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Population Dynamics of *Heracleum mantegazzianum*

JAN PERGL,[1] JÖRG HÜLS,[2] IRENA PERGLOVÁ,[1] R. LUTZ ECKSTEIN,[2] PETR PYŠEK[1,3] AND ANNETTE OTTE[2]

[1]Institute of Botany of the Academy of Sciences of the Czech Republic, Průhonice, Czech Republic; [2]Justus-Liebig-University Giessen, Giessen, Germany; [3]Charles University, Praha, Czech Republic

> *Around every river and canal their power is growing*
>
> (Genesis, 1971)

Introduction

The aim of this chapter is to summarize existing knowledge on the dynamics of populations of *Heracleum mantegazzianum* Sommier & Levier in regions where it is an invasive species, with particular emphasis on survival, growth and reproduction. The data come from populations studied in the Czech Republic and Germany. Unfortunately, corresponding information on the population biology of *H. mantegazzianum* in its native distribution range in the Western Greater Caucasus is still incomplete, because population studies require long-term observations in a wide range of habitats and environmental conditions. Nevertheless, there is some information on the population biology of *H. mantegazzianum* in its native range, which can be compared with corresponding data from the invaded range, such as population age structure, which is a crucial characteristic of monocarpic plants (Pergl *et al.*, 2006).

Because population dynamics involve a variety of processes, this chapter is presented in sections dealing with seedling dynamics, relative growth rate of seedlings, population stage structure and mortality, analysis of life tables and effects of stand structure on population dynamics. Implications of these results for the long-term population dynamics are outlined. Together with other biological characteristics, which affect the population dynamics of *H. mantegazzianum* and are dealt with elsewhere (seed bank – Moravcová *et al.*, Chapter 5, this volume; Krinke *et al.*, 2005; reproductive biology – Moravcová *et al.*, 2005 and Chapter 5, this volume; timing of flowering – Perglová *et al.*, 2006 and Chapter 4, this volume), this provides the most complete picture of the population dynamics of this species. Knowledge of the population biology of *H. mantegazzianum* will: (i) provide insights into spread

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dynamics at various scales based on field data; (ii) help to determine what makes this species such a successful invader; and (iii) enable us to analyse the complete life cycle of this invasive herb with the aim of finding possible weak events in its life cycle that can be targeted for weed control. In addition, data on population dynamics can be used in models with the aim of making both generalized and site-specific predictions (see Nehrbass and Winkler, Chapter 18, this volume; Nehrbass *et al*., 2006).

Population studies in the Czech Republic were conducted in the western part of the country, in the Slavkovský les Protected Landscape Area (see Moravcová *et al*., 2005; Müllerová *et al*., 2005 for characteristics of the region, and Perglová *et al*., Chapter 4, this volume, for overview of the localities). *Heracleum mantegazzianum* was introduced to this area in 1862 as an ornamental species. The invasive behaviour of the species accelerated when the majority of the inhabitants of this area were moved out after World War II. This led to radical changes in land use, with considerable increase in the proportion of unmanaged habitats. Historical dynamics of the invasion of this region by *H. mantegazzianum* were reconstructed based on a series of aerial photographs covering a period of 50 years from World War II (start of the invasion at the studied sites) up to the present (Müllerová *et al*., 2005). The history of the *H. mantegazzianum* invasion of the Czech Republic is described in detail elsewhere (Pyšek, 1991; Pyšek and Prach, 1993; Pyšek and Pyšek, 1995; Pyšek *et al*., 1998; see Pyšek *et al*., Chapter 3, this volume).

In Germany, population studies were conducted on paired open and dense stands of *H. mantegazzianum* in five populations (Hüls, 2005). These were situated at an altitude of 155–335 m in the low mountainous region of Hesse, central western Germany, which is characterized by a temperate sub-oceanic climate with annual average temperatures of 7.6–9.0°C and annual precipitation of 609–767 mm (for details see Hüls, 2005).

Seedling Dynamics

The seedling stage is the most vulnerable in the life cycle of a plant. Young seedlings suffer a high mortality due to attack by herbivores and pathogens, as well as from intra- and interspecific competition or unsuitable environmental conditions such as frost or drought (Harper, 1977; Crawley, 1997). Because reproduction in *H. mantegazzianum* is exclusively by seed (see Perglová *et al*., Chapter 4 and Pyšek *et al*., Chapter 7, this volume), seedlings represent the only means of colonization of new sites and subsequent population recruitment. Data on seedling dynamics are available for a wide range of sites, including dominant stands of *H. mantegazzianum*, with only a few ruderal species and a high proportion of bare ground in spring at the time of seedling emergence, to those covered with grass and with a sparse occurrence of *H. mantegazzianum*. These sites are the same as those at which the data on reproduction ecology and seed bank were collected (see Perglová *et al*., Chapter 4 and Moravcová *et al*., Chapter 5).

High percentages of the seeds of *H. mantegazzianum* germinate; Moravcová *et al.* (2005) give an average of 91% for seed collected at a range of study sites in the Slavkovský les region and germinated in laboratory conditions. Prior to germination, the seeds need cold and wet stratification to break the morphophysiological dormancy. Under experimental conditions (Moravcová *et al.*, 2005 and Chapter 5, this volume) this process takes about 2 months, but once dormancy is broken seeds germinate in conditions suitable for cold stratification. Under natural conditions at the study region the cold period lasts longer than the minimum of 2 months needed for stratification. Thus all non-dormant seeds are ready to germinate in early spring (see Moravcová *et al.*, Chapter 5, this volume; Krinke *et al.*, 2005). A study of the dynamics of seedling emergence conducted in 2002–2004 (J. Pergl *et al.*, unpublished) shows that massive germination occurred a few days after the snow melted. In 2002 the peak density of seedlings occurred during the first census on 5 April at six out of 11 localities. In 2003, some seedlings already had true leaves on 20 April, despite the presence of scarce snow cover; at the same time, the rosettes of previous year(s)' plants reached about 10 cm in diameter. The peak number of seedlings occurred about 10 days after the last snowfall (30 April 2003). A week later, the ground was overgrown by leaf rosettes of the older *H. mantegazzianum* individuals, which shaded out the seedlings of this and other plant species. No new seedlings with cotyledon leaves were observed after May. This accords well with the results of seed bank studies and germination experiments (see Moravcová *et al.*, Chapter 5, this volume; Krinke *et al.*, 2005), which show that the seed bank is depleted in early spring and germination under higher temperatures later in the season does not occur. The minimum morning ground temperatures recorded at the nearest meteorological station (Mariánské Lázně; Czech Hydrometeorological Institute) in 2002 reveal that in this year, the massive germination occurred 5 days before the temperatures increased and remained above freezing. A similar pattern is reported for the milder oceanic climate of the British Isles, where seedlings start to emerge from January to March (Tiley *et al.*, 1996).

