7 Regeneration Ability of *Heracleum mantegazzianum* and Implications for Control

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Hurry now, we must protect ourselves and find some shelter
(Genesis, 1971)

Introduction

As populations of *Heracleum mantegazzianum* Sommier & Levier can only reproduce via seed (Tiley *et al.*, 1996; Krinke *et al.*, 2005; Moravcová *et al.*, 2005), control measures applied before flowering and fruit set will limit recruitment to subsequent generations (Nielsen *et al.*, 2005). The possibility of controlling this species by reducing fruit production has been repeatedly considered, assuming that if applied systematically over a number of years it would ultimately deplete the seed bank. Several studies have investigated the regeneration capacity of *H. mantegazzianum* (Pyšek *et al.*, 1995; Tiley and Philp, 1997, 2000; Otte and Franke, 1998; Caffrey, 1999, 2001; Nielsen, 2005; Pyšek *et al.*, 2007).

Unfortunately, the majority of the data on regeneration come from papers where this issue is only part of descriptive studies aimed at providing information on biomass production, fecundity and basic population parameters (Tiley and Philp, 1997; Otte and Franke, 1998). Four studies (Pyšek *et al.*, 1995, 2007; Tiley and Philp, 2000; Nielsen, 2005) focus explicitly on the response of *H. mantegazzianum* to the removal of tissues. The quality of these data may in some cases be compromised by: (i) regeneration being a secondary subject of the research; (ii) the need for a practical solution resulting in less rigid experimental design; and (iii) technical difficulties resulting from the size of the plants, which makes designing experiments and obtaining sufficient replicates difficult. Some papers dealing with these issues do not use statistical analysis (e.g. Tiley and Philp, 2000) or the response to the treatments is only described verbally (Otte and Franke, 1998). All but two (Caffrey, 1999; Pyšek *et al.*, 2007) were conducted at a single locality and do not consider the effect of site conditions, and all but one (Pyšek *et al.*, 2007) do not go beyond estimates of fruit number and size, i.e. they do not explore the germination ability of seeds produced after regeneration. Caffrey (1999) measure fruit length and width, and Tiley and Philp (1997) refer to seed from regenerated plants being viable, albeit without providing any data or evidence. Pyšek *et al.* (2007) is the only study we are aware of that explores in detail the quality of fruits and seeds produced by regeneration, in terms of fruit mass and germination characteristics.

In the present chapter the literature on regeneration in *H. mantegazzianum* is reviewed. In addition, primary data from two experiments are reported. The first experiment explored whether or not plants of *H. mantegazzianum*, in which flowering was initiated, could survive until the next year if damaged (a phenomenon previously reported and often cited, see Tiley *et al.*, 1996) and how they responded to repeated removal of tissues. The second experiment focused on the potential for fruit production of umbels removed from plants and left at a site, and considered not only fruit quality but also how it was affected by the time the umbels were removed.

As to the geographical coverage, data on species response to removal of organs come from Scotland, Ireland, Denmark, Czech Republic and Germany, and with one exception they state when and at what phenological stage the treatments were applied (Table 7.1). This allows the drawing of some general conclusions, valid for various regions, and the comparison of results from different parts of Europe.

Effect of Organ Removal on Mortality

From the management point of view, the ultimate aim is to kill the plant before it fruits. Tiley and Philp (1997) investigated the effect of cutting at different root depths and stem heights on regeneration and found that only cutting the tap root 15 cm below ground killed plants in the vegetative or reproductive stage so that none of them regenerated and produced flowers. Cutting the plants 5 cm below the soil surface or at ground level allowed regrowth of shoots from axillary buds below ground (Tiley and Philp, 1997).

No mortality was recorded among plants cut to ground level in Ireland (Caffrey, 1999), but treatment in this study was applied at an early phenological stage to plants that would have flowered that year (Table 7.1). Cutting plants at ground level at later phenological stages results in some mortality, but the pattern is fairly inconsistent among treatments (Table 7.2). Data from 2 subsequent years in the Slavkovský les region, Czech Republic, indicate that mortality may be affected by site conditions. Of ten plants treated in 2002 (one at each of 10 sites), only three set fruits, compared to 9–10 (from one site) that set fruits in 2003; interestingly, the average fruit number was the same in both years (Table 7.2).

