Population ecology of the invasive alien plant *Heracleum mantegazzianum*

Ph. D. Thesis

Charles University
Faculty of Science
Department of Botany

Jan Pergl
2006

Supervisor: doc. RNDr. Petr Pyšek, CSc.

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Hereby I declare that I have not submitted or presented any part of this thesis for any other degree or diploma.

Jan Pergl

Průhonice, November 2006

Acknowledgements

With a considerable help from my friends...

This thesis could not be completed without help and support from many people. First of all, I would like to thank my supervisor Petr Pyšek and my wife Irena for excellent conditions I had for my work.

My thanks goes to Irena for her patient help in collecting field data, comments on the work and being with me not only at work. Petr Pyšek played very important role in the process of creation of the thesis and my professional growth. I thank him for his contribution not only as a supervisor and organizer of funding but also for a human dimension. He was always patient when reading my manuscripts and kindly and marveously improved my English. I am grateful to him for opening for me the window of opportunity to work in European scientific community.

I appreciate the role of the whole GIANT ALIEN project team, who showed me the cooperative and multidisciplinary work within an international project. I would like to thank them for stimulation of my work and valuable comments. I highly acknowledge the support of the Russian colleagues who took the best care I had during a field work. Sorry Irena ;-)

My special thanks goes to co-authors of presented papers for their collaboration and to several reviewers for valuable comments on the manuscripts. I also thank to colleagues from the Institute of Botany in Průhonice for their help, support and open doors I had for my questions and needs. I especially appreciate the consultations with Vojta Jarošík, Honza Wild and Lenka Moravcová.

I thank to my parents, brother and sister and apologize that I spent so little time with them in the last years.

The research was mainly supported by the project 'Giant Hogweed (*Heracleum mantegazzianum*) a pernicious invasive weed: developing a sustainable strategy for alien invasive plant management in Europe', funded within the 'Energy, Environment and Sustainable Development Programme' (grant no. EVK2-CT-2001-00128) of the European Union 5th Framework Programme. Funding from ALARM (GOCE-CT-2003-506675) made it possible to complete the work after the GIANT ALIEN project has been completed in April 2005.

Jan Pergl
November 2006

Introduction

Biological invasions are not only possible threat to biodiversity and human well-being (Pimentel 2002, Millenium Ecosystem Assesment 2005, Mooney *et al.* 2005) but also provide an excellent source of data for studying species interactions and evolution in real time (Sax *et al.* 2005). Not all introduced species became naturalized or invasive, or pose problem in their new distribution range (Richardson *et al.* 2000) and this inequality in the establishment rate of introduced species gave rise to the main questions in invasion ecology: what makes a species invasive, what makes a community more vulnerable to invasion and what is the impact of invasive species (Rejmánek *et al.* 2005). Although the proportion of problematic invasive species is rather small, the publicity they receive is high. One of the species belonging to the "top ten" of plants invasive in Europe is *Heracleum mantegazzianum* Sommier & Levier (giant hogweed). This species was introduced from the Western Greater Caucasus to Europe in the first half of the 19th century and soon became a popular ornamental plant which was spread across many European gardens. Later it started to spread into the wild (Tiley *et al.* 1996).

From 2002 to 2005 a project GIANT ALIEN was running, targeted at developing sustainable strategy for control of *Heracleum mantegazzianum*, and funded by the 5th Framework of the European Union. Giant hogweed was chosen as a model species because of its high profile among invasive species in Europe. The attention it receives is not only due to the exotic appearance and enormous size (flowering plants up to 5 m high) but also because of the impact this species exerts on human health. The plant produces sap containing photosensitising fouranocoumarins, which can, after contact with human skin and in combination with ultraviolet radiation, cause severe burnings (photodermatitis). The GIANT ALIEN project provided a good opportunity to join basic research with applied aspects of plant invasions, by linking various disciplines from population biology of plants and plant-insect interactions to fungal pathogens and management of invasive aliens.

The papers in this thesis resulted from research on the biology and ecology of *H. mantegazzianum* carried out within this project, which was designed so as to cover all important parts of the life cycle of the species. Starting from the stage of a seed, studies completed within the project framework described the dynamics of seed bank (Krinke *et al.* 2005, Moravcová *et al.* 2006) and the pattern of seed germination (Moravcová *et al.* 2005, 2007). Then, along the continuing life cycle, seedling dynamics, survival of plants and timing of flowering were addressed - these topics that are covered by Chapters 1–2 of this thesis. The patterns of flowering and seed production is covered by other study (Perglová *et al.* 2007). The seeds are then dispersed across landscape, which affects the population dynamics at a larger scale. For *H. mantegazzianum* there was a unique opportunity to study large-scale population dynamics using aerial photos, because large and conspicuous inflorescences allowed to identify individual plants or their populations and analyse population dynamics in relation to the land-use and history of study sites (Chapter 3 of this thesis). Long-distance dispersal and amount of randomly dispersed seeds are assumed to be key processes affecting the population dynamics, but are rarely studied due to the methodological problems (Cain *et al.* 2000). These processes were estimated by using Individual Based Models (IBM) and set of aerial photos from one selected locality in Chapter 4. By this study, the hypothetical life cycle is completed and returns to the stage of a seed. Furthermore, the life cycle can be modified by applying control mechanisms which affect population dynamics (Nehrbass & Winkler 2007). The last part of the thesis (Chapter 5) gives a methodological view on studies of population dynamics by comparing simple matrix models and more complex stochastic individual-based models.

This comprehensive list of topics that were addressed in the GIANT ALIEN projects indicates that papers in this thesis are pieces of the puzzle towards understanding the successful invasion of *H. mantegazzianum* and developing a sustainable strategy of its control. Although the work is focused on a single species, the outputs from the studies contribute to understanding the processes determining the establishment of newly introduced species.

Outline of the thesis

Chapter 1

Population ecology

This chapter summarizes up-to-date knowledge about the population dynamics of *H. mantegazzianum*. Population biology can help us to explain what are the characteristics that make this species such a successful invader and, on the other hand, what are possible weak links in the life cycle which could be targeted by appropriate control measures. Furthermore, a detailed description of small-scale dynamics can serve as a guidance to understanding the spread of the species on a larger scale (see Chapters 4 and 5).

This chapter is mostly based on long-term field observations of *H. mantegazzianum* populations in its invaded distribution range in the Czech Republic and Germany. Main areas covered by this chapter are those that affect the survival and growth of individuals: seedling dynamics, RGR of seedlings, population stage structure and mortality and analysis of life tables. Although the title of the chapter may imply that all aspects of the life cycle are included, some are not because they are addressed in separate papers on seed ecology (Moravcová *et al.*, 2005, 2007) and reproduction (Perglová *et al.* 2006, 2007).

