Regeneration in *Heracleum mantegazzianum* – response to removal of vegetative and generative parts

Regenerace *Heracleum mantegazzianum* po odstranění vegetativních a generativních částí

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Response of *Heracleum mantegazzianum* to removal of leaves and flowers was studied in the Křivoklát Protected Landscape Area, central Bohemia, Czech Republic. In June 1993, i.e. at the peak of flowering period, plants were subjected to the following treatments: A. removal of all umbels and leaves, B. removal of all umbels, C. removal of the terminal umbel, and D. control. Regeneration was assessed at the end of August. By that time, the plants defoliated in June (treatment A) compensated for 12.4 % of the leaf area, and the seed production of plants of A and B treatments reached on average 5.75 and 2.88 %, respectively, of the number of flowers present in June. Removal of the terminal umbel did not decrease the total fecundity. Regeneration in plants of the treatments A and B occurred through (a) new branches on the plant's main stem, and/or (b) new shoots from the stem base. The plants subjected both to defoliation and umbel removal (treatment A) produced more new shoots from the stem base than plants that were only deflorated (treatment B) but their fruitlet (= one-seed portion of the fruit) weight was significantly reduced. Frequency distributions of fruitlet weights in all treatments were bimodal due to a certain portion of very small fruitlets produced. Stem branches had a high proportion of these small fruitlets but, when large fruitlets were analysed separately, those coming from regenerating branches were heavier than those produced on control plants.

K e y w o r d s : *Heracleum mantegazzianum*, compensatory growth, leaf area removal, flower removal, fecundity, seed size

Introduction

Some plants can compensate for the effect of tissue removal (Belsky 1986, Verkaar 1988) but the extent varies between individual plants and depends on (1) the extent of the damage, (2) its timing, and (3) conditions under which the plant is growing (Crawley 1983). The effects the timing of the removal of both vegetative and generative parts can have on seed production have been largely documented (see Crawley 1983 and references therein) and the most serious impact may be expected when developed flowers are removed (Begon et al. 1986).

Since one of the objectives of the present study was to contribute to the knowledge necessary for successful eradication of *Heracleum mantegazzianum*, the timing of the treatment applied in the present study was directed at making these treatments as effective as possible in terms of fecundity reduction. Hence the removal was carried out at the peak of the flowering period.

The present study was aimed at quantifying the regeneration potential of *Heracleum mantegazzianum* in terms of leaf area and seed production and addresses the question whether the removal of plant parts carried out at the time of maximum plant development can be, in terms of eradication, as effective as the cutting the whole plant.

Material and methods

Study site

The study site was located in the Křivoklátsko Landscape Protected Area, Czech Republic, 7 km SE from the town of Rakovník (latitude 50°06', longitude 13°51') at the altitude of 420 m a. s. l. The mean annual temperature is 6.9 °C, precipitation 522 mm (50 years average, Lány meteorological station). The field work was conducted in the pheasantry Amálie which is closed to the public and seriously infested by *Heracleum mantegazzianum* plants (Kolbek et al. 1994). The study site was a moist meadow adjacent to oak forest on one side and to willow scrub on the other. The community consisted of the following species: *Urtica dioica* L., *Cirsium arvense* (L.) Scop., *Lathyrus pratensis* L., *Galium aparine* L., *Poa trivialis* L., *Rubus idaeus* L., *Salix fragilis* L.

Study species

Heracleum mantegazzianum Somm. et Levier (*Apiaceae*) is a monocarpic perennial with a thick taproot, stout stem reaching up to 5.5 m height, large pinnate leaves (up to 3 m) and usually 7–10 umbels bearing oval-elliptical, broadly winged fruits 9–11 mm in size (Tutin et al. 1968). Its seed production per plant may reach up to several tens of thousands (Neiland 1986, Brondegaard 1990, but see Table 5). In the study area, the species germinates in early spring (April), flowering period starts in May, fruits appear in July and are being shed from September onwards.

The species was introduced into the Czech Republic, as to other European countries (Lundström 1984, Wright 1984) in the 19th century from the western Caucasus (Pyšek 1991, 1994, Pyšek et Pyšek 1994). The species forms extensive monospecific stands and may cause serious problems; at present, it represents one of the most noxious alien weeds in Europe (Williamson et Forbes 1982, Lundström 1984, Wright 1984, Bingham 1990, Dodd et al. 1994, Tiley et Philp 1994). Replacement of native vegetation (Kolbek et al. 1994, Pyšek et Pyšek 1995) and injuries to human skin, caused by juices photosensitive in sunlight (Tutin et al. 1968, Drever and Hunter 1970) are the main reasons for efforts to eradicate the species from infested areas (de Waal et al. 1994).