Table 7.1. Overview of the studies on the regeneration capacity of *H. mantegazzianum* plants after removal of tissues. n.g. = not given.

Country (region)	Author	Number and type of treatments	Timing of treatments	Number of sites	Number of plants/ treatment	Characteristics assessed
Czech Republic (C Bohemia)	Pyšek *et al.* (1995)	3: Removal of umbels and/or leaves	1: Peak of flowering	1	8	Leaf area, fruit number, fruit mass
Scotland (Ayr River)	Tiley and Philp (1997)	6: Cut at different heights, incl. at ground level[1]	1: Flowering time	1	4	Mortality, weight of fruiting umbels
Germany (Lahn River)	Otte and Franke (1998)	2: Cut at two heights, incl. removal of plants at ground level[2]	2: Peak of flowering, cut off regenerated flowers	1	n.g.	Height, inflorescence size[3]
Ireland (Portmarnock and Mulkear Rivers)	Caffrey (1999)	1: Cut at ground level	2: Late March (vegetative stage of flowering plants), early May (beginning of flowering)[4]	2	15–30	Mortality, plant height, fruit number, fruit size[5]
Scotland (Ayr River)	Tiley and Philp (1997)	4: Cut at ground level; at 50 cm; umbels or leaves removed	1: Flowering time	1	4	Fruit mass, fruit number
Czech Republic (Slavkovský les region)	Pyšek *et al.* (2007)	9: Removed umbels, leaves or all above-ground organs	1: Peak of flowering	10	10	Mortality, fruit number, fruit mass, germination percentage, rate of germination
Czech Republic (Slavkovský les region)	Pyšek *et al.* (2007)	2: Cut at ground level or above rosette	3: Terminal umbel bud, peak of flowering, fruit formation	1	10	Mortality, fruit number, fruit mass, germination percentage
Czech Republic (Slavkovský les region)	This study	2: Removal of terminal umbels/flowering stems, and leaving cut parts at the site	3: Terminal umbel in receptive stigma/ post-receptive/ fruit development stage	1	4–6	Germination percentage
Czech Republic (Průhonice)	This study	2: Cut at ground level at two different times, then continuous removal of flowering shoots	First cut at early terminal bud stage/after it opened and inflorescence emerged, then continuously	1	10	Number of regenerating shoots and the date of their appearance, survival of the plants into next year

[1]Cut at six different levels from 15 cm below ground to below terminal inflorescence bud. [2]Cut at ground level and at the first node. [3]Not tested statistically, only verbally described. [4]Inferred from phenological data in the paper, not stated explicitly. [5]Fruit size (length and width) was only measured at one site.

Table 7.2. Regeneration of *H. mantegazzianum* after removal of all umbels. Treatment and phenological stage at which it was applied is indicated. Data come from Pyšek et al. (2007). Treatments 1–4 are different combinations of removal of leaves and flowers, treatments 5–10 are two treatments applied at three different times. Ten plants were subjected to the treatments, one at each of ten sites in the Slavkovský les region, Czech Republic (1–4) or ten plants at one locality (5–10) (see Table 7.1 for details of this study). Number of plants that regenerated and produced some fruit is indicated (*n*) and the values (mean ± SD) are based on those plants.