The following features of population dynamics deserve to be highlighted: germination of seeds starts early in spring, few days after the snow has melted.

Seedlings reach high densities with subsequent thinning during the season and none of them were found to germinate in autumn. After the germination, the seedlings of *H. mantegazzianum* grow relatively fast (RGR), compared with other species, about twice as fast as those of the native congener *H. sphondylium* but their RGR reaches only two thirds of that reported for a competitively strong native dominant of disturbed habitats, *Urtica dioica*. Survival to the next season, as well as the probability of flowering depends on size in the previous year, and is little affected by neighbouring members of the population. *Heracleum mantegazzianum* reproduces once in its life-time, usually at the age of 3 to 5 years (for details see Chapter 2). Analysis of life tables and matrix models revealed that highest elasticity values are related to growth and stasis rather than to fecundity. Seed production is diminished by poor establishment and high mortality of seedlings. The establishment of seedlings is higher in open and disturbed habitats than in grasslands with closed canopy. The growth rate of studied populations as obtained from matrix models is characterized by the values of λ slightly below one, with high fluctuations among years. A more detailed insight into the outputs of matrix models and their comparison with those of the Individual Based Model and the role of stochasticity is provided in Chapter 5.

The results presented in this chapter do not point to any special feature which might be responsible for the successful invasion of this species or to a marked weak link in its life history. The invasive potential of *H. mantegazzianum* is associated with its fast growth and ability to successfully colonize ruderalised or disturbed habitats which are mostly of human origin. Strictly monocarpic behaviour and reproduction exclusively by seed have important implications for planning sustainable control strategy based on preventing flowering plants from producing seed (Pyšek *et al.* 2006, 2007).

Chapter 2

Population age structure in native and invaded distribution ranges

This chapter relates the population dynamics of *Heracleum mantegazzianum* to the reproductive behaviour and compares the results from the native and invaded distribution range. In contrast to other chapters, this study is based on a single time slice taken in the populations studied. Nevertheless, the time scale is included by the information on age structure of sampled populations. Generative reproduction an important characteristics affecting species' invasion success (see Pyšek & Richardson 2007 for a review), especially in those that do not reproduce vegetatively (Baker 1965, Noble 1989, Roy 1990, Saxena 1991). *Heracleum mantegazzianum* reproduces entirely by seed and is monocarpic – it reproduces only once in its life-time. The phenomenon of a single opportunity to reproduce raises interesting questions. In general, monocarpic species live between two "decisions": to reproduce as early as possible and minimize the risk of death without reproduction, or wait and prolong the period of resource accumulation which can potentially result in more seed and offsprings (Metcalf *et al.* 2003).

In invasion ecology, several approaches are used to determine why some species became successful invaders. A promising direction is to compare behaviour of a species in its native and invaded distribution range, i.e. the biogeographical approach (Hierro *et al.* 2005). There are several hypotheses proposing that alien species in invaded range may escape from their specialized enemies, which may increase their competitive ability in the new region (Keane & Crawley 2002, Wolfe 2002, Blossey & Nötzold 1995, Rogers & Siemann 2004). If this is the case, introduced species are supposed to grow faster, produce more seeds, grow taller and at higher densities in the new region than in their native distribution range, although this pattern is not always consistent (Thébaud & Simberloff 2001).

The study presented in this chapter is based on the comparison of reproductive strategy and population characteristics, such as age structure, density of stands and proportion of flowering plants, in native (Caucasus) and invaded (Czech Republic) distribution ranges of *H. mantegazzianum* and between different habitat types (managed vs. unmanaged). In both distribution ranges, managed habitats were cattle and sheep pastures. Unmanaged sites were high-mountain meadows or forest clearings (possibly the natural sites of *H. mantegazzianum*) in the native distribution range (Otte *et al.* 2007) and sites left for a long-term spontaneous development in the invaded region. Age of individual plants was assessed by using herb-chronology, a method based on counting annual rings in the xylem of root (von Arx & Dietz 2006). In total, 302 individual plants were sampled and their age at the time of flowering determined.

All flowering plants found during the study were at least 3 years old. In unmanaged sites in the invaded distribution range majority of plants flowered between their 3rd or 4th year (median = 3 years). The maximum age of 12 years was recorded in an extremely dry locality in the Czech Republic, where the majority of plants flowered between the 5th and 8th year. In unmanaged habitats in the native distribution range plants flowered significantly later than in unmanaged habitats in the Czech Republic and the median age was 4 years. In managed sites, the age at flowering was 5 years regardless of the distribution range. The shift in flowering age between distribution ranges can be explained by harsher climatic conditions in the native region; this was illustrated by a significant effect of altitude added to the model as a covariable. Population density was highest in unmanaged sites within the invaded range, but did not affect the age of flowering plants. The analysis of reproductive output of flowering plants did not show a significant difference between distribution ranges nor it confirmed the hypothesis that older plants produce more seed. This indicates the existence of a common threshold in the amount of resources needed to trigger flowering.

Results from this study indicate, that the studied species is rather plastic in terms of the timing of flowering; more favourable conditions in the invaded distribution range accelerate its life-cycle and thus promote the rate of invasion. Additionally, the knowledge of the population age structure allows to verify and improve theoretical models gained from long-term field observations (Chapter 1, 4, 5). Another important point concerns control issues; the data show that at managed sites, flowering is postponed for at least one year, which consequently prolongs the time needed for post-control monitoring of the site (Pyšek *et al.* 2007).

Chapter 3

Historical regional dynamics assessed by aerial photographs

The first chapter illustrates that at a small scale populations of *H. mantegazzianum* reach the local carrying capacity and then the rate of population growth decreases, leading to the development of a stable stage structure. Chapter 3 deals with the population dynamics at larger spatial and time scales; the population dynamics are explored at tenths of hectares and over 50 years. The long-term and historical perspective of invasion dynamics of *H. mantegazzianum* is interesting from the methodical point of view: since most invasions are recognized at rather advanced stage, they are studied *post hoc* data capturing the beginning of invasion are rarely available. Past invasion dynamics are usually reconstructed, depending on the scale of the study, by using information on species distribution derived from floristic sources or herbaria (e.g. Weber 1998, Mandák *et al.* 2004). By using remote sensing techniques, few studies covered the entire invasion process of some species from the beginning (Robinson 1965, Lonsdale 1993), and this is true also for the *H. mantegazzianum* study presented in this chapter. The dynamics of invasion was reconstructed in landscape sections of 60 ha and the first photographs were taken when the species did not occur in particular sites, i.e. prior to invasion. The invasion of *H. mantegazzianum* in the Slavkovský les Protected Landscape Area was analysed by using a series of aerial photographs from 11 sampling dates from 1947 to 2000.