Autumn emergence of seedlings was not observed in the study sites in the western part of the Czech Republic, although it is reported from Poland (Cwiklinski, 1973, cited in Tiley *et al.*, 1996), Ireland (Caffrey, 1999) and Scotland (Tiley and Philp, 1994). Nevertheless, the small proportion of non-dormant seed in the seed bank in autumn at some localities (Krinke *et al.*, 2005) indicates that germination in autumn is possible under suitable climatic conditions.

To estimate the dynamics of seedling emergence and their survival at each site, the number of seedlings was counted at one permanent plot in three consecutive seasons in early spring (Fig. 6.1). Five censuses were made in 2002, and three in 2003 and 2004. The maximum density of 3700 seedlings/m^2 was found in one plot in 2004. The mean values for the sites were (mean ± SD per m^2) 671.8 ± 439.2 (2002), 734.3 ± 441.7 (2003) and 1613.9 ± 1322.1 (2004). The seedling densities were not related to characteristics of the maternal population, such as total or adult density or to those characteristics of the seed bank, such as number of total, live or non-dormant seeds

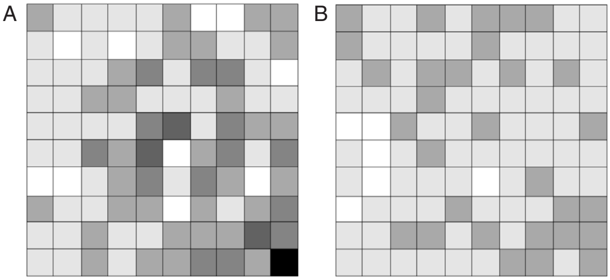

Fig. 6.1. Spatial distribution of seedlings in one of the permanent plots (1 × 1 m) in (A) early (5 April 2002 – first census) and (B) late (1 May 2002 – last census) spring. Each permanent plot was divided into 100 subplots in which the number of seedlings was counted. The censuses were carried out at weekly intervals until the beginning of May, when the leaf canopy of the rosettes closed and prevented further observations. Number of seedlings: □ 0, ░ 1–3, ▒ 4–6, ▓ 7–8, ▩ 9–11, ■ 12–15.

(J. Pergl *et al.*, unpublished). The density of seedlings, defined as new plants with a lamina width of < 3.5 cm, in ten plots in a population close to Giessen, Germany, in 2003 was 504.0 ± 363.3 per m^2 (Hüls, 2005). Other available data for seedling densities come from Scotland, where Tiley *et al.* (1996) found 400 seedlings/m^2.

However, seedling survival is low. In the Czech Republic and Germany, less than 1% of the seedlings survive until the next spring (J. Pergl *et al.*, unpublished; Hüls, 2005). In Scotland there is a rapid decrease in seedling density from 400 seedlings/m^2 in spring to 33 surviving plants in autumn (Tiley *et al.*, 1996). Caffrey (1999) records survival of seedlings within the range of 1.2–13.7%. In another study, the survival rate of seedlings and immature plants from March to June was approximately 2.5% (Caffrey, 2001: estimated from his Fig. 2).

Seedling emergence and survival indicate that established populations are not seed limited. Seedling survival is related to microclimatic conditions, intraspecific competition and stochastic events. Seedling establishment is promoted by favourable conditions of open ground, where competition from co-occurring species, particularly grasses, is low. As stands of *H. mantegazzianum* are often visited by game animals (deer, hogs), seeking shelter and food, the soil surface is disturbed and the herb layer removed, which increases the probability of establishment and survival of seedlings and decreases competition from other species. In undisturbed grasslands and other vegetation types with a dense cover, the probability of seedling establishment and survival to the end of the first growing season is very low; in the dense cover of grasses, the average number of seedlings found in midsummer in a 1 m^2 plot next to a plant that flowered the previous year was 56 (J. Pergl and I. Perglová, unpublished). As *H. mantegazzianum* is a monocarpic perennial plant and dies after seed release, seedlings do not have to compete with the mother plant. Thus, small seedlings can take advantage of a safe place in close proximity to a dead, decaying flower stem, which creates a patch of disturbed ground even in otherwise compact vegetation. Suitable conditions for germination and survival are also found at wet sites, such as riverbanks, where there are sufficient nutrients, moisture and suitable patches of disturbed ground (Ochsmann, 1996; Tiley *et al.*, 1996).

The germination of *H. mantegazzianum* seeds very early in spring provides this species with an advantage. Seedlings are adapted to climatic conditions in the native distribution range, and hence are not sensitive to frost. Early germination allows the seedlings to cover patches of open ground and reach a sufficiently advanced stage before they are overgrown by adult plants of *H. mantegazzianum* or other species. The mortality of seedlings is high, but comparable with those generally observed in other plants (Harper, 1977).

Seedling RGR

To evaluate the growth potential of *H. mantegazzianum*, seedling relative growth rate (RGR) was measured using standard procedures (Grime and Hunt, 1975). Thus, it is possible to compare the RGR of *H. mantegazzianum* with that of native species and explore whether early germination is associated with fast growth and rapid accumulation of biomass.