Treatment/phenological stage	*n*	Fruit number	% of control	Fruit mass	% of control	% germination	% of control
1. All flowers removed/peak of flowering	6	110.3 ± 250.6	1.1	10.6 ± 4.8	81.8	34.3 ± 35.5	40.0
2. All flowers and half leaf area removed/peak of flowering	5	52.6 ± 63.5	0.5	15.5 ± 8.9	119.7	57.0 ± 38.1	66.3
3. All flowers and all leaves removed/peak of flowering	4	32.5 ± 28.7	0.3	13.5 ± 5.9	104.3	65.7 ± 34.5	76.4
4. Cut at ground level/peak of flowering	3	268.9 ± 433.3	2.8	10.8 ± 1.8	83.3	81.3 ± 22.7	94.6
Control 1–4	10	9613.7 ± 9183.1	–	13.0 ± 3.6	–	85.9 ± 9.0	–
5. Cut at ground level/development of flowering stem	9	1631.8 ± 1247.3	16.5	14.4 ± 4.6	109.7	84.1 ± 14.6	108.3
6. Cut at ground level/peak of flowering	10	289.3 ± 395.4	2.9	9.4 ± 4.5	71.8	48.6 ± 43.1	62.6
7. Cut at ground level/formation of fruit	9	476.3 ± 611.1	4.8	11.9 ± 2.5	90.5	56.6 ± 22.7	72.9
8. Cut above rosette/development of flowering stem	9	4989.0 ± 4205.0	50.6	17.7 ± 7.1	135.0	64.0 ± 26.2	82.5
9. Cut above rosette/peak of flowering	9	652.8 ± 770.4	6.6	19.7 ± 7.4	150.2	61.3 ± 30.1	79.0
10. Cut above rosette/formation of fruit	7	407.9 ± 413.6	4.1	16.7 ± 5.3	127.5	64.0 ± 20.6	82.5
Control 5–10	10	9863.1 ± 5215.9	–	13.1 ± 2.6	–	77.6 ± 15.4	–

Flowering Plants of *Heracleum mantegazzianum* Do Not Survive into the Next Season

Although there is recent evidence that *H. mantegazzianum* is strictly monocarpic in both its invaded and native distribution ranges (Pergl *et al.*, 2006 and Chapter 6, this volume), it is reported to be polycarpic in Russia (Shumova in Tiley *et al.*, 1996). Moreover, Tiley *et al.* (1996) state that damaged flowering plants, which are not allowed to set fruit, may survive for one or more seasons.

To clarify this issue, an experiment to test the effect of removing regenerating shoots on the survival of plants was set up in the experimental garden of the Institute of Botany, Academy of Sciences of the Czech Republic, Průhonice. Ten plants growing in an experimental bed were cut at ground level shortly after the flowering stem appeared (7 June 2004; maximum height of plants was 60 cm), and another ten when the terminal bud opened and the inflorescence emerged from sheathed bracts (14–21 June 2004); then regenerating shoots were removed as they appeared during the rest of the growing season.

None of these plants survived until the following year. This, together with several years of observations at field sites in the Czech Republic, can be considered as evidence that *H. mantegazzianum* is strictly monocarpic in the invaded distribution range. As far as the native area is concerned, the same conclusion can be drawn from the estimates of age at flowering based on examining the roots of 473 plants (Pergl *et al.*, 2006). None of these plants exhibited any signs of repeated flowering.

Effect of Organ Removal on Vegetative Growth and Regeneration

The pattern of regeneration of flowering plants depends on the type of treatment. Plants cut to ground level regenerate from the stem base, while those with a stem or part of a stem left, mostly branch and produce new flowering shoots from leaf nodes between petioles and the stem (Tiley and Philp, 1997, 2000; Otte and Franke, 1998).

The only study that measured the ability of *H. mantegazzianum* to compensate for removal of leaves (Pyšek *et al.*, 1995) found that on average 12.4% of the leaf area removed at flowering time was regenerated by the end of the growing period (corresponding to 2752 cm^2/plant). In August, at the time of fruit ripening, plants that had their leaves removed in June had three times more leaf area than control plants, which at that time had lost most of their leaf area due to senescence (Pyšek *et al.*, 1995).