The mean rate of areal spread of *H. mantegazzianum* was 1261 $m^2.yr^{-1}$, while that of the linear spread 10.8 $m.yr^{-1}$. The resulting population size (expressed as the area occupied by *H. mantegazzianum*) was directly more affected by the rate of invasion than by the residence time, but there was a slight difference between the overall (direct and indirect) effects of both factors. A high proportion of pastures and fields was invaded (more than 80%), less so in forests and scrub.

The study showed that *H. mantegazzianum* is easily detectable on aerial photos if they are taken in the flowering or early fruiting period. This made it possible to estimate its distribution with reasonable precision, although limited to flowering individuals. Analysis of aerial photos has not only a scientific relevance, but can be used by land managers for planning and prioritising control measures.

Chapter 4

The role of long-distance dispersal determined by simulation model of invasion

The previous chapter illustrates how aerial photographs can be used for studying the population dynamics at landscape scale; Chapter 1 reports about the small-scale dynamics. The present chapter is based on the intersection between these two approaches. One of the most frequently asked questions in population ecology concerns the role of long-distance and random seed dispersal. Seed dispersal in the close vicinity of mother plant has long been studied in many species, but random events that allow invasive species to colonize distant areas have been rarely addressed because of methodological constraints (Cain *et al.* 2000).

The proportion of randomly dispersed seed was studied using combination of the monitoring of population dynamics in permanent plots and analysis of aerial photos covering 50 years of invasion (see Chapter 3). Population dynamics of the species in the same area as that covered by aerial photographs was monitored since 2002 to 2005 and fate of individual plants, their survival and emergence followed. An Individual Based Model (IBM) was based and parameterized based on these data (see Chapter 5). The simulations were run on a grid where the quality of individual cells and their suitability to invasion by *H. mantegazzianum* was classified on the basis of the species' occurrence as determined on aerial photos. Real data on the distribution of *H. mantegazzianum* in the landscape were used to parameterise long-distance and random dispersal at one selected site. The questions addressed in this chapter focus on (i) the role of long-distance dispersal in regional invasion dynamics, and (ii) the effect of land-use changes on the progress of invasion.

Three scenarios were used: (1) standard, with the proportion of seed dispersed randomly set to 2.5%; (2) long-distance scenario aimed at estimating the proportion of randomly dispersed seed that best fits the real population dynamics recorded on aerial photographs; and (3) the scenario testing the effect of land-use change by using habitat structure prior to invasion. Run simulations showed remarkable influence even of a small amount of randomly dispersed seed on the colonization rate and with over-proportional effect. The best fit of the number of colonized cells (simulations were run on a grid) with observed distribution was found for 2.5% of randomly dispersed seed. The effect of land-use change was obvious only in a landscape that became highly saturated by *H. mantegazzianum*. This effect was a function of actual habitat saturation and hence of the percentage of randomly dispersed seeds.

Chapter 5

Matrix vs. individual-based model

There are several ways of analysing data on population dynamics; matrix and individual-based models represent two main approaches. Predictions and analyses of population dynamics are valuable in planning control or conservation measures, as they allow to specify the most vulnerable life stage or transition between stages. Nevertheless, the results must be carefully interpreted with regard to local conditions and with limits of the collected data borne in mind.

This chapter illustrates how predictions of the population dynamics can be affected by using different analytical methods, even if they are based on the same set of data. Data presented in Chapter 1 show that at a small scale of inner parts of invading populations, stable equilibrium has been reached with rates of population growth fluctuating around one. At a large scale, illustrated by Chapter 3, the populations yet show the dynamics behaviour with stable increase in the area occupied. Thus, the results obtained from the analysis of basic matrix model and more complex individual based model with the stochastic and spatial component included indicate that different approaches are suitable for different questions and scales. The matrix models are better suited for elasticity and sensitivity analysis, while individual-based model for answering the questions related to spatial spread.

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Population ecology

6 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 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 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, this volume).

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 the 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 nondormant 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 scarce snow cove; 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 nondormant 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

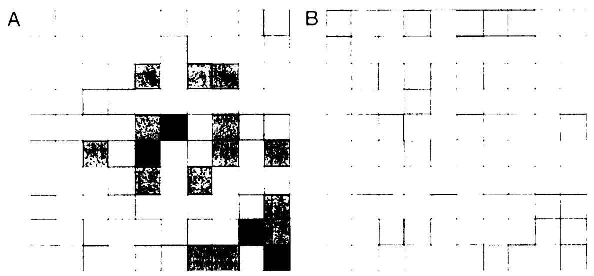

Fig. 6.1. Spatial distribution of seedlings in one of the permanent plots (1 × 1 m) in (A) early (5 April 2002 – first census) and (B) late (1 May 2002 – last census) spring. Each permanent plot was divided into 100 subplots in which the number of seedlings was counted. The censuses were carried out 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.

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 (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 mid summer 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 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, seedling 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).

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

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 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 the 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 area that are not invaded.

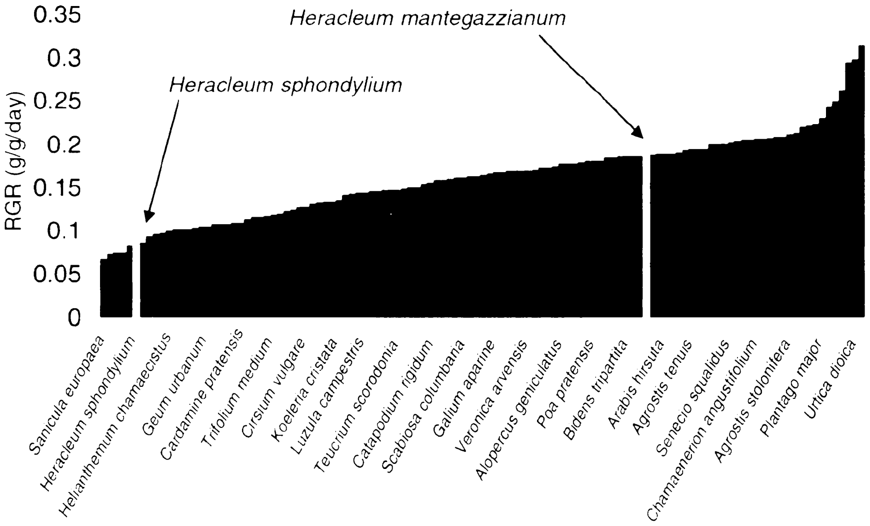

Fig. 6.2. Position of invasive *H. mantegazzianum* and its native congener *H. sphondylium* in a continuum of 117 herbaceous species ranked according to increasing seedling RGR. Data for the other species from Grime and Hunt (1975). Only one species in five is labelled by name. For *H. mantegazzianum*, 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. *Heracleum 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 Germany it is 0.8 (min. 0.0; max. 2.1) and in the open stands only 0.3,