In *H. mantegazzianum*, fruits are produced in umbels of various orders and positions within the plant (see Fig. 4.2). The final contribution of an individual umbel to the overall fitness of a plant is a function of its fruit set, the germination capacity of the seeds and their ability to survive to flowering. While germination is not, fruit mass is significantly affected by umbel position (Moravcová *et al.*, 2005). To determine the role of umbel position on population growth and offspring fitness, the RGR of seedlings from different umbels was compared (Perglová *et al.*, unpublished).

Ripe fruits were collected in 2004 at the site Žitný I (see Perglová *et al.*, Chapter 4, this volume; Müllerová *et al.*, 2005) from randomly selected individuals. They were collected separately from the primary umbels (hereafter referred to as ‘terminals’) and secondary umbels on satellites (‘satellites’), stem branches (‘stem branches’) and branches growing from the base of the flowering stem at ground level (‘basal branches’). One umbel per plant was sampled. After 1 month of storage, seeds were stratified in Petri dishes on wet sand (for details of stratification see Moravcová *et al.*, 2005). After emergence of the radicule, seedlings were placed in pots filled with sand, moved to a climate chamber (Fitotron, Sanyo) with a standard regime (day/night: 12 h/12 h, 22°C/15°C), watered with Rorison nutrient solution (Hendry and Grime, 1993) and harvested after 7 or 21 days. RGR was calculated according to Hoffmann and Poorter (2002) and Hunt *et al.* (2002).

Seedlings from basal branches showed considerably high variation in RGR (Table 6.1), which accords with the observation that terminal umbels on these branches are generally highly variable in terms of size, fruit

Table 6.1. Relative growth rate (RGR) of seedlings of *H. mantegazzianum* grown from seeds produced by different types of umbels. Different letters indicate significant differences ($P = 0.05$) tested using multiple t-tests with Bonferroni's correction.

	Seedling RGR (g/g/day)		
Umbel position	Mean	SD	
Terminal	0.186	0.0497	a
Satellite	0.184	0.0598	ab
Stem branch	0.155	0.0667	b
Basal branch	0.156	0.0803	ab

mass, fecundity and proportion of male flowers. Some terminal umbels on basal branches resemble primary umbels (terminals) in appearance, while others resemble secondary umbels (see Perglová *et al.*, Chapter 4, this volume). RGR differed significantly only between the seedlings grown from seed from terminals and stem branches, with the growth of the former being quicker (Table 6.1). RGR of seedlings from satellites and basal branches did not differ significantly from others. However, seedlings from satellites differed marginally significantly ($P = 0.1$) from those from stem branches. Unexpectedly, there was no difference in the RGR of seedlings from terminals and satellites, i.e. from the umbels of a different order that differed significantly in seed mass.

In order to consider the RGR values in the context of plant communities invaded by *H. mantegazzianum*, its growth rate was compared with that of co-occurring species or of those found in the close vicinity of invaded sites.

The following RGR values (using data from Grime and Hunt, 1975) are reported for common species in communities invaded by *H. mantegazzianum* (M. Hejda, unpublished data from the Slavkovský les region): *Urtica dioica* L. 0.314 g/g/day, *Dactylis glomerata* L. 0.187, *Galium aparine* L. 0.167, *Geum urbanum* L. 0.104, *Poa trivialis* L. 0.200, *Anthriscus sylvestris* (L.) Hoffm. 0.074, *Heracleum sphondylium* L. 0.083 and *Alopecurus pratensis* L. 0.184. Seedlings from terminal umbels of *H. mantegazzianum* have an RGR of 0.186 g/g/day, which is less than that of *Urtica dioica*, but higher than or similar to that of other common species. In contrast, the RGR of the native *Apiaceae*, *H. sphondylium* and *Anthriscus sylvestris*, is only half of that of *H. mantegazzianum*.

The RGR of *H. mantegazzianum* seedlings, grown from seeds produced by terminal umbels, is the 34th highest in the set of 117 herbaceous species studied in the UK (Fig. 6.2). This relatively high RGR allows seedlings to establish themselves in dense *Heracleum* stands within the short period between germination and when they are overgrown by leaf rosettes. Also this RGR is similar to that of grasses, which seem to be the most important competitors in neighbouring areas that are not invaded.

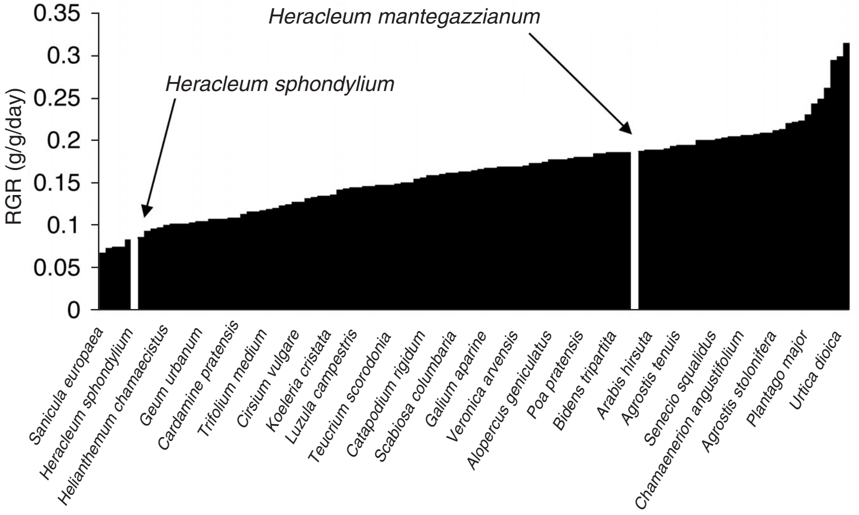

Fig. 6.2. Position of invasive *H. mantegazzianum* and its native congener *H. sphondylium* in a continuum of 117 herbaceous species ranked according to increasing seedling RGR. Data for the other species are from Grime and Hunt (1975). Only one species in five is labelled by name. For *H. mantegazzianum*, the value reported is that of seedlings developing from seeds from terminal umbels (0.186 g/g/day).