Plants in the experiment reported in the previous section did not survive to the next year but differed widely in the level of regeneration effort. Those cut when the flowering stem appeared produced an average of 7.6 ± 4.0 regenerating branches (mean ± SD, $n = 10$), while those cut after the terminal bud had opened produced 5.1 ± 3.6 (Fig. 7.1A). The difference was

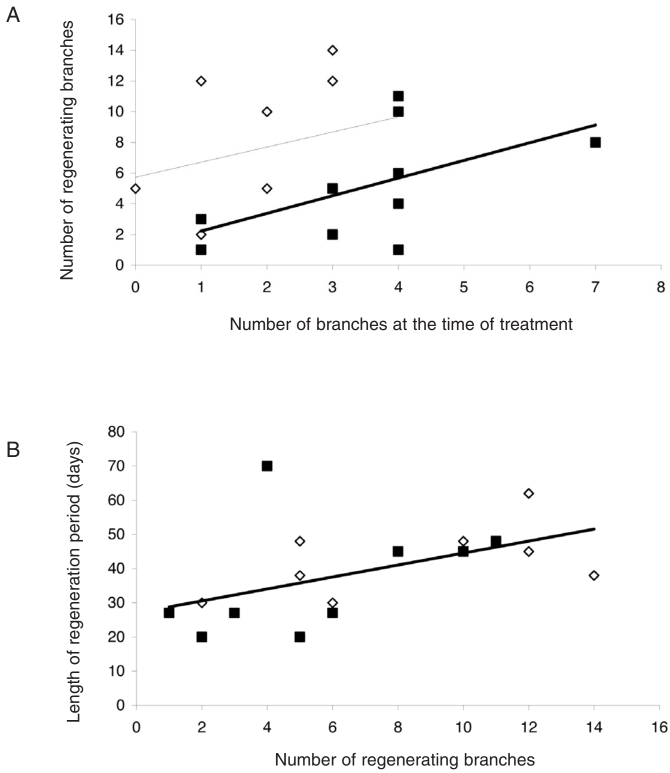

Fig. 7.1. (A) Vigorous plants are likely to regenerate better than weak plants. Ten plants were cut at ground level shortly after the flowering stem appeared (diamonds, dotted line), another ten when the terminal bud opened and the inflorescence emerged from sheathed bracts (solid square, solid line). The number of branches plants had at the time of the treatment is used as a proxy for plant vigour. Regeneration is measured as the number of branches that a plant produced under continuous branch removal. Branches were removed immediately as they developed. (B) Measures of regeneration effort are correlated. Plants that made many regeneration attempts over a long period regenerated more branches. This is indicated by a significant correlation between these measures ($r = 0.492$, $P < 0.05$). Note that the slopes are not significantly different and hence not distinguished in the plot. Symbols for the two treatments as in (A). Based on original data.

significant (t = 2.36; df = 18, P = 0.03), indicating that early treated plants have more resources that could be mobilized and allocated to regeneration. In addition, the regeneration effort in terms of the number of branches produced marginally significantly depended on plant vigour at the time of treatment (t = 2.02, df = 18, P = 0.06). Strong plants produced more regenerating branches than plants that were less vigorous at the time of tissue removal (Fig. 7.1A). The period over which regeneration occurred did not depend on the timing of the treatment (t = 0.94, df = 18, P = 0.36); plants produced new branches over 38.2 ± 14.0 days (mean ± SD, n = 20). Neither was the length of this period affected by plant vigour ($t = 0.51$, $df = 18$, $P = 0.62$). Nevertheless, both measures of regeneration effort are significantly correlated, which indicates that there might be an advantage of being large, manifested both in the period of time over which and extent to which regeneration occurs (Fig. 7.1B).

Effect of Organ Removal on Fecundity

All studies evaluated regeneration in terms of fecundity (the number of fruits produced) and in the majority umbels were removed at flowering (Tables 7.1–7.3). This in general led to marked reductions in fecundity, ranging from 2.8 to 9.9%, depending on whether or not the leaf rosette was also removed.

Data from Slavkovský les region, Czech Republic, suggest that cutting plants to ground level may be less effective in terms of reduction in fruit numbers than removing the umbels and leaving stems (Pyšek *et al.*, 2007). The former treatment yielded more than twice as much regeneration and the difference is even more marked when not only flowers but also leaves are removed (Table 7.2). Although these differences are not significant (Pyšek *et al.*, 2007), presumably because of low numbers of regenerating plants and high variation (Table 7.2), they should be taken into account when considering control measures. This result accords with the pattern of regeneration described above: plants regenerating from stem bases sometimes produce vigorous branches with umbels that are more fecund than those produced on branches, that result from the regrowth of the main stem.