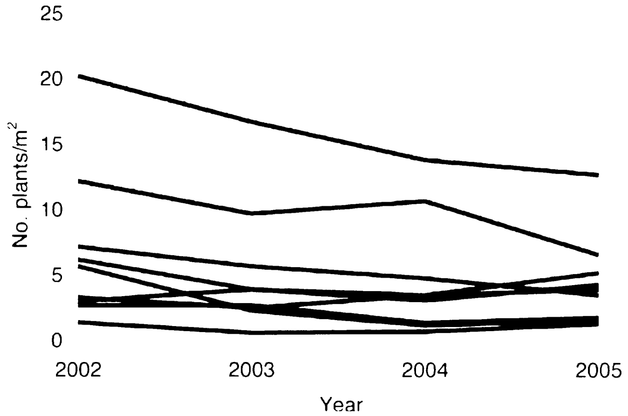

Fig. 6.3. Changes in population density of *H. mantegazzianum* over 4 years at eight sites studied in the Czech Republic. Each line represents one site. Number of plants was counted on permanent plots, 1 × 10 m in size. Only plants with leaves longer than 8 cm were counted.

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

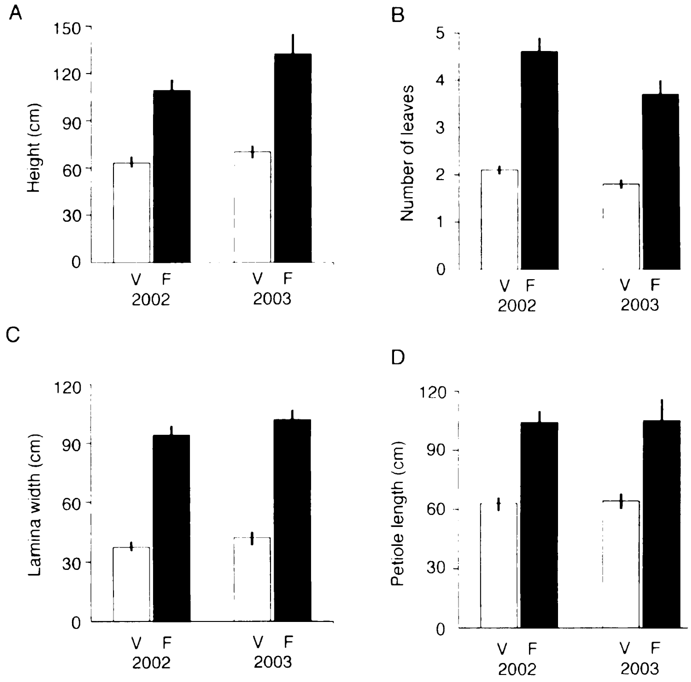

Fig. 6.4. Average height (A), number of rosette leaves (B), width of largest rosette leaf (C) and petiole length of largest rosette leaf (D) of plants in 2002 and 2003 that did not flower (V, white bars) and flowered (F, black bars) the following year. Error bars denote 95% confidence intervals. Differences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

was found in an extremely dry 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 uses the year-to-year transitions for the years 2002–2005 in the Czech Republic and 2002–2004 in Germany.

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.

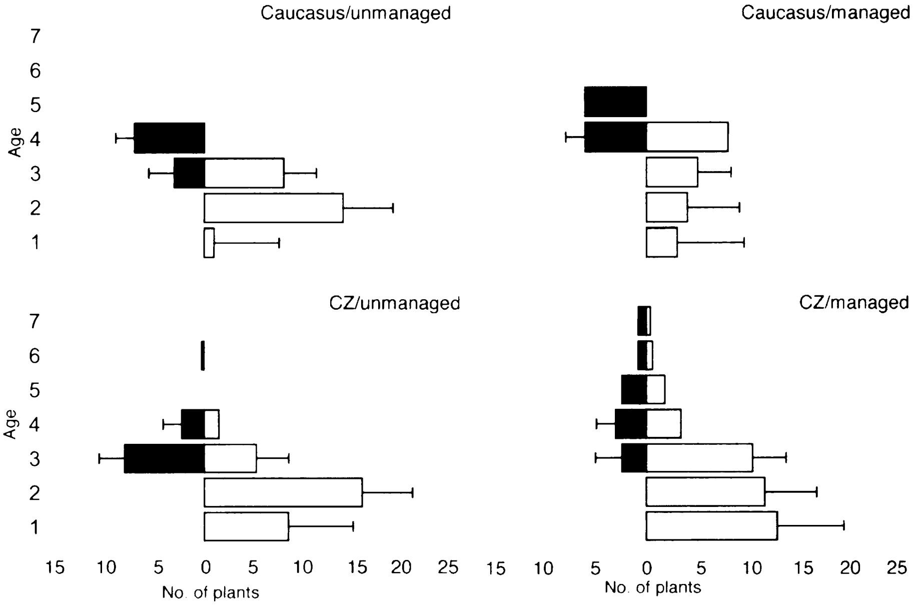

Fig. 6.6. Age structure of *H. mantegazzianum* populations at managed (pastures) and unmanaged sites in the native (Caucasus) and invaded (CZ – Czech Republic) distribution ranges. White bars represent mean number of plants (whiskers = SD) per sample plot. Black bars represent flowering plants. For details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

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 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. A 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 population 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

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 number 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 (Manly, 2001; Dixon, 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

stochasticity. Extremely hot and dry conditions in the 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 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 production is diminished by the poor establishment and high mortality of seedlings. This accords with the fact that within established populations there is little

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

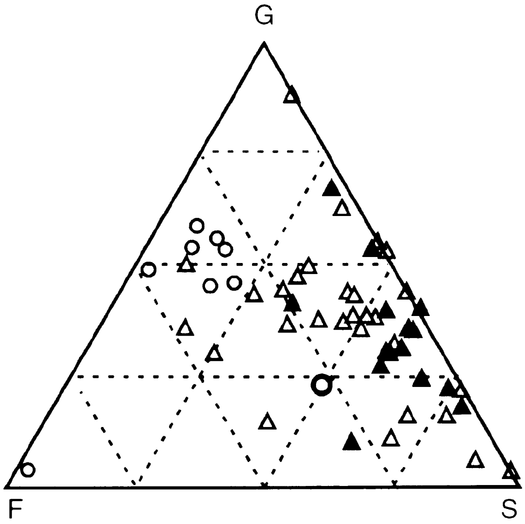

Fig. 6.7. Position of *H. mantegazzianum* in a rescaled elasticity space based on vital rates survival (S), growth (G) and fecundity (F) using species from Franco and Silvertown (2004). Note that values of S, G and F are not simply sums of elasticity matrix elements; ○ *H. mantegazzianum* (pooled across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

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 the 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 no. 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. *Heracleum 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, exert 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 their first year. *Heracleum 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.