Population Structure, Mortality and Flowering

What can the structure of populations tell us about the species' life history? Can we determine the reasons why *H. mantegazzianum* is such a successful invasive species? Can an understanding of the main drivers of population dynamics help us develop an efficient control strategy? To answer these questions, the fate of individual plants was followed in permanent plots in the Czech Republic and Germany. Although *H. mantegazzianum* has been the object of many studies in the past (for review see Tiley *et al.*, 1996), there is little information on its population biology and life history. Moreover, this information was based on a limited number of plants (Otte and Franke, 1998), on observations under artificial conditions (Stewart and Grace, 1984) or was anecdotal (Tiley *et al.*, 1996). Another source of information is short notes on occasional observations by botanists and land managers (Morton, 1978; Brondegaard, 1990) or studies on control (for review see Pyšek *et al.*, Chapter 7, this volume). Finally, the studies on *H. mantegazzianum* and closely related species as fodder plants do not record the fate of individual plants or information on population biology, but focus on standing crop, biomass productivity and suitability for livestock (Satsyperova, 1984).

Population density of *H. mantegazzianum* is highly variable, ranging from isolated plants in sparse and small populations to dense and large populations covering several hectares. *H. mantegazzianum* occurs in many habitats, particularly those affected by former or present human activity: along transportation corridors (rivers, roads and railways), and abandoned meadows or forest edges (Pyšek and Pyšek, 1995; Thiele, 2006; Thiele *et al.*, Chapter 8, this volume). Thus, populations were studied in a range of environmental conditions in both the Czech Republic and Germany. In Germany the populations were classified as open and dense stands on the basis of the density of mature plants and extent of *H. mantegazzianum* cover (see later for details). In 2002, permanent plots were established in both regions. In Germany, 2–8 replicates of 1 × 2.5 m permanent plots were established at five sites and monitored every year for 3 years. This produced demographic data for two annual transitions. In the Czech Republic, eight 1 × 10 m plots were established and sampled at the beginning of summer and at the end of the vegetation season. These plots were monitored for 4 years yielding data for three transition periods.

When referring to 'population density', it should be noted that, for practical reasons, only plants above a certain threshold size (plants with leaves at least 8 cm long) were considered. This omits the majority of current year seedlings, which are unlikely to survive until the following spring. The stands in the Czech Republic had a mean density across sites and years of 5.4 plants/m^2 (min. 0.4; max. 20.2). In Germany, the dense and open stands harboured on average 7.7 (min. 1.3; max. 31.2) and 2.0 (0.3; 7.0) plants/m^2, respectively. Changes in density over time for particular localities in the Czech Republic are shown in Fig. 6.3. The decreasing trend in population densities, particularly in the overcrowded populations, agrees with projections of matrix models (see below). However, because the duration of the study was only 4 years, these results must be interpreted with care (Nehrbass *et al.*, 2006).

The proportion of plants that flowered varied considerably between years in the Czech populations and is difficult to interpret. The mean density, pooled across sites and years, is 0.7 flowering plants/m^2. In the dense stands in

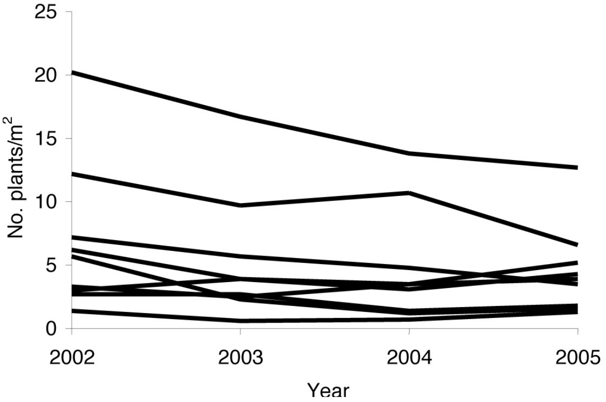

Fig. 6.3. Changes in population density of *H. mantegazzianum* over 4 years at eight sites studied in the Czech Republic. Each line represents one site. Number of plants was counted on permanent plots, 1 × 10 m in size. Only plants with leaves longer than 8 cm were counted.

Germany it is 0.8 (min. 0.0; max. 2.1) and in the open stands only 0.3, averaged across sites and years (min. 0.05; max. 0.8). Published reports correspond to our observations: one flowering plant per 0.5–1.0 m^2 (Tiley *et al.*, 1996) or 4–7 flowering individuals/m^2 in established stands (Gibson *et al.*, 1995, cited by Tiley *et al.*, 1996). Although the density of flowering plants is highly variable, the total number of seeds in the seed bank is related to the number of flowering plants (Krinke *et al.*, 2005).

To determine the effect of the size of a plant on its survival, the number of leaves and the length of the longest leaf were used as proxies of plant size in logistic regressions. For populations in the Czech Republic, both factors significantly and positively affected the probability of surviving to the following year. The survival was not dependent on the distance of the tested plant from the nearest neighbour or to the size of its Thiessen's polygon (J. Pergl *et al.*, unpublished). This indicates that survival is similar in the range of habitats studied and does not depend on local conditions.

The survival of *H. mantegazzianum* individuals in summer and winter was compared for the same stage classes as used in matrix models (see below). Survival of newly emerged seedlings (with the lamina of the largest leaf longer than 8 cm) was on average 22% during summer and 50% during winter. It was higher for larger plants (with 2–4 leaves) and varied between 60% and 67% for newly recorded plants at a given census and between 81% and 85% for those that were recorded previously. Large vegetative plants (with the longest leaf larger than 140 cm or with more than four leaves) have a slightly higher probability of surviving over summer (93%) than over winter (90%).

Similar to survival, flowering in *H. mantegazzianum* appears to be size dependent, which in turn is closely linked to the age of a plant and the time required to accumulate the necessary resources (Pergl *et al.*, 2006; Perglová *et al.*, Chapter 4, this volume). The results of studies in Germany (Hüls, 2005) (Fig. 6.4) and the Czech Republic (J. Pergl *et al.*, unpublished) suggest that the trigger for flowering is the size of the plant the 'previous' year and that the majority (90–100%) of plants that reach the minimal size flower.