Some studies combine removal of varying proportions of flowers and/or leaves (Table 7.1). Complete removal of leaves at the time of flowering always results in a reduced fruit set, but more vigorous individuals are able, after the loss of leaves, to produce more fruits than those that are weak at the time of treatment (Pyšek *et al.*, 2007).

Effect of Organ Removal on Seed Quality

Surprisingly, only recently have studies explored the germination of seed produced by regenerating plants. Because Tiley and Philp (1997) only note that such fruits are viable and do not give any figures or details on how this was assessed, the study by Pyšek *et al.* (2007) provides the first detailed information on this issue. In plants that rely exclusively on generative reproduction, not only the number of fruit produced is important but also their quality in terms of size and germination capability, which is even more crucial for population survival (Pyšek, 1997).

Removal of all leaves at the time of flowering (but not of flowers) reduces fruit mass (see also Tiley and Philp, 2000, not supported by a statistical analysis) but neither germination percentage nor the rate of germination are affected in a consistent way (Pyšek *et al.*, 2007). In general, removal of different proportions of the leaf canopy and flowers affected both final germination percentage and germination rate (assessed as the time needed for 50% of

Table 7.3. Comparison of the extent of regeneration reported in studies where plants of *H. mantegazzianum* were cut at ground level or above the basal rosette of leaves. Phenological stage at which the treatment was applied is indicated. Numbers are values recorded in particular treatments relative to control, and those reported as significant in the original studies are shown in bold. All plants, i.e. including those that did not regenerate, are included in the calculation of means. See Table 7.1 for details on particular studies.

Treatment	Application stage	Fruit number	Fruit size	Germination	Country	Source
Cut at ground level	Vegetative: early	**49.5**	**107.0**[1]		Ireland	Caffrey (1999)
Cut at ground level	Vegetative: development of flowering stem	**14.9**	98.7[2]	108.3	Czech Republic	Pyšek *et al.* (2007)
Cut at ground level	Flowering: beginning	**12.5**	**89.8**[1]		Ireland	Caffrey (1999)
Cut at ground level	Flowering: peak	9.9	63.8		Scotland	Tiley and Philp (2000)
Cut at ground level	Flowering: peak	**4.3**[3]			Scotland	Tiley and Philp (1997)
Cut at ground level	Flowering: peak	**2.8**	83.2[2]	94.6	Czech Republic	Pyšek *et al.* (2007)
Cut at ground level	Flowering: peak	**2.9**	71.8[2]	62.6	Czech Republic	Pyšek *et al.* (2007)
Cut at ground level	Fruit formation	**4.3**	81.5[2]	72.9	Czech Republic	Pyšek *et al.* (2007)
Cut above rosette	Vegetative: development of flowering stem	45.5	121.5[2]	82.5	Czech Republic	Pyšek *et al.* (2007)
Cut above rosette	Flowering: peak	16.3	48.6		Scotland	Tiley and Philp (1997)
Cut above rosette	Flowering: peak	15.8[3]			Scotland	Tiley and Philp (1997)
Cut above rosette	Flowering: peak	**6.0**	135.2[2]	79.0	Czech Republic	Pyšek *et al.* (2007)
Cut above rosette	Fruit formation	**2.9**	89.2[2]	82.5	Czech Republic	Pyšek *et al.* (2007)

[1] Expressed as fruit length.
[2] Expressed as fruit mass.
[3] Expressed as weight of fruiting umbels.

seed to germinate), but not significantly. This indicates that the reproductive characteristics of *H. mantegazzianum* are little affected by the loss of a large proportion of the leaves and flowers (Pyšek *et al.*, 2007). This accords well with previous findings that this plant is little affected by environmental conditions, which favours this species' invasion of Europe (Moravcová *et al.*, 2005 and Chapter 5, this volume; Müllerová *et al.*, 2005).