Acknowledgements

We thank Hansjörg Dietz and Miguel Franco for comments on the manuscript, Zuzana Sixtová for technical assistance and land owners for permission to study *H. mantegazzianum* on their private land. Tony Dixon kindly improved our English. The study was supported by the project 'Giant Hogweed (*Heracleum mantegazzianum*) a pernicious invasive weed: developing a sustainable strategy for alien invasive plant management in Europe', funded within the 'Energy, Environment and Sustainable Development Programme' (grant no. EVK2-CT-2001-00128) of the European Union 5th Framework Programme, by institutional long-term research plans no. AV0Z60050516 from the Academy of Sciences of the Czech Republic and no. 0021620828 from Ministry of Education of the Czech Republic, and grant no. 206/05/0323 from the Grant Agency of the Czech Republic, and the Biodiversity Research Center no. LC0607.

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Population age structure in native and invaded distrinution ranges

American Journal of Botany 93(7): 1018–1028. 2006.

POPULATION AGE STRUCTURE AND REPRODUCTIVE BEHAVIOR OF THE MONOCARPIC PERENNIAL *HERACLEUM MANTEGAZZIANUM* (APIACEAE) IN ITS NATIVE AND INVADED DISTRIBUTION RANGES[1]

JAN PERGL,[2,5] IRENA PERGLOVÁ,[2] PETR PYŠEK,[2,3] AND HANSJÖRG DIETZ[4]

[2]Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice, Czech Republic; [3]Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-128 01 Praha 2, Czech Republic; and [4]Institute of Integrative Biology ETH, Universitätsstrasse 16, CH-8092 Zürich, Switzerland

Many invasive species are benign in their native region—are there interactions between their key traits and the new habitats that explain invasion success? The giant perennial herb *Heracleum mantegazzianum* is a problematic invader in Europe and is also naturalized in North America. We compared its population structure and reproductive behavior in the native (W. Caucasus) and invaded (Czech Republic) areas in managed (pastures) and unmanaged sites. The age structure of the populations and age at flowering were analyzed using herb-chronology, a method based on counting annual rings in the secondary xylem of roots. The species was strictly monocarpic; most plants in unmanaged sites in the invaded range flowered in the third and fourth yr (maximum 12 yr). In unmanaged habitats, plants from the native range flowered later than those from the invaded range. In both ranges, flowering was delayed in managed sites where the population density was higher and most plants flowered around the fifth year. Reproductive output of individual plants was neither related to population density nor to age at flowering. More favorable climatic conditions in the invaded region, together with increased chances for dispersal in a densely colonized central Europe, seemed to allow the massive invasion.

Key words: biogeography; Caucasus; Czech Republic; demography; habitat type; *Heracleum mantegazzianum*; herb-chronology; invasive alien plant.

Biological invasions, that is, the spread of introduced species into non-native areas, rank among the most important factors and consequences of global change, threatening native biodiversity (Dukes and Mooney, 1999). It is, therefore, imperative to gain a thorough understanding of the mechanisms underlying biological invasions and the key traits of invasive species for informed management decisions. A promising direction for studying the characteristics of invasive species (sensu Richardson et al., 2000; Pyšek et al., 2004) is to compare their behavior in the native and introduced ranges. This biogeographical approach is important for understanding the principles underlying plant invasions (for a review, see Hierro et al., 2005), yet it has been rarely used. For example, it has been suggested that alien species escape from their specialized herbivores and enemies, which may increase their performance in the new region (Keane and Crawley, 2002; Wolfe, 2002) or may even result in the evolution of increased competitive ability (Blossey and Nötzold, 1995; Blair and Wolfe, 2004; Rogers and Siemann, 2004). In their native regions, several species have been reported to grow at lower population densities (Bastlová-Hanzélyová, 2001), produce fewer seeds (Noble, 1989; Rees and Paynter, 1997), have lower growth rates, and are smaller (Blossey and Nötzold, 1995; Bastlová-Hanzélyová, 2001; Siemann and Rogers, 2001; Jakobs et al., 2004), although these patterns are not always consistent (Thébaud and Simberloff, 2001; Agrawal and Kotanen, 2003; Hierro et al., 2005).

It is particularly important to investigate possible differences in the reproductive behavior of species between their native and introduced ranges because reproductive traits have often been identified as crucial for the invasion success of introduced plants (Baker, 1965; Noble, 1989; Roy, 1990; Saxena, 1991; Rejmánek, 1996; Rejmánek and Richardson, 1996; Pyšek, 1997). Invasive plants that are unable to reproduce vegetatively depend entirely on seed production (Pyšek, 1997; Moravcová et al., 2005). In these species, timing of flowering and life span are particularly important traits for successful naturalization and spread (Baker, 1965; Noble, 1989; Roy, 1990; Saxena, 1991; Rejmánek, 1996). Species that adopt a monocarpic strategy are convenient study subjects from an evolutionary point of view, as the 'decision' of when to flower involves a trade-off between flowering as early as possible vs. accumulating more resources leading to a higher seed set, but with an increased risk of dying before reproduction (Childs et al., 2003; Metcalf et al., 2003). The strategy thus depends on the balance between the risk of death and the profit from delayed reproduction and differs between distinct habitat conditions or management regimes (Bullock et al., 1994; Crawley, 1997). Hence, the time of reproduction in monocarpic plant species seems to be more closely related to developmental stage or plant size than to plant age (Harper, 1977; Gross, 1981; Kachi and Hirose, 1985; Lacey, 1986; Crawley, 1997).

However, the important question remains whether there are differences among habitats in the plant age at which sufficient

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[1] Manuscript received 20 September 2005; revision accepted 25 April 2006.

The authors thank J. Jernstedt and two anonymous reviewers for comments on the manuscript, J. M. Alexander for improving our English, V. N. Portenier and the members of the Russian team for logistic support during the field research in the Caucasus, and V. Jarošík for valuable comments and help with data analysis. The study was supported by the project "Giant Hogweed (*Heracleum mantegazzianum*) a pernicious invasive weed: developing a sustainable strategy for alien invasive plant management in Europe," funded within the Energy, Environment and Sustainable Development Programme (grant no. EVK2-CT-2001-00128) of the European Union 5th Framework Programme. Additional support was provided by the institutional long-term research plans no. AV0Z60050516 from the Academy of Sciences of the Czech Republic and no. 0021620828 from the Ministry of Education of the Czech Republic (to P. P.).