Timing of flowering is crucial for monocarpic plants, so Pergl *et al.* (2006) used annual rings in the roots (Fig. 6.5) to determine the age structure of *H. mantegazzianum* populations in its native (Caucasus) and invaded (Czech Republic) distribution ranges. This study revealed that flowering occurred later in the native distribution range (Caucasus) and managed habitats (pastures) than in unmanaged sites in the Czech Republic. The later time of flowering in the native distribution range seems to be due to the higher altitude there, hence shorter period of growth compared to the sites in the invaded range. Grazing significantly prolonged the time needed for accumulating the resources necessary for flowering. The age structures of the populations in the different habitats in the Caucasus and Czech Republic are shown in Fig. 6.6. The number of 1–year-old plants is underestimated, as only plants with leaves at least 8 cm long are included. Interestingly, although plants from unmanaged sites in the Czech Republic flowered on average significantly earlier than those from other habitats, the oldest flowering plant was found in an extremely dry

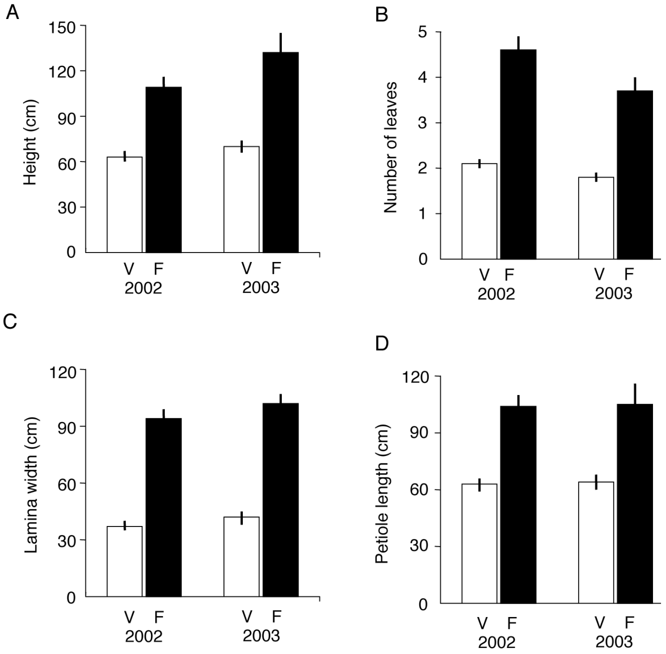

Fig. 6.4. Average height (A), number of rosette leaves (B), width of largest rosette leaf (C) and petiole length of largest rosette leaf (D) of plants in 2002 and 2003 that did not flower (V, white bars) and flowered (F, black bars) the following year. Error bars denote 95% confidence intervals. Differences between all the groups were statistically significant (logistic regressions: $\chi^2 > 34$, $df = 1$, $P < 0.001$). Data from Hüls (2005).

locality in the Czech Republic. These results suggest that the species is very tolerant and plastic in its response to environmental conditions and is able to postpone flowering for many years (up to 12 years) (for details see Pergl *et al.*, 2006; Perglová *et al.*, Chapter 4, this volume).

Matrix Model Approach: Life Tables from the Czech Republic and Germany

The populations and their dynamics based on data from Germany and the Czech Republic were compared by analysing the outputs from matrix models. The matrix models are based on transition probabilities between categories that were defined in terms of size categories rather than age. Despite slight differences in the sampling procedure used in these countries, plants were assigned to one of four size categories: seedlings (in the Czech Republic)/small vegetative plants (in Germany); juveniles/medium-sized vegetative plants; adult non-flowering plants/large vegetative plants; flowering plants (in both countries). The matrix model with data obtained at the end of each growth season

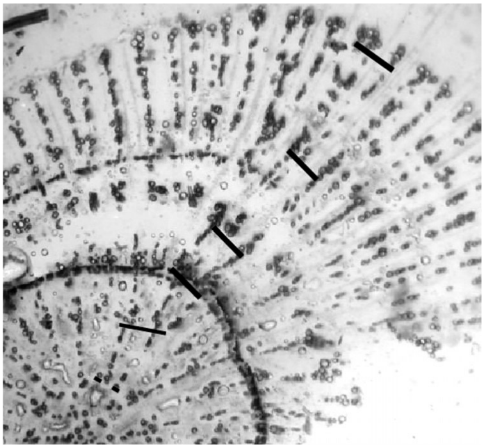

Fig. 6.5. Annual early wood rings in the secondary root xylem of *H. mantegazzianum* make it possible to determine the age of both vegetative and flowering plants. Age of plants was estimated by herb-chronology (Dietz and Ullmann, 1997, 1998; von Arx and Dietz, 2006). The figure shows annual rings in a cross-section of the root of a 7-year-old individual. Lines indicate the transitions between late wood of the previous year and early wood of the following year.

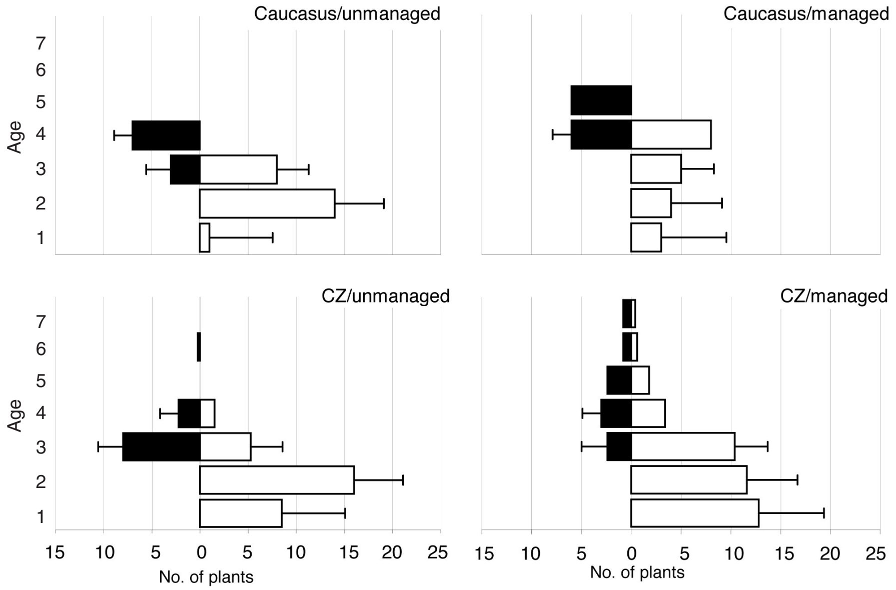

Fig. 6.6. Age structure of *H. mantegazzianum* populations at managed (pastures) and unmanaged sites in the native (Caucasus) and invaded (CZ – Czech Republic) distribution ranges. White bars represent mean number of non-flowering plants (lines = SD) per sample plot. Black bars represent flowering plants. For details of the sampling and method used to determine age see Pergl *et al.* (2006).

uses the year-to-year transitions for the years 2002–2005 in the Czech Republic and 2002–2004 in Germany.