Being the largest central European forb, part of the competitive superiority of *Heracleum* over other plants is ascribed to its size and ability to shade the surrounding vegetation with huge ground leaves. Large seed set with dispersal by water, wind, animals and human-related factors (Jehlík et Lhotská 1970, Pyšek and Prach 1993) also contributes to its rapid spread into various vegetation types.

Sampling and data analysis

Eight blocks of 4 plants each were selected in the study site on 24 June, 1993, at the peak of the flowering period. The density of *Heracleum* plants was similar in each block. The plants were marked using plastic tags and their height (246.4 ± 6.1 cm, mean ± S.E., n = 32) and basal diameter (5.86 ± 0.20 cm) were recorded. The diameter of all umbels

was recorded for each plant. The following treatments were imposed on the plants within each block: A. removal all of umbels and leaves, B. removal of all umbels, C. removal of the terminal umbel, D. control (no organs removed). The position of plants subjected to different treatments was randomized within each block. The umbels and leaves were cut off at the upper part of flowering stalks and petioles, respectively.

Thirty umbels were sampled from non-experimental plants present in the site to make the non-destructive estimate of fecundity possible. The umbels were selected in order to cover the range of sizes of umbels occurring on experimental plants. Flowers were counted and the following regression between the number of flowers and umbel diameter was used to estimate the number of flowers in experimental plants:

NUMBER OF FLOWERS = 101.76 DIAMETER + 205.92, $r = 0.90$, $P<0.0001$, $R^2 = 80.75$ %. The non-destructive estimate was also used for plants that had their flowers removed in order to be comparable to those whose flower heads were allowed to grow.

Leaves removed from plants were oven-dried at 80°C for 48 hrs and their dry weights recorded. Leaf area was estimated on the basis of dry leaf weight (Rychnovská et al. 1987).

On 18 August, 1993, umbel diameters were recorded for control plants and for those with only the terminal umbel removed. In plants completely deflorated in June, the number of newly produced branches on the main stem and that of new shoots resprouting from the stem base were recorded and regenerated umbels were harvested. In these umbels, seeds were counted. Thirty umbels were sampled from control plants following the same criteria as for the June sampling to obtain the regression for estimating seed production in control and terminal-cut plants:

NUMBER OF SEED = exp (5.226 +0.0523 DIAMETER), $r=0.92$, $P<0.0001$, $R^2= 84.95$ %.

Leaves were harvested from all plants and leaf area estimated corresponding to the June sample.

Fruit samples were taken from the following positions on plants: (1) terminal umbels of control plants, (2) lateral umbels of control plants, (3) lateral umbels of plants with the terminal umbel previously removed, (4) regeneration from new branches on the main stem, and (5) regeneration from new stems from the stem base. One-seed portion of the fruit (i.e. monachenium or mericarp), further termed as fruitlet, was considered. One hundred fruitlets were taken randomly from each group and weighed.

Regeneration rate was expressed as follows: (a) for leaf area as a ratio between the leaf area obtained by August sample and leaf area removed in June from the same plant; (b) for fecundity as a ratio between the number of seeds recorded in August and number of flowers estimated for the respective plant in June.

Data were analysed using standard methods (Sokal and Rohlf 1981).

Results

Effect of treatment on leaf area and seed production

The number of umbels per plant and number of seeds per umbel were both significantly reduced by August regardless of whether flowers and leaves had been removed in June or flowers only. This resulted in a dramatic reduction in the number of seeds which was, on average, 95.9 % in plants both defoliated and deflorated and 95.0 % in those deflorated only (Table 1, 2).

Table 1. Vegetative and reproductive characteristics of *Heracleum mantegazzianum* plants sampled in August given for the treatments applied in June. Means ± S.E. (n = 8) are shown for the August sample. Means followed by the same letters rowwise were not significantly different in multiple range analysis (Tukey test, $P<0.05$).