[5] Author for correspondence (e-mail: pergl@ibot.cas.cz)

size for flowering is attained. Habitat conditions that are conducive to rapid growth and hence early attainment of the threshold size for flowering may be particularly important for the invasion process in introduced monocarpic perennials. The recently developed method of herb-chronology (analysis of annual rings in the secondary root xylem of perennial forbs) allows efficient age determination in perennial forbs that have annual rings in the permanent main roots (Dietz and Ullmann, 1997, 1998; Dietz, 2002; von Arx and Dietz, 2006). Therefore, the use of this method makes it possible to relate individual age directly to reproductive investment in invasive perennial forbs.

The present study provides the first information on the age at which the monocarpic invasive species *Heracleum mantegazzianum* flowers and sets seed in the native and invaded distribution ranges and compares reproductive output and other related population characteristics between both ranges. *Heracleum mantegazzianum* is one of the major plant invaders in Europe (Tiley et al., 1996). Despite an increasing number of studies that have helped to reconstruct its invasion history (Pyšek, 1991, 1994; Pyšek et al., 1998; Müllerová et al., 2005) and contributed to understanding its biology and ecology (Pyšek et al., 1998; Moravcová et al., 2005; Krinke et al., 2005), there is virtually no information about the biology and behavior of this species in its native range. The only exceptions are studies associated with the use of the *Heracleum* species as agricultural crops, without any relevance to invasion dynamics (Satsyperova, 1984). Although grazing has been recommended to control invasive populations of *H. mantegazzianum* (Nielsen et al., 2005), its effect on the life cycle and demography of this species remains unknown. The need for studying plant invasions in relation to grazing is further accentuated by the fact that the effect of grazing on alien species may vary and does not always lead to their suppression (Petryna et al., 2002; Kimball and Schiffman, 2003; Dorrough et al., 2004)

By studying the population structure and reproductive effort of *H. mantegazzianum* among distinct habitats in its native (Caucasus) and invaded (Czech Republic) distribution ranges, we aimed to answer the following questions: (1) Does the population age structure and the related age at flowering of *H. mantegazzianum* differ between the native and the invaded ranges? (2) Is reproductive output related to age at flowering? (3) How do these patterns vary between managed and unmanaged habitats in the two ranges?

MATERIALS AND METHODS

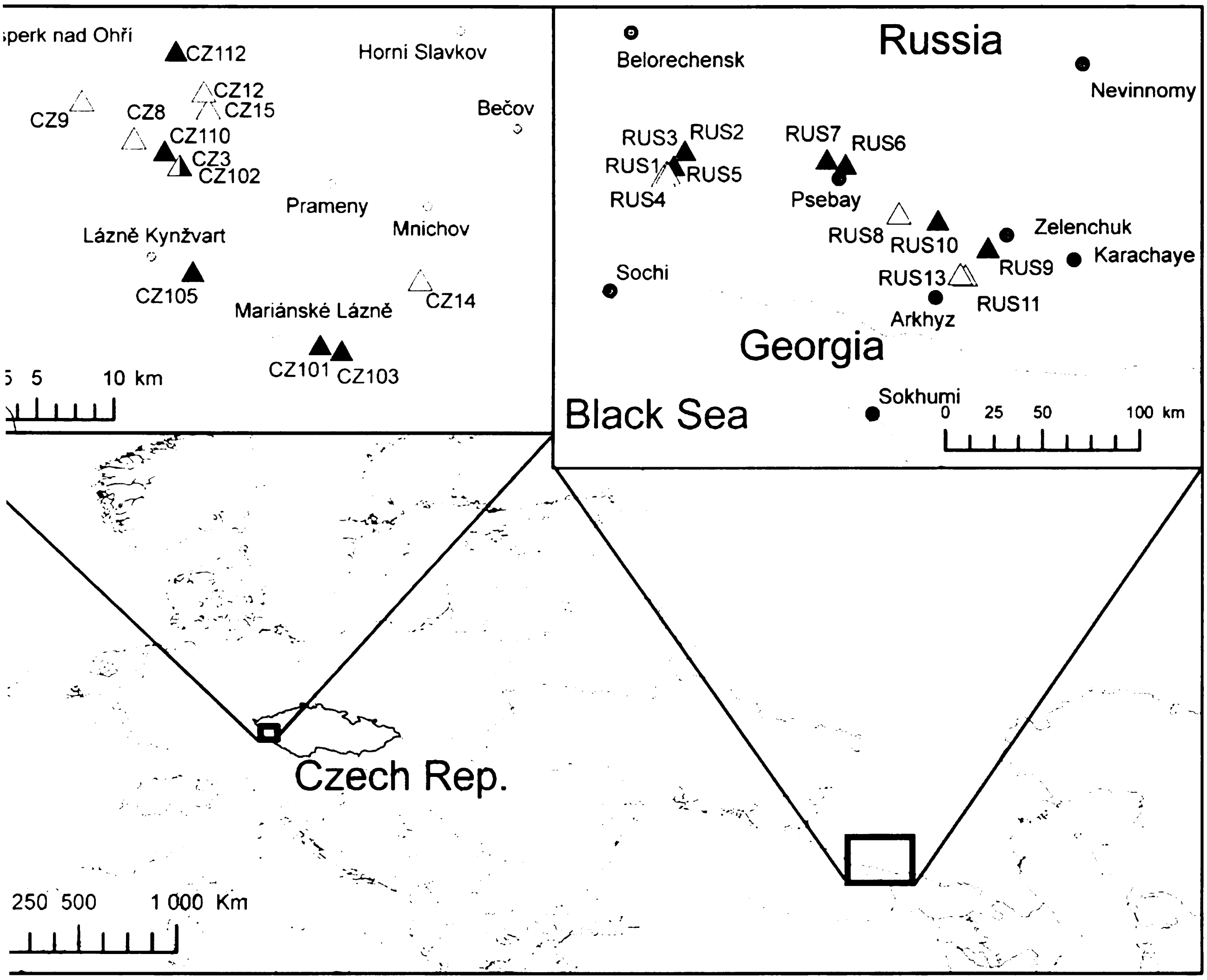
Study species—The monocarpic perennial *Heracleum mantegazzianum* Sommier et Levier (Apiaceae, Giant hogweed) is the tallest herbaceous species in Europe; it reaches 200 to 500 cm in height with leaves up to 300 cm long. The plant develops a thick but relatively soft, permanent taproot with an additional two to five parallel vertical roots, which usually develop in the following years and eventually give rise to a flowering stem that may reach up to 15 cm in diameter. The flowers (compound umbels of four orders; Moravcová et al., 2005) are insect-pollinated and protandrous, but self-fertilization within the same plant and the same umbel is possible (Perglová et al., 2006). *Heracleum mantegazzianum* produces a large number of fruits, which split into two-winged mericarps, each containing one seed (Moravcová et al., 2005). Estimates of seed production range from 5000 to more than 100 000 seeds per plant (Pyšek et al., 1995; Tiley et al., 1996), however, the values of 10 000–20 000 seem to be the most common average in Europe, with maxima occasionally reaching around 50 000 fruits (Perglová et al., 2006). *Heracleum mantegazzianum* reproduces exclusively by seed and forms a short-term persistent seed bank. A small proportion (less than 3%) of the seeds remain viable in the soil for at least 2 years (Krinke et al., 2005). Seeds released from parent plants are morphophysiologically dormant; i.e., a period of emb growth is required and dormancy is broken by wet and cold conditions o winter. After dormancy is broken, the germination rate is about 90% regard of where on the parent plant the seeds were produced (Moravcová et al., 20