As the data are for a limited number of transitions and sites, and the matrix models do not incorporate the spatial component of spread, the prediction of a decrease on population development in the future needs to be interpreted with caution (for a discussion of the differences between outputs from matrix and individual based models based on the same data, see Nehrbass *et al*., 2006). The estimated population growth rates for individual sites, and the number of individuals used for each transition matrix within each plot, are summarized in Table 6.2. For seven out of the eight populations studied in the Czech Republic, it was possible to construct a pooled matrix across 2002–2005. For the majority of sites, however, the number of individuals within a plot was insufficient for constructing a robust transition matrix every year (Table 6.2). The values for the finite rate of population increase (λ) at particular sites pooled across years varies from 0.550 to 1.099. Those for particular sites and years are within the range 0.684–1.286 (Pergl *et al*., unpublished). Pooled across years, values of λ are 1.15 and 1.16 for open and dense stands in Germany (Hüls, 2005). Populations in open stands have λ values of 0.76 and 1.24 for transitions 2002–2003 and 2003–2004 and in dense stands values of 0.75 and 1.38, respectively (Table 6.3). These population growth rates indicate stable or slightly decreasing local populations, which is to be expected as these populations invaded these sites a long time ago. Large-scale invasion dynamics depend on regional-scale processes such as seed dispersal, including long-distance dispersal and successful establishment of new populations. The populations that reach and remain at the carrying capacity act as sources for further invasions. It is clear that once a population

Table 6.2. Summary of finite rates of population increase (λ) based on matrix models for populations of *H. mantegazzianum* in the Czech Republic. For each locality and year, number of analysed plants (Plant no.) is shown as number of living/total number of individuals. Values marked with * are based on insufficient numbers of plants (missing data in diagonal or subdiagonal matrix elements); NA (not available). Numbers of localities correspond to those in the overview in Perglová *et al*., Chapter 4, this volume.

	Pooled		2002–2003		2003–2004		2004–2005	
Locality	λ	Plant no.	λ	Plant no.	λ	Plant no.	λ	Plant no.
3	0.749	59/93	0.93*	27/35	0.25*	14/34	1.052*	18/24
6	0.551	51/103	0.376*	23/59	NA	12/24	1.233*	16/20
8	1.099	112/151	0.924	25/45	NA	35/44	NA	52/62
9	0.994	111/157	1.08	39/51	0.684	33/56	1.286	39/50
12	NA	24/39	NA	6/14	NA	5/8	NA	13/17
13	0.878	433/600	0.945	167/234	0.867	140/195	0.849	126/171
15	0.83	113/170	0.721	39/66	0.842	31/49	1.012	43/55
16	0.796	140/200	NA	57/80	NA	48/65	NA	35/55
Pooled	0.84	1043/1513	0.935	383/584	0.813	318/475	0.953	342/454

Table 6.3. Finite rate of population increase (λ), bootstrap estimate of λ (λ_b) with lower and upper 95% confidence intervals in brackets (Dixon, 2001; Manly, 1993), expected numbers of replacements (R_0), stage distribution (ssd, stable stage distribution; osd, stage distribution observed during the second year of the transition interval), and Keyfitz's Δ (distance between observed and stable stage distribution) of dense and open stands of *H. mantegazzianum* in 2002–2003 and 2003–2004. Abbreviations of life cycle stages: sv – small vegetative; mv – medium vegetative; lv – large vegetative; fl – flowering. Matrix analyses were based on paired permanent plots of 1 × 2.5 m established in dense and open stands at five study sites in Hesse, Germany (Hüls, 2005).

Interval	Stand type	λ	λ_b	R_0	Stage distribution sv/mv/lv/fl	Keyfitz's Δ
2002–2003	Dense	0.75	0.74 (0.56–0.87)	0.24	ssd: 0.29/0.32/0.24/0.15 osd: 0.24/0.29/0.27/0.20	0.07
	Open	0.76	0.73 (0.39–0.99)	0.45	ssd: 0.09/0.17/0.36/0.37 osd: 0.04/0.10/0.40/0.46	0.12
2003–2004	Dense	1.38	1.31 (0.70–1.63)	6.45	ssd: 0.38/0.34/0.24/0.04 osd: 0.64/0.23/0.10/0.02	0.25
	Open	1.24	1.07 (0.72–1.40)	3.94	ssd: 0.23/0.21/0.48/0.07 osd: 0.70/0.13/0.15/0.03	0.46

of *H. mantegazzianum* reaches carrying capacity there is no potential for further growth. The variability in population growth rate at sites in Germany (Hüls, 2005) seems to be closely related to annual climatic variation and stochasticity. Extremely hot and dry conditions in summer 2003 strongly reduced primary productivity across Europe (Ciais *et al*., 2005), inducing dramatic changes in the population structure of *H. mantegazzianum* due to increased mortality and low seedling establishment. This resulted in an increase in recruitment of new plants in gaps and high population growth rates between 2003 and 2004 (Table 6.3).