	Flowers and leaves removed	Flowers removed	Terminal umbel removed	Control
Number of seeds	671.7 ± 253.7a	805.1 ± 500.4a	17870.0 ±4468.1b	16139.9 ±2617.2b
Number of umbels	3.62 ± 1.25a	4.37 ± 0.84a	12.75 ± 3.91b	7.87 ± 0.71ab
Number of seeds per umbel	222.6 ± 83.5a	152.5 ± 98.7a	1464.9 ± 179.8b	1964.9 ± 231.7b
Leaf area (cm^2)	2752.3 ±1870.7a	17839.1 ±5601.0b	865.3 ± 382.9a	837.9 ± 470.6a
Number of regenerating shoots[1]	0.87 ± 0.29a	0.12 ± 0.12b	–	–
Number of regenerating branches	0.37 ± 0.26a	0.50 ± 0.33a	–	–

[1]new shoots resprouting from the stem base

Table 2. Summary of ANOVAs showing the effects of treatments (A – flowers and leaves removed, B – flowers removed, C – terminal umbel removed, D – control) on *Heracleum mantegazzianum* characteristics. F-value and significance level (P) are given. LN – log-transformed data used to achieve normality.

Characteristic	Treatments compared	d.f.	F-value	P
Number of seeds LN	A,B,C,D	3,28	12.94	<0.0001
Number of umbels LN	A,B,C,D	3,28	5.82	0.0032
Number of seeds/umbel	A,B,C,D	3,28	31.92	<0.0001
Leaf area LN	A,B,C,D	3,28	7.82	0.0029
Number of new shoots[1]	A,B	1,14	5.47	0.034
Number of new branches	A,B	1,14	0.09	0.773

[1]new shoots resprouting from the stem base

In August, the leaf area of plants with only flowers removed was an order of magnitude greater than that of those affected by other treatments and this difference was highly significant (Table 2). These plants still had 68.1 % of the maximum leaf area achieved by *Heracleum* at the stage of the full development of vegetative organs, i.e. in June (mean ± S.E. 26,207.0 ± 5,058.1, n = 8). By this time, both the controls and plants with only terminal umbels removed had already lost a significant proportion of their leaf area due to senescence and this leaf area was also smaller (though not significantly) than that produced from June to August by plants that had had their leaves removed in June (Table 1).

Regeneration, of both vegetative and generative organs, in plants completely deflorated at the peak of the flowering period occurred through the production of (a) new branches on the plant's main stem, and/or (b) new shoots from the stem base. The number of regenerating shoots was higher in plants with both flowers and leaves removed than in those with only flowers cut. Both treatments did not differ in the number of regenerating branches produced (Table 1, 2).

The removal of the terminal umbel had no effect on the total number of seeds produced if compared to control plants (Table 1). Plants with the terminal umbel removed had less seeds per umbel (Table 1) but tended to produce more umbels (mean + S.D. 12.8 ± 11.1) than control plants (7.9 ± 2.0) and showed much higher variation in the umbel number (the coefficient of variation was 86.9 % compared to 25.7 % in the control).

Table 3. Summary of allometric relationships between the characteristics investigated and some measures of plant size. Data were pooled for plants with umbels completely removed in June, and also the data from terminal removal treatment were pooled with the controls as there were no significant differences in response to the treatment. Values of the correlation coefficient (n = 16) and its significance level are given (* P<0.05, ** P<0.01, *** P<0.001, NS – not significant). The relationships fitted better by the exponential model Y=exp(a+bX) are indicated by E. Leaf area is not included as by the August sample, the degree of senescence might have varied among the plants. Regeneration ratio is a ratio between values obtained by August sample and those removed in June (see Fig. 1).

	Control plants		Complete umbel removal	
	Diameter	Height	Diameter	Height
Number of seed	0.78 ***	0.61 * E	0.01 NS	0.29 NS
Number of umbels	0.81 *** E	0.52 * E	–0.31 NS	–0.13 NS
Number of seeds per umbel	0.21 NS	0.25 NS	–0.38 NS	–0.18 NS
Number of regenerating shoots[1]	–	–	–0.33 NS	–0.18 NS
Number of regenerating branches	–	–	0.68 **	0.41 NS
Leaf area regeneration ratio	–	–	–0.07 NS	–0.05 NS
Fecundity regeneration ratio	–	–	0.14 NS	0.40 NS

[1]new shoots resprouting from the stem base

Effect of plant size on regeneration characteristics

The number of umbels and total number of seeds produced by a plant were highly significantly correlated with its basal diameter in both the control and terminal-umbel--only-cut treatments. Both characteristics were also correlated with plant height, though less significantly (Table 3). In plants with complete flower removal, no significant relationships between these characteristics and either of both measures of plant size were found. However, the post-cut production of regenerating branches increased significantly with plant diameter ($r = 0.68$, $P<0.01$).

