al. 2006), even a seriously limited fruit set supplies the population with enough viable seed to ensure population regeneration in the following years.

The advantage of being large: the position matters

Larger size allows a plant of *H. mantegazzianum* to more efficiently compensate. Plants that were more vigorous at the time of treatment application produced more fruit at the end of the growing period. If no flowers but all leaves were removed, the positive effect of plant size on fruit production was more pronounced than after treatments with only half of the leaves lost. Obviously, the more extreme the treatment, the more pronounced the advantage of being large.

However, if half of the umbels were removed, the effect of plant vigour on compensation was more difficult to interpret. Simultaneous loss of half of the flowers and either all or none of the leaves triggered the same response as if no flowers were removed: large plants did better. However, the effect was non-significant after the treatment with both half of flowers and half of leaves removed. Similarly, there was some inconsistent effect of compensation treatments on fruit weight and final germination percentage.

As shown in a previous study, terminal inflorescences produce more and heavier fruits, but the final germination is always high (91% on average), regardless of fruit position on a plant. However, seed from heavier fruits germinate at a faster rate, hence seed produced by terminal umbels germinated faster than those from satellite and branch umbels (Moravcová et al. 2005). These findings were confirmed by the present study: terminal umbels produced significantly more fruits that were heavier with faster germinating from satellites and branches. However, plant vigour at the time of treatment interacted with position of an umbel on the plant, and exerted effects on both quantity and quality of fruit produced.

In terms of the number of fruit produced, the more vigorous of those plants that had no flowers and all leaves removed were more fecund (Fig. 2a). This effect was significant on all types of umbels but most pronounced on terminals (Fig. 2c). But, larger individuals within plants that lost half of the flowers allocated resources preferentially to satellite and branch umbels making the effect of plant vigour detectable only on these umbel types but not on terminals (Fig. 2d).

Mean fruit weight always increased with plant vigour (Fig. 2e), regardless of umbel type, but the final germination percent exhibited an interesting and rather complicated response. For seed produced on satellite and branch umbels, percent germination increased with size of the largest leaf, i.e. the measure of vegetative vigour. At the same time, however, germination of satellite and branch-produced seed decreased with the size of the terminal inflorescence at the time of treatment. Although measures of vegetative and generative vigour are correlated in plants (Crawley 1996), plants with large terminal inflorescences had already allocated a large proportion of resources to generative reproduction at the time of treatment. In addition, terminal umbels are the main seed suppliers for the population (Perglová et al. 2006) and terminal diameter is closely correlated with the number of fruit produced (Pyšek et al. 1995). It appears that if leaves are removed, which is a situation simulating a rather heavy herbivore load, plants with large terminals have allocated enough resources to terminal umbels such that fruit production in terminals is unaffected or even increased. This strategy exerted a negative effect on fruit numbers produced by umbels other then terminal. Nevertheless, plants with enough vegetative vigour, reflected by large leaves, were able to compensate for this preferential post-treatment allocation of resources to the terminal better than less vigorous individuals. This ''terminal-first'' strategy is further supported by the fact that the final germination percentage of fruits from terminal umbels was unaffected by the size of the terminal and length of the largest leaf—terminal umbels appear to be never negatively affected. Comparison of these results with those of a previous study further indicates that terminals are mobilized to exert their dominant position in resource allocation only when plants are exposed to extreme situations. In normally developing plants, size of the terminal umbel has no effect on germination characteristics (Moravcová et al. 2005).

Timing changes everything: implication for the control

Control measures applied to alien plants reproducing by seed typically target the flower; hence the regeneration portion of the present study is more relevant from the practical point of view. Plants from regeneration experiments performed in both years responded consistently to the removal of all umbels at the peak of flowering: regeneration in terms of number and weight of fruit produced was not affected by whether and how much of the leaves were removed at the same time. This contradicts the result of a previous study on *H. mantegazzianum* (Pyšek et al. 1995) and some others (Maun and Cavers 1971b) that complete defloration at the flowering time leads to the production of larger fruits. The reasons for this difference could be that the previous study on the same species was conducted in a single locality, eliminating any variation in site conditions at particular localities. However, the presence of leaves during the regeneration process in Experiment 1 affected characteristics related to germination, since both the final germination percentage and the rate of germination were only negatively affected if leaves were missing. Nonetheless it is clear that the effect of timing in treatment application, and subsequent germination characteristics, depends on the phenological stage at which organs are removed. In 2003, when the last treatment was applied a little earlier compared to Experiment 1 in 2002, neither percentage nor rate of germination was affected by the treatments; seed produced was of the same quality as that from control plants.

That the timing of treatment is crucial is further validated by a comparison of both experiments conducted in this study. The time of tissue removal in Experiment 1 roughly corresponds to Time 3 of Experiment 2 (9–10 July and 2 July, respectively, taking between-year phenological differences into account); in phenological terms it was the peak flowering time, with fruits on terminal starting to develop. Yet the extent of regeneration was quite different: while 30–60% of plants with umbels completely removed produced some fruit in 2002, 80% did so in 2003. Translating approximately a week difference in timing into fruit production indicates that plants treated later, at later stage of fruit development on terminal, produced about four times less fruit. Targeting plants at the beginning of fruit development is probably insufficient: The most devastating treatment lead to 80% of regenerating plants that on average produced about 450 seeds with 60% germination. Tissue removal is therefore more efficacious when fruits on the terminal umbel are almost fully developed and those on secondary umbels are at full blossom (Pyšek et al. 2006). These results also emphasize need for repeated visits and a second cut of regenerating reproductive structures after which the fruits were reported not to develop (Otte and Franke 1998; Pyšek et al. 2006).

Another important message of this study, from the viewpoint of control strategies, is that there is no difference between treatment efficiency when applied during the flowering and early fruiting stage of terminal umbels, and that cutting the rosette does not add to the overall effect. Cutting the stem and leaving rosette in its place results in the same effect and is technically more feasible.

The present study is also the first to evaluate previous anecdotal reports that seeds of *H. mantegazzianum* are able to ripen even if left at the locality after the inflorescences are cut. The extent of this ability is not negligible. Umbels from 85% of plants produced viable seed, although much less and of lower quality compared to control (18.6% of its number and 43.8% of its mean weight). Still, these umbels provided on average 1840 fruits per plant and the seed germinated to 24.1%. Each terminal umbel cut-off and left at a site would therefore contribute an average of 442 viable seeds available for the regeneration of the invading population. These results clearly indicate that umbels removed from plants must be transported from the locality and measures taken, for example burning (Nielsen et al. 2005), to prevent fruit from completing development. It must also be kept in mind that there is a trade-off between the danger of post-treatment development of seed and the efficiency of treatment depending on plants' phenology. Early removal of umbels provides an opportunity for substantial regeneration. Later umbel removal leads to more efficient reduction in fecundity but the removed fruits are more developed and would ripen into seed of a better quality. Moreover, late removal of umbels is associated with the danger of release of individual fruits during the treatment procedure and subsequent transport of plant material from the locality.

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