Heracleum mantegazzianum is native to meadows, clearings, and fo margins at higher altitudes in the western Caucasus (Russia, Geor (Mandenova, 1950) where it grows in species-rich, tall-herb moun meadows up to the treeline (at ca. 2000 m). Due to its size and ex appearance, it became popular as a garden ornamental and was introduce many European countries. Now it is naturalized or invasive in many Europ countries and central Russia (Tiley et al., 1996; Nielsen et al., 2005). It is naturalized in Canada and the United States (Morton, 1978; Ochsmann, 19 Kartesz and Meacham, 1999). The first record in the Czech Republic dates b to 1862 (chateau in Lázně Kynžvart in W. Bohemia). In later years, it spr spontaneously across the country and became invasive (Pyšek, 1991; Pyšek Pyšek, 1995; Pyšek et al., 2002; Müllerová et al., 2005). The species o develops large stands (Müllerová et al., 2005), dominates invaded sites, a replaces the native vegetation (Pyšek and Pyšek, 1995; Tiley et al., 19 Besides threatening biodiversity and landscape management in the inva area, its phytotoxic chemicals can harm humans and livestock (Drever a Hunter, 1970; Tiley et al., 1996). So far programs to control the spread of species have only had limited success (Nielsen et al., 2005).

Study areas—The study was conducted in the Caucasus (native distribu range) and the Czech Republic (invaded distribution range). The study are the Caucasus was located in the western part of the Russian territory (Fig between 570 and 1735 m a.s.l. (Table 1). Climatic data are only available for localities in the Arkhyz area, but reasonably reflect the climate in the wh region; the January temperature varies between −36 and 16°C and the J temperature between −3 and 35°C. Total annual precipitation is 863 mm (3 average, Russian Hydrometeorological Institute). The study area in the Cz Republic was located in the Slavkovský les Protected Landscape Area, Bohemia (see Krinke et al., 2005 for details), in the vicinity of the introduction of *H. mantegazzianum* to the country in 1862 (Pyšek, 1991). altitudinal range of the study area is 370–980 m a.s.l. (Kos and Maršák 1997; Table 1). The climate is temperate with January temperatures betw −5.1 and −0.2°C (min/max) and July temperatures between 10.5 and 21.5 The total annual precipitation is 1094 mm (Mariánské Lázně meteorolog station, 50-yr average). Strong invasion of the region by *H. mantegazzia* started in the 1940s, following an 80-yr lag phase (Pyšek and Prach, 1993). extensive areas are heavily infested by the species (Müllerová et al., 2005

In both study areas, populations of *H. mantegazzianum* were sample unmanaged and managed habitats. Unmanaged habitats in the Caucasus mountain meadows or former clearings located between the altitudes of 90 1700 m a.s.l. and harboring tall-herb communities. To simplify compariso between ranges, we use the term unmanaged for possibly natural sites of t species (Mandenova, 1950; Tiley et al., 1996) as well as for sites where huma created forest clearings and left them without further management. The spec does not form dense stands in these habitats in Caucasus but rather populatio of scattered plants in species-rich communities with *Angelica purpurascen* *Cirsium* sp., *Dactylis glomerata*, *Petasites* sp., *Pulmonaria* sp., *Rumex alpin* and *Telekia speciosa* as dominant species (J. Pergl and I. Perglová, unpublishe data). In submontane areas of the Caucasus, *H. mantegazianum* spreads in river valleys, abandoned fields, and pastures. Six pastures, located betwe 500-1300 m a.s.l., were included as managed habitats in the native range. these sites, the cover of *H. mantegazzianum* was higher than at the unmanag sites (Table 1). In each region, the study sites were distributed so as to cover t range of variation in environmental conditions and management. Within th Czech Republic, unmanaged sites were grasslands and abandoned settleme and their surroundings; these sites were located where populations have be developing undisturbed for several decades (Müllerová et al., 2005). In bo areas studied, managed habitats were cattle and sheep pastures, but grazing wa more intensive and regular in the Czech Republic (pastures are fenced an overgrazed three times a year) than in Caucasus where extensive grazing traditionally applied (smaller droves of livestock or individual animals mov freely in unfenced areas). In both managed and unmanaged habitats in th Czech Republic, *H. mantegazzianum* forms dense stands with a more or le closed canopy (Table 1).

Population sampling—Six sites (populations) were sampled for ea combination of distribution range (native/invaded) and habitat type (manage unmanaged) during 2003 and 2004 (Table 1). To cover a wider range of habi



Location of the study areas in the native (Caucasus) and invaded (Czech Republic, Central Europe) distribution ranges; ▲ managed, △ d habitats.

in which the species occurs (Krinke et al., 2005; Moravcová et al., l et al., 2006), an additional site was sampled in the Czech Republic, ed in analyses because it was on extremely dry soil. Because soil have been reported to affect the age of flowering in some species 1997), representative soil samples were taken in each study site and sing standard methods for pH_{H_2O}, pH_{KCl}, content of Mg, Ca, K, P, tage of N and C (Page et al., 1982; Moore and Chapman, 1986). Soil ere collected at 10–20 cm depth, air-dried, sieved (2 mm mesh sieve), in paper bags. Although the soil parameters varied largely among not shown), we did not find any significant relationships with the d population parameters of *H. mantegazzianum* and therefore did not n further analyses.

ver possible, we sampled the central part of the population at each imize edge effects. The area used for sampling was small relative to extent of the populations. Therefore, for low-density populations, no differences between the edge and inner parts, so that the bias due edge effect could be avoided. We established a plot of a minimum ^{2} within which all plants with leaves larger than 5 cm were recorded. reshold was set to avoid collecting plants that had germinated in the npling. The sampling area was gradually extended to 2, 4, 6, 9, 12, , respectively, until at least 30 plants (vegetative or flowering) were o measure the density of vegetative and flowering plants in very ulations, the position of individual plants was mapped without plots, and x and y coordinates. If the number of flowering plants within the plots was below 10, we collected flowering individuals from the nearest neighborhood of the plot until the sample size of 10 individuals was reached. Only at the RUS 5 site was the number of plants too low to sample 30 individuals. In each population, we recorded the population density and determined the age, stage, and the reproductive score (vigor) of each sampled individual. Plants from the neighborhood were not considered in analyses related to the density and age structure of populations.