The relative measures of regeneration (leaf area and fecundity regeneration ratios, see Methods for definition) were correlated with neither plant diameter nor its height (Table 3).

Level of regeneration

The plants defoliated at the flowering time produced by August 12.4 ± 8.7 % (mean ± S.E.) of their June leaf area (with the maximum value recorded 72.2 %).

Regeneration rate with respect to seed production was 2.9 ± 1.3 % for those plants with both flowers and leaves removed in June; the respective figure for the plants deflorated only was 5.8 ± 5.1 %. There was an extremely high variation in the regeneration rate among individual plants (Fig. 1). Two plants of the former group and three of the latter did not produce any regenerating seeds and, with one exception in the former group (41.4 %) the regeneration rate of any particular plant did not exceed 11.0 %.

Effect of treatment on fruitlet size

There was a highly significant effect of the part of the plant in which a fruitlet was produced on its weight as revealed by ANOVA ($F_{4,495} = 13.81$, $P<0.0001$). The fruitlets produced on shoots from the stem base, having originated as a response to removal, were lighter than the others. Regeneration from new branches on the main stem, however, produced the fruitlets of the same weight as controls. There was no difference in the weight of fruitlets

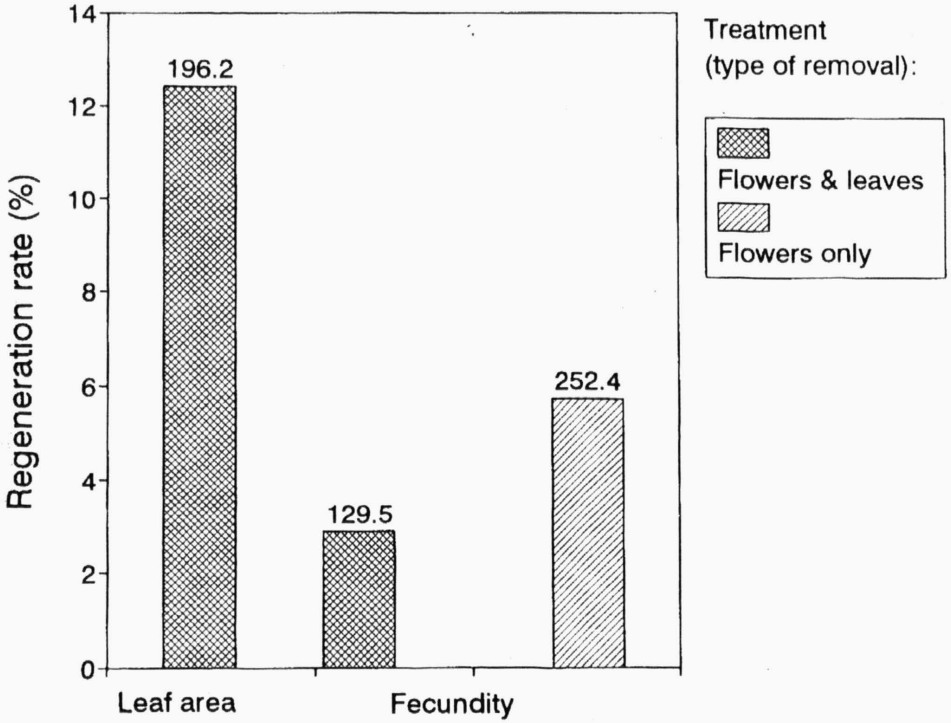

Fig. 1. Regeneration in *Heracleum mantegazzianum* assessed for vegetative and reproductive characteristics. Leaf area regeneration rate was expressed as a ratio between the leaf area obtained by August sample and leaf area removed in June from the same plants. For fecundity, regeneration rate stands for the ratio between the number of seeds recorded in August and number of flowers estimated for the respective plants in June. Coefficient of variation (%) is given on top of each bar. Note that the figures for leaf area and fecundity cannot be directly compared as (a) each female flower is producing two seeds, and (b) male flowers do not produce any, so that comparing the number of flowers and seeds can only be used as a relative measure.