Matrix models make it possible to estimate a theoretical stable population stage structure, which can be compared with the observed stage of distribution. When the data are pooled across years, G-tests indicate no significant differences between the predicted and observed stage structures for each locality in the Czech Republic (Pergl *et al*., unpublished). However, when the test was performed using data for individual years, most differences were significant. This suggests that, although there is a significant year-to-year variation in stage structure, the populations show stable long-term dynamics. This is supported by the results from Germany. The perturbation caused by the extreme climatic conditions in 2003 resulted in large deviations between observed and expected stage structures in 2004 (measured as Keyfitz's delta; Table 6.3). Over this period, both open and dense stands showed similar stage structures and population dynamics. However, the differences between the observed and predicted stable stage distributions were smaller in 2002–2003, when populations experienced average weather. This was particularly true for dense stands, which were very close to equilibrium conditions, whereas open stands showed larger deviations from the expected stage structure.

The accuracy of matrix model projections can be verified by comparing expected and observed population age structure or age at reproduction if available (Cochran and Ellner, 1992). This was done by estimating the age at flowering (based on data from Czech Republic) using the program STAGECOACH (Cochran and Ellner, 1992) and the results of a study on the age structure of *H. mantegazzianum* (Pergl *et al*., 2006). Results for a site in the Czech Republic indicated an estimated age at flowering of 4.36 ± 1.41 years (mean ± SD), while the observed median age was 3 years, with the oldest plant being 4 years old (Pergl, J. *et al*., unpublished). This is corroborated by the results from the German study that indicate a generation time (age at flowering in monocarpic species), estimated according to Caswell (2001), of about 3 years for dense stands for the transition 2002–2003 (Hüls, 2005). The close match between the observed data and the results of independent matrix analyses for two regions indicate that, although there are some limitations in the use of simple, time-invariant, deterministic matrix models (Hoffmann and Poorter, 2002; Nehrbass *et al*., 2006), they accurately describe the essential properties of the *H. mantegazzianum* populations studied. Elasticity analysis of these matrix models (Caswell, 2001) was used to identify transitions in the life cycle that have large effects on population growth rate, which might be used for developing management or control measures. Elasticity matrices for pooled populations in the Czech Republic and two stand types in Germany are shown in Table 6.4. The elasticity matrices averaged across years are similar in both regions and the highest elasticities are related to growth (transition to higher stage classes, i.e. sub-diagonal) and stasis (remaining within the same stage class, i.e. matrix diagonal). However, when analysed separately for each year-to-year transition, dense stands exhibit a high elasticity for stasis and open stands high elasticity for growth (Hüls, 2005). These results suggest that despite the enormous seed production, survival is crucial; the role of seed

Table 6.4. Elasticity matrices of *H. mantegazzianum* for pooled data from the Czech Republic, and for open and dense stands in Germany averaged across years and sites. Abbreviations: seedl – seedlings; juv – juveniles; ros – rosette plants; flow – flowering plants; sv – small vegetative; mv – medium vegetative, lv – large vegetative. Although the definition of stage classes varied slightly between regions, seedlings and small vegetative plants, juveniles and medium vegetative plants, and rosettes and large vegetative plants are considered to be equivalent developmental stages.

Czech Republic					Germany (open stands)					Germany (dense stands)			
	seedl	juv	ros	flow		sv	mv	lv	flow	sv	mv	lv	flow
seedl	0.07	0.03	0	0.11	sv	0.01	0	0	0.17	0.05	0.01	0.00	0.13
juv	0.11	0.13	0.02	0.07	mv	0.11	0.03	0	0.05	0.11	0.10	0	0.06
ros	0.04	0.13	0.11	0	lv	0.06	0.15	0.16	0.02	0.03	0.16	0.15	0.01
flow	0	0.04	0.14	0	flow	0	0	0.23	0	0	0	0.19	0

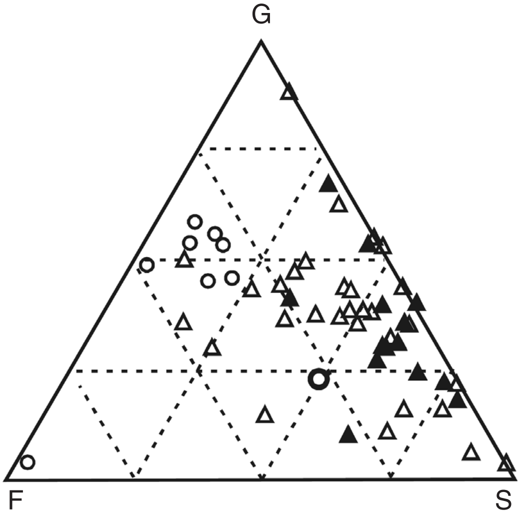

Fig. 6.7. Position of *H. mantegazzianum* in a rescaled elasticity space based on vital rates of survival (S), growth (G) and fecundity (F) using species from Franco and Silvertown (2004). Note that values of S, G and F are not simply sums of elasticity matrix elements; **O** *H. mantegazzianum* (pooled across localities and years; data from the Czech Republic), ▲ iteroparous (polycarpic) forest herbs, △ iteroparous herbs from open habitats, ○ semelparous (monocarpic) herbs.

production is diminished by the poor establishment and high mortality of seedlings. This accords with the fact that within established populations there is little recruitment, while in the open the role of colonization is high. Compared to the other species, *H. mantegazzianum* fits near the group of polycarpic perennials in the fecundity, survival and growth 'elasticity space' (Hüls, 2005). Although the strictly monocarpic behaviour of *H. mantegazzianum* is confirmed and its average age at reproduction is between 3 and 5 years, this species seems to be rather isolated from the other short-lived monocarpic species analysed by Franco and Silvertown (2004) (Fig. 6.7).

Comparison of Open and Dense Stands of *Heracleum mantegazzianum*

Individual plants, linear stands, sparse, open populations and dense populations of *H. mantegazzianum* occur in nature (Thiele, 2006). Since the density of a population is not simply a function of time since its establishment (Müllerová *et al.*, 2005), understanding what determines the density of stands and if there are differences in the life cycles of plants in open and dense stands may provide guidelines for management and control. This is also important in the context of eradication of *H. mantegazzianum*, because control measures have so far focused mainly on dominant stands (Nielsen *et al.*, 2005). There is little information on whether open stands occur in suboptimal environmental conditions or represent initial population stages. An analysis of the variation in the life cycles of plants in dense and open stands using matrix population models was used to identify morphological traits and environmental conditions associated with this life-cycle variation. The data are from a field study of paired dense and open stands in five populations in Germany (Hüls, 2005).