Timing of Control is Crucial

Of the studies reviewed, three explicitly consider the timing of the treatment as crucial for regeneration and manipulated this factor. However, Caffrey (1999) applied treatments at two different times, which are not explicitly related to a phenological stage; from the description of the population development in Ireland, it can be inferred that both treatments were applied early and with little effect, in terms of fruit production, if compared to other studies where the treatment was carried out later in the season (Table 7.3). Otte and Franke (1998) treated plants twice during the course of a growing season: new umbels produced by the post-treatment regrowth were also removed. Although this paper does not give quantitative assessment of regeneration, it provides important practical information – if umbels produced by regrowth were removed, no fruit was produced in this growing period. However, the results of the experiment reported in the section 'Effect of organ removal on vegetative growth and regeneration' (Fig. 7.1) indicate that the second cut is probably only effective if applied later to umbels with fruits already initiated (but no details of this are given by Otte and Franke, 1998). If the branches bearing regenerating flowering umbels are cut too early, regeneration continues (Fig. 7.1).

In spite of the different experimental designs and methods of assessment, some general conclusions can be drawn from a continental-wide comparison of studies that used the same sort of treatment, i.e. removal of all aboveground organs by cutting at ground level (Table 7.1). If regeneration is expressed as the number of fruits produced relative to the control (Fig. 7.2), there seem to be two qualitative thresholds. If plants are cut at an early vegetative stage (late March in Ireland from where the only data are available; Caffrey, 1999), fruit set is reduced by about 50%. Applying the treatment later, when the flowering stem has emerged and the flowers start to develop (phenological stages 2–3 on Fig. 7.2), results in a substantial reduction in fruit set and yields of 12.5–14.9% of the control. A further reduction is achieved if treatment is at peak flowering or beginning of fruit formation; the values of regeneration drop to 2.8–4.3% of the control for all but one data set (Fig. 7.2).

The effect of not removing leaf rosettes seems to disappear gradually as treatments are applied to phenologically more developed plants. The large difference observed in plants treated when the terminal bud forms (at this stage plants with rosettes produce three times more fruit than those with rosettes removed) is less obvious and insignificant when applied at the peak of flowering (Pyšek *et al.*, 2007) and indetectable when applied when fruits start to develop (Fig. 7.2).

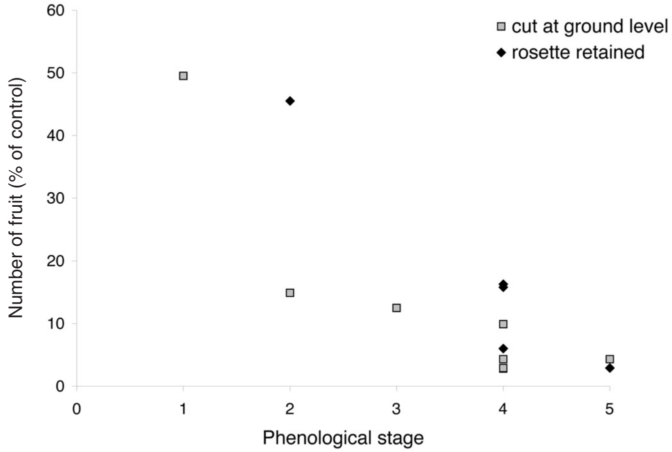

Fig. 7.2. Data from published studies allow exploration of the effect of phenological stage on the number of fruits produced by regenerating plants cut at ground level (squares) or with rosette leaves retained (diamonds). The later the cut is applied, the lower the number of fruits produced relative to the control. When both treatments were applied at the same phenological stage, diamonds positioned above squares indicate that up to stage 5 (fruit formation), leaving the basal rosette of leaves resulted in more regeneration. Phenological stages: 1: early vegetative; 2: vegetative (development of flowering stem); 3: beginning of flowering; 4: peak of flowering; 5: formation of fruits. Studies were carried out in the Czech Republic, Scotland and Ireland. See Table 7.1 for details of studies and Table 7.3 for data.