In late July and August, we determined individual age by means of herbchronology, i.e., analysis of annual rings in the secondary root xylem of perennial forbs (Fig. 2; Dietz and Ullman, 1997; Dietz and Schweingruber, 2002). For this the primary (main) root of each sampled plant was obtained from at least 15 cm below the top of the root. Only the core (xylem) part of the root was collected, stored in a cold environment, and analyzed within the next 3 days. Thin cross-sections of the root xylem were cut 10 cm from the root crown. Annual rings were counted immediately after staining the cuttings with phloroglucinol-HCl (Dietz and Ulmann, 1997). A minimum of two sections was analyzed for each plant. To verify the results from the field, annual rings were also analyzed in plants of known age that were grown from seedlings in the experimental garden of the Institute of Botany, Průhonice, since 2002. In these plants annual rings were reliably formed, confirming the annual nature of root rings in *H. mantegazzianum*.

For technical reasons, it was impossible to count the number of fruits of *H. mantegazzianum* in the field. We therefore developed an alternative approach to determine and compare the reproductive vigor of the plants. The complex

TABLE 1. Location and characteristics of study sites and population parameters for *Heracleum mantegazzianum* in its native (RUS, Caucasus) a invaded (CZ, Czech Republic) distribution ranges. Habitat type: man = managed, unm — unmanaged. Analyzed plants: Veg = vegetative, Flow Flowering. na = not available.

Location	Region	Latitude (N)	Longitude (E)	Altitude (m a.s.l.)	Habitat type	Population density (plants/m²)	Median plant age (maximum)	No. analyzed plants		Mean reproductive s (± SD)
								Veg	Flow	
RUS2	Lago-Naki	44°14′	40°07′	877	man	3.7	5 (6)	20	13	—
RUS3	Lago-Naki	44°10′	40°04′	1285	man	4.2	5.5 (7)	20	10	—
RUS6	Psebay	44°10′	40°52′	572	man	8.5	4 (5)	29	13	—
RUS7	Psebay	44°11′	40°46′	672	man	2.9	3.5 (4)	28	10	—
RUS9	Arkhyz	43°47′	41°31′	1061	man	7.5	4 (5)	29	10	—
RUS10	Pregradna	43°55′	41°17′	943	man	3.2	4.5 (5)	20	12	—
RUS1	Lago-Naki	44°08′	40°02′	1431	unm	11.0	4 (6)	36	10	11.94 ± 1.8
RUS4	Lago-Naki	44°07′	40°01′	1465	unm	7.3	3 (4)	40	10	12.42 ± 1.75
RUS5	Lago-Naki	44°08′	40°02′	1455	unm	0.3	5 (7)	14	10	14.21 ± 2.54
RUS8	Pregradna	43°56′	41°07′	922	unm	5.5	3 (4)	21	10	10.65 ± 1.91
RUS11	Arkhyz	43°39′	41°25′	1735	unm	1.7	5 (6)	20	10	10.68 ± 1.1
RUS13	Arkhyz	43°04′	41°24′	1500	unm	0.6	4 (4)	23	10	15.43 ± 3.7
CZ102	Slavkovský les	50°40′	12°38′	790	man	12.3	5 (7)	61	10	—
CZ103	Slavkovský les	49°57′	12°44′	660	man	12.0	4 (5)	37	12	—
CZ105	Slavkovský les	50°00′	12°38′	630	man	9.0	5 (7)	48	13	—
CZ110	Slavkovský les	50°04′	12°37′	710	man	14.5	4 (5)	28	10	—
CZ111	Slavkovský les	50°04′	12°44′	778	man	12.0	5 (7)	48	10	—
CZ112	Slavkovský les	50°08′	12°37′	553	man	7.3	4 (5)	33	10	—
CZ3	Slavkovský les	50°04′	12°38′	788	unm	6.2	3 (4)	38	10	na
CZ8	Slavkovský les	50°05′	12°36′	643	unm	3.3	3 (4)	31	10	13.26 ± 2.0
CZ9	Slavkovský les	50°06′	12°34′	506	unm	6.5	3 (4)	28	10	13.14 ± 1.05
CZ12	Slavkovský les	50°06′	12°39′	596	unm	1.3	3 (3)	22	10	13.42 ± 1.51
CZ14	Slavkovský les	49°59′	12°46′	752	unm	3.8	3 (4)	34	10	13.23 ± 1.56
CZ15	Slavkovský les	50°06′	12°38′	596	unm	3.0	3 (4)	18	12	11.98 ± 1.44

Note: The reproductive score was not determined for plants in managed habitats because the levels of damage and regeneration of the abovegrou plant mass varied. Codes for localities in the Czech Republic correspond to the numbering used in Moravcová et al. (2005) and Krinke et al. (2005)

flowering architecture of *H. mantegazzianum* (Tiley et al., 1996; Moravcová et al., 2005) results in each umbel contributing differently to the overall seed set. To estimate the reproductive output of individual plants, coefficients reflecting the relative importance of umbels of particular order were developed, based on seed production of umbels on 100 test plants studied in the field. The proportional contribution of the terminal umbel (first order), satellite and terminal umbels of branches (second order), and umbels of third order to overall seed set was 5 : 1 : 0.05 (I. Perglová, unpublished data). These coefficients were summed for each plant yielding a reproductive score based on all umbels of all orders. The reproductive score was not determined for grazed plants on pastures because plants at different sites were in different stages of recovery from damage by grazing. This made it impossible to estimate the number of potential umbels and seeds produced.

Statistical analysis—All analyses were performed with S-PLUS (2001). We tested for differences in the age of flowering plants between distribution ranges and habitat types using factorial ANOVA with interactions. All six sites per range/habitat type combination were included in the analysis. Habitat type and distribution range were included as fixed factors. As sites in the native and invaded ranges as well as within habitat types differed in altitude (ANOVA; distribution range: $F_{1,20} = 5.687$, $P = 0.027$; habitat: $F_{1,20} = 24.422$, $P < 0.001$), its effect was filtered out from the model by replacing the age with residuals from a linear regression of the age on altitude ($F_{1,22} = 4.357$, $P = 0.048$). This approach was used due to the relatively small number of replicates within a group, compared to the number of tested factors. Preliminary analysis showed significant interactions between habitat types and sites nested within ranges that cannot be reasonably interpreted, so the age of flowering plants was averaged within sites to avoid the nested design. This allowed for simplifying the model without losing any important information. Means across sites were transformed by reciprocal transformation, which was checked for appropriateness by the Box-Cox method (Crawley, 2002) and by normal probability plots of the fitted values.