Table 4. Differences in the weight of fruitlets (in mg) with respect to the position on a plant. Means ± S.E. are given; those not significantly different in multiple range comparison (Tukey test, $P<0.05$) are bearing the same letter columnwise. Only the fruitlets bigger than 8 mg (number of which is given as N) are shown in the second column.

	Full set (N=100)	Fruitlets > 8 mg	N
Control plants – terminal	14.80±0.48a	15.66±0.37a	87
Control plants – lateral	13.90±0.49a	15.87±0.27a	83
Lateral after terminal cut	13.99±0.41a	15.14±0.26a	89
Branch regeneration	14.82±0.57a	17.50±0.39b	76
Stem regeneration[1]	10.48±0.32b	11.56±0.22c	85

[1]new shoots resprouting from the stem base

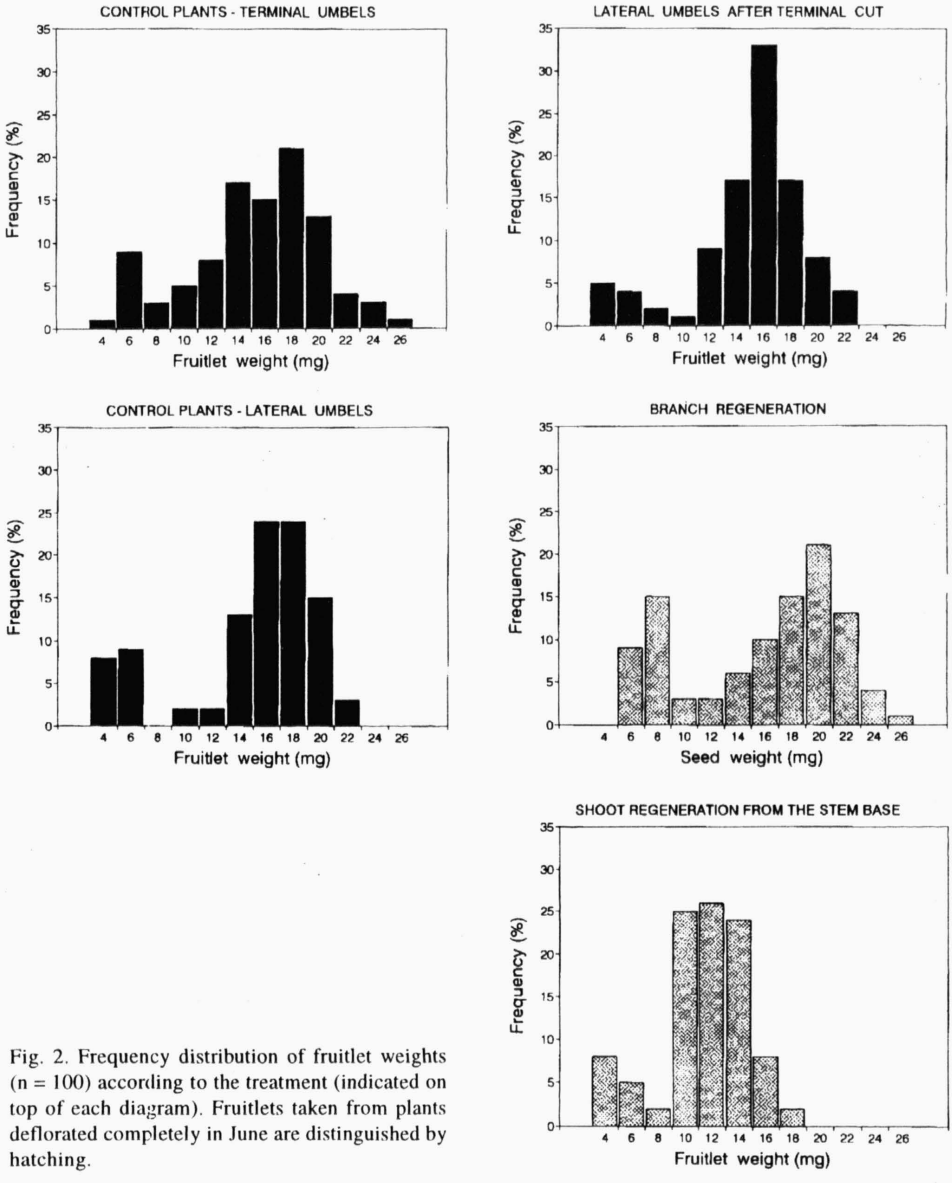

Fig. 2. Frequency distribution of fruitlet weights (n = 100) according to the treatment (indicated on top of each diagram). Fruitlets taken from plants deflorated completely in June are distinguished by hatching.