The study of Pyšek *et al.* (2007) makes it possible to assess the effect of timing of the treatment not only on the number of fruit produced by regenerating plants, but also their quality, in terms of size and germination. Mean fruit mass, although varying widely among treatments, both in absolute terms and relative to the control (Table 7.2), was not significantly affected by the treatment, and the same was true for the percentage of seed that germinated. This has important practical implications. Relative fecundity of treated plants is severely reduced by losing flower structures at some stage of development, but given the extraordinarily high number of fruits produced by plants of *H. mantegazzianum* (Perglová *et al.*, 2006 and Chapter 4, this volume) the absolute number of fruits that are available for recruitment of invading populations is very high (Table 7.2). Even plants subjected to the most effective of all treatments (the removal of all above-ground organs at ground level), which reduces the number of fruits down to 3–4% (Table 7.3), bear several hundred seeds (Table 7.2) that are viable and do not differ in size and germination characteristics from those produced by untreated plants (Pyšek *et al.*, 2007).

Removed Umbels Left at a Site Produce Viable Seeds

Two studies considered the possibility that cut-off umbels left at a site can produce viable fruits. The extent of this post-treatment fruit ripening is a warning. Pyšek *et al.* (2007) show that 85% of terminal umbels cut off at the beginning of fruit formation produce some fruits – less and of lower quality than the control (18.6% in terms of number and 43.8% in weight), but nevertheless producing an average of 1840 fruits per plant of which 24% germinated. That is, although cutting umbels off at the stage of fruit formation in the terminal umbel reduces fecundity of newly produced umbels to less than 5% of the controls (see Table 7.2), this may be ineffective if the umbels are not removed from the site. However, since there is no principle difference between treatments applied at the peak of flowering and early fruiting (Fig. 7.2; Pyšek *et al.*, 2007), the former seems to be the better management strategy, because umbels cut at flowering are less likely to give rise to fruits.

The above study, however, did not determine the effect of the time of removal on post-treatment fruit ripening in removed umbels. To explore this issue, an experiment was performed at the Slavkovský les research area in 2002 (for example, see Müllerová *et al.*, 2005 and Perglová *et al.*, Chapter 4, this volume, for details of the region). Umbels were removed at three phenological stages: (i) late stigma receptivity; (ii) post-receptive; and (iii) fruit development, with ovaries already of a flat shape but not with final fruit size. Two treatments were applied at each stage: (i) only the terminal umbel was removed and left lying on the ground until harvest; or (ii) the flowering stem was cut at ground level and left at the site; in the latter case, the umbels remained attached to a cut stem. The removed umbels were enclosed in a fine mesh to prevent loss of ripe fruits and left on the ground within the *H. mantegazzianum* stands until the end of August (fruit ripening time) to simulate mechanical control. Although many fruits decayed in the wet microclimate within the ground vegetation layer, some fruits matured. The umbels that remained attached to flowering stems produced seeds, many of which germinated (Fig. 7.3). The percentage germination was not significantly affected by the timing of the treatment and even flowers cut as early as the end of stigma receptivity produced viable seeds provided they were connected to a stem (Fig. 7.3).

The type of treatment had a significant effect. A significantly higher percentage of seeds from umbels that remained attached to a stem germinated: 9.0% (max. 20.0%) if removed at the earliest phenological stage, 19.0% (max. 30.0%) at the later stage and 15.0% (max. 50.0%) at the fruit development stage. Corresponding values for isolated umbels were 0.0%, 1.7% (max. 10.0%) and 3.3% (5.0%), respectively (Fig. 7.3). A probable explanation is that fruits attached to stems are supplied with resources for an extended period following the treatment. It is also possible that the rigid stem kept some umbels above the soil level and away from the wet conditions.