In contrast to dense stands, where *H. mantegazzianum* cover approaches 100%, the cover of *H. mantegazzianum* in open stands is less than 10%. All individuals of *H. mantegazzianum* were marked in summer 2002, assigned to one of four life-cycle stages, i.e. small, medium, large vegetative and flowering plants, and revisited in the summer of 2003 and 2004. Soil samples, from areas adjacent to the permanent plots, were analysed for total nitrogen, available phosphorus, potassium, magnesium and pH. The height, number of rosette leaves and the length and width of the largest rosette leaf were recorded for each vegetative plant within a sample plot. The product of number of leaves × length × width served as a proxy for leaf area.

An analysis of stage-based (Lefkovitch) population matrices revealed that open stands of *H. mantegazzianum* did not have higher intrinsic population growth rates than dense stands (Table 6.4). Therefore, this could lead to the conclusion that open stands cannot be considered to be expanding populations or the front of an expanding population. Furthermore, there were considerable and biologically relevant differences in population dynamics, stage structure and elasticities between stand types (see above), at least during the transition 2002–2003, when populations developed under average climatic conditions. Nevertheless, these results must be interpreted with care; data used in this analysis are only for two transitions and established populations. However, there were no significant differences in abiotic environmental conditions, i.e. pH and soil nutrients, between the stand types. It is therefore possible that the differences result from the effect of a high density and biomass of *H. mantegazzianum*, which changes local abiotic conditions; the species acts as an ‘ecosystem engineer’ sensu Crooks (2002) (Hüls, 2005). In addition, a large survey of 202 stands in Germany (J. Thiele, unpublished) revealed no significant differences in environmental conditions between stand types.

The analysis of stand structure suggests that in open stands *H. mantegazzianum* exerts a strong competitive effect on the surrounding vegetation. By elongating its petiole the species is able to place its leaf area just above the resident vegetation and thus monopolize the light resource (Hüls, 2005). A considerable proportion of the young *H. mantegazzianum* plants are able to reach the leaf canopy in open stands. As a result they have a faster development and shorter generation time in open stands and outcompete the shade-intolerant grassland species (Kolbek *et al.*, 1994; Gibson *et al.*, 1995; Thiele, 2006). This successful competitive growth strategy is amplified by an early phenological development (Otte and Franke, 1998; Perglová *et al.*, Chapter 4, this volume). The structural and compositional changes, which occur in invaded communities, gradually result in species-poor or dense monospecific stands. In the course of this development, stand height and petiole length, but not leaf area, increase significantly (Hüls, 2005). The intensity of intraspecific competition increases and only a small fraction of the population reaches the closed leaf canopy. Consequently, the development of small individuals, growing in the shade of the canopy, is slowed down, which leads to protracted generation times, higher proportions of small- and medium-sized plants and a higher mortality of small individuals (Hüls, 2005).

Concluding Remarks and Future Perspective

This chapter summarizes the information on the population biology of *H. mantegazzianum* in various habitat types within its invaded distribution range in the Czech Republic and Germany. *H. mantegazzianum* is a monocarpic perennial (Pergl *et al.*, 2006; Perglová *et al.*, Chapter 4, this volume) with a poor seed bank (Moravcová *et al.*, Chapter 5, this volume). Although this species is invasive, once an area is colonized the population growth rate shows little variation between habitat types and fluctuates around $\lambda = 1$. As in many other plant species, environmental stochasticity, especially extreme climatic conditions, exerts a strong influence on population dynamics. In undisturbed conditions, a close match between the observed and stable stage distributions and a high elasticity for stasis suggest that dense monospecific stands have reached the carrying capacity of the habitat. In contrast, in open stands growth transitions have a large effect on the population growth rate. However, population dynamics in dense and open stand types respond similarly to disturbance. Gaps in the stand that result from drought, for example, are quickly filled by increased seedling establishment and recruitment. Although the time series of field observations is short, the predictions based on the data accord with reality. Invasive behaviour is associated with successful colonization of sites mostly resulting from human land use change and disturbance (Müllerová *et al.*, 2005; Thiele *et al.*, Chapter 8, this volume), especially increased abandonment (ruderalization) of landscapes. A similar invasive behaviour was observed at sites in the native range of *H. mantegazzianum* intensively used by humans, such as pastures.

The analyses presented here did not identify any special features responsible for the successful invasion of this species or a weak link in its life history on which control measures could focus. Future control measures need to consider every stage of the life cycle of *H. mantegazzianum*. Although a single *H. mantegazzianum* plant is able to produce thousands of seeds (see Perglová *et al.*, Chapter 4, this volume; Perglová *et al.*, 2006), their survival is site-dependent. For example, when competing with other species in managed meadows seedling survival is extremely low, particularly during the first year. *H. mantegazzianum* only reproduces by seed; such strictly monocarpic behaviour offers some possibilities for its eradication, e.g. by preventing seed release by depletion of mature plants at a site (Pyšek *et al.*, 2007 and Chapter 7, this volume).

Although the whole life cycle of *H. mantegazzianum* has been considered here, some issues remain to be studied. Namely the effect of various control measures on particular phases of the life cycle, employing long-term experiments and observations. Similarly, although regional landscape-scale dynamics over a historical time scale have been recently analysed (Müllerová *et al.*, 2005), metapopulation dynamics as well as the role of long-distance dispersal need to be addressed. Since some invasive species produce allelopathic substances (e.g. Hierro and Callaway, 2003), there is a need to determine whether *H. mantegazzianum* produces such substances and whether they are released from seed, decomposing litter or root exudates. Finally, a detailed study of seedling establishment and survival over a wider range of habitats and regions than considered here may improve our understanding of the population dynamics and invasion success of *H. mantegazzianum* in relation to land use.

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