produced in lateral and terminal umbels of control plants and also the removal of the terminal umbel did not affect the size of fruitlets produced on lateral umbels after then (Table 4).

Frequency distributions of fruitlet weight were clearly bimodal reflecting the fact that fruits of *Heracleum* derived from one flower are often asymmetric in terms of size, producing one bigger and one smaller achene (Fig. 2). The visual inspection of frequency distributions indicates that the small fruitlets are concentrated in size classes up to 8 mg.

The proportion of small fruitlets was highest in seeds originating from branch regeneration (24 %, see Table 4). When the larger fruitlets (> 8 mg) were analysed separately, the differences in their weight were also significant (ANOVA, $F_{4,415} = 47.95$, $P<0.0001$) and, moreover, the fruitlets produced on regenerating branches were heavier than all the others (by 10.3 and 11.7 % than those coming from lateral and terminal umbels of control plants, respectively, and by 51.4 % than fruitlets from shoot regeneration from the stem base, Table 4).

Discussion

Pattern of compensatory growth

The effects of removal of either vegetative and/or generative organs from plants have been mostly analysed with respect to herbivory, be it addressed in studies on natural level of herbivory or in those involving experimental tissue removal (Crawley 1983, Dirzo 1985, Pimentel 1988).

In the present study, the pure defloration (with assimilation apparatus allowed to grow) yielded a high variation in seed size but these plants produced the heaviest fruitlets found in the experiment and their regrowth was almost exclusively on the main stem. On the other hand, where the leaves were also removed, regeneration occurred rather by new shoots from the stem base and tended to follow a pattern as if the plants were cut at the ground level (though some regeneration also occurred on the main stem); these shoots were only able to produce remarkably light fruitlets. Removal of flowers also delayed senescence, in terms of leaf die back: at the time control plants had only about 3 % of their leaf area green, the plants with flowers removed still had 68.1 % green.

These results correspond to the major responses found in some herbivory studies (see Crawley for review and discussion): increase in seed size after defloration (Maun et Cavers 1971b in *Rumex crispus*, but see Hendrix 1979), decrease following defoliation (Maun et Cavers 1971a, Lee et Bazzaz 1980 in *Abutilon theophrasti*, Bentley et al. 1980 in *Rumex crispus*), delayed flowering (Collins et Aitken 1970 in *Trifolium subterraneum*, Pyšek 1992 in *Senecio ovatus*) which may lead to reduced seed production (Crawley 1983), regeneration by regrowth shoots (Cameron 1935, and Zahirul Islam 1981 cited by Crawley 1983 in *Senecio jacobaea*).

The present study did not find any difference in fecundity (a) between *Heracleum* plants subjected to both defloration and defoliation and those deflorated only, and (b) between those with the terminal umbel cut and the control. Although the complete removal of both flower heads and leaves may lead to zero seed production in that year (Cameron 1935, Crawley 1983), *Heracleum* plants produced the same number of seed as when the leaves were allowed to grow and the difference between both treatments was manifested in terms of mean fruitlet weight. However, small fruitlet (and consequently small seed) need not necessarily mean competitive disadvantage as in these, dispersal or escape from predation may be favoured (Crawley 1983, Morse et Schmitt 1985). Indeed, Bentley et al.(1980) have found that smaller seeds in *Rumex crispus*, the reduction in size of which was due to defoliation, did not show any decrease in germination rate.

Removal of the terminal umbel (which contributed 37.8 ± 2.7 % to the total number of seeds in control plants) was compensated by the increase in the number of lateral umbels and the seed size did not differ from the control either (but see Hendrix 1979 who found,

Table 5. Summary of available data on fecundity in *Heracleum mantegazzianum*.