These results further emphasize that timing of treatment is critical. From a management point of view, there is a 'trade-off' between the risk of fruit developing and reduction in fecundity. This trade-off is affected by the phenology of the plant. Very early removal of umbels results in high levels of regeneration. Removal of umbels later in a season results in a marked reduction in fecundity but the removed fruits are likely to provide viable seeds. In addition, when manipulating umbels later in a season, it is difficult to avoid ripe fruits being released.

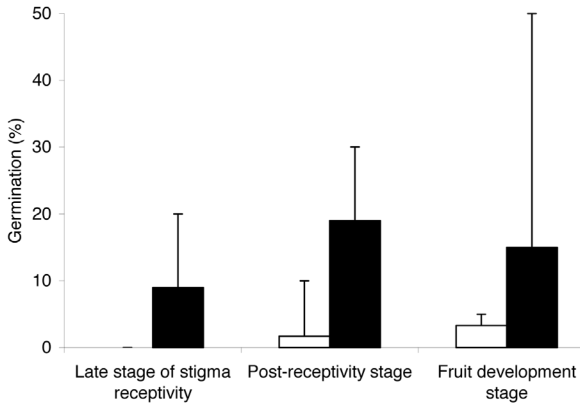

Fig. 7.3. Percentage of seeds that germinated of those maturing in umbels cut off at three phenological stages. Two treatments were adopted: either the whole flowering stem (dark columns) or only umbels (light columns) were cut and left at the site. Deletion tests revealed a significant difference between treatments ($F = 5.35$, $df = 1,12$, $P = 0.039$) but no effect of the timing of removal. Umbels attached to the cut-off stems produced seeds that germinated better than that those produced by cut-off umbels. Based on original data.

Conclusions: Guidelines for Control

Plants of *H. mantegazzianum* have a high regeneration capacity, which allows them to survive some control measures. Comparison of previous studies on this topic (Pyšek *et al.*, 1995, 2007; Tiley and Philp, 1997; Otte and Franke, 1998; Caffrey, 1999; Nielsen *et al.*, 2005) and the results of the experiments reported here identify certain principles that should be considered when designing a strategy for mechanical control.

1. The only treatment that immediately kills plants of *H. mantegazzianum* is cutting the tap root 15 cm below ground (Tiley and Philp, 1997). Any treatment that does not kill the plants, such as cutting at ground level, always results in a proportion of treated plants regenerating (Pyšek *et al.*, 1995, 2007; Caffrey, 1999).

2. Whatever the strategy for mechanical control, the life stage of the plants targeted for control is critical. Above-ground cutting of the vegetative (rosette) stage will not kill plants, but extends their life span by postponing the time of flowering. Vegetative plants can only be killed by cutting the root. In the case of flowering plants, it is not necessary to cut the root below the soil surface as once flowering is initiated these plants will not survive until the next year. Therefore, the best strategy is to kill plants at the rosette stage by cutting their roots and preventing those at the flowering stage from producing fruits. Alternatively, if a long-term programme is feasible, only flowering plants need to be targeted until the population is depleted (but see Pergl *et al.*, 2007 and Chapter 6, this volume, for data on life span).

3. Timing of the treatment is crucial. If carried out too early, plants will regenerate to a high level. Removal of umbels is effective if carried out at the peak of flowering or at the beginning of fruit formation. Subsequent cutting of regenerated flowering umbels, as they emerge, prevents plants from producing fruit. Removal of leaf rosette does not increase the effect of this treatment; there is some evidence that cutting flowering plants at ground level is less efficient than removing flowers and leaves from the stems (Pyšek *et al.*, 2007).

4. Umbels must be removed from the site. Even umbels cut at late flowering or early fruiting are able to produce viable seeds and thus should be collected and destroyed (burnt). Cutting whole flowering stems and leaving them at a site is not recommended.

5. Because of the extraordinary fecundity of *H. mantegazzianum* (see Perglová *et al.*, 2006 and Chapter 4, this volume), even a severe reduction in the number of fruits produced by regenerating plants, relative to the control, still results in large quantities of fruit in absolute numbers. More importantly, these seeds are generally of a good quality, in terms of size and viability (Pyšek *et al.*, 2007).

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