Source	Number of seeds	Country
Williamson et Forbes (1982)	>5000	UK
Warde (1985)	14000–29000	Ireland
Brondegaard (1990)	max. 27000	Germany
Caffrey (unpubl. data)	max. 107984	Ireland
Pyšek et al. (this study)	aver. 16139, max. 25894	Czech Republic

in *Pastinaca sativa*, compensation via increased number of seed on lateral umbels producing smaller seeds).

One of the ways the compensatory growth may work is by the mobilization of stored reserves to form regrowth tissues (Crawley 1983). Plants of the same species from different habitats may show compensation and regrowth to different degrees (Crawley 1983) but in *Heracleum*, there is usually at least some regeneration (even plants cut at the time of full seed maturity are able to produce a tiny umbel of flowers at the stem base – P. Pyšek, unpublished data). Comparison with other cutting experiments (J. Caffrey, personal communication) indicates that, as in other species (Begon et al. 1986), the timing of tissue removal plays a decisive role in *Heracleum*.

Possible consequences of reduction in fecundity

Although the data on seed production in *Heracleum* vary considerably (Table 5), it may be concluded that despite high variability between plants in the same site and between different sites in the same region (J. Caffrey, unpublished data) the fecundity is sufficient to ensure continuous input of seeds into the soil seed bank in infested sites. Even if losses in the seed bank and due to seedling mortality are taken into account (the latter is reported to vary between 77.0 and 88.8 %, see Warde 1985, and J. Caffrey, unpublished data), 5 % regeneration in terms of fecundity (which represents input of 671.7–805.1 seeds left per plant in the present study, see Table 1) is still enough to keep the site heavily infested for years.

The efficient control of *Heracleum* in any infested site would thus require (a) complete prevention of seed input, and (b) control of the site in the years following the treatment. Unfortunately, no data on the longevity of seeds in the seed bank are available which would indicate the approximate time necessary for complete eradication of the species from a given site.

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Souhrn

V CHKO Křivoklátsko byla sledována regenerační schopnost druhu *Heracleum mantegazzianum*. V červnu 1993, na vrcholu květní fenofáze, byly odstraněny všechny okolíky a listy (zásah A), všechny okolíky (B), pouze terminální okolík (C); poslední skupina rostlin byla ponechána jako kontrolní (D). Na konci srpna byla hodnocena regenerace. V té době rostliny, jimž byly odstraněny v červnu listy, znovu vytvořily 12.4 %

funkční listové plochy; produkce semen u rostlin s odstraněnými okolíky dosáhla 2.88–5.75 % počtu v červnu přítomných květů. K regeneraci docházelo prostřednictvím (a) nových větví vyrostlých na hlavní lodyze a/ nebo (b) nových prýtů vyrůstající z báze hlavní lodyhy. Semena vytvořená na regenerujících větvích hlavní lodyhy byla větší než semena na kontrolních rostlinách.

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Ještě před ukončením prvního vydání souborného díla Flora Europaea (Vol. 1–5) vznikla potřeba dalšího, přepracovaného vydání. Bylo třeba provést opravy nejrůznějšího rázu, akceptovat nejnovější taxonomické i nomenklatorické poznatky, doplnit dílo o nově popsané druhy a subspecie a upřesnit rozšíření mnoha druhů v Evropě.

Pro nové vydání bylo třeba vytvořit i nové organizační předpoklady, protože řada botaniků dřívějšího vydavatelského komitétu zemřela nebo odešla do důchodu. Předsedou nového komitétu se stal N. A. Burges a jeho sekretářem J. R. Edmonton, dalšími členy jsou J. R. Akeroyd, F. A. Bisby, A. O. Chater, V. H. Heywood, S. L. Lury, D. M. Moore a S. M. Walters. M. E. Newton byl jmenován „Flora Europaea Research Officer". Sekretariát je v Department of Botany at Liverpool Museum, jež je součástí National Museums and Galleries on Merseyside. Revizí prvního dílu byl pověřen J. R. Akeroyd.

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Přestože jde o knihu vysoké odborné úrovně, dovoluji si upozornit na některé drobnosti.

V kapitole „List of standard floras" by bylo vhodné doplnit díla: Květena České republiky (již 4 svazky) a Flóra Slovenska (doposud 8 svazků). Dostálova dvoudílná Nová květena z roku 1989 je uzavřený celek, který nebude pokračovat dalšími svazky jak je zde naznačeno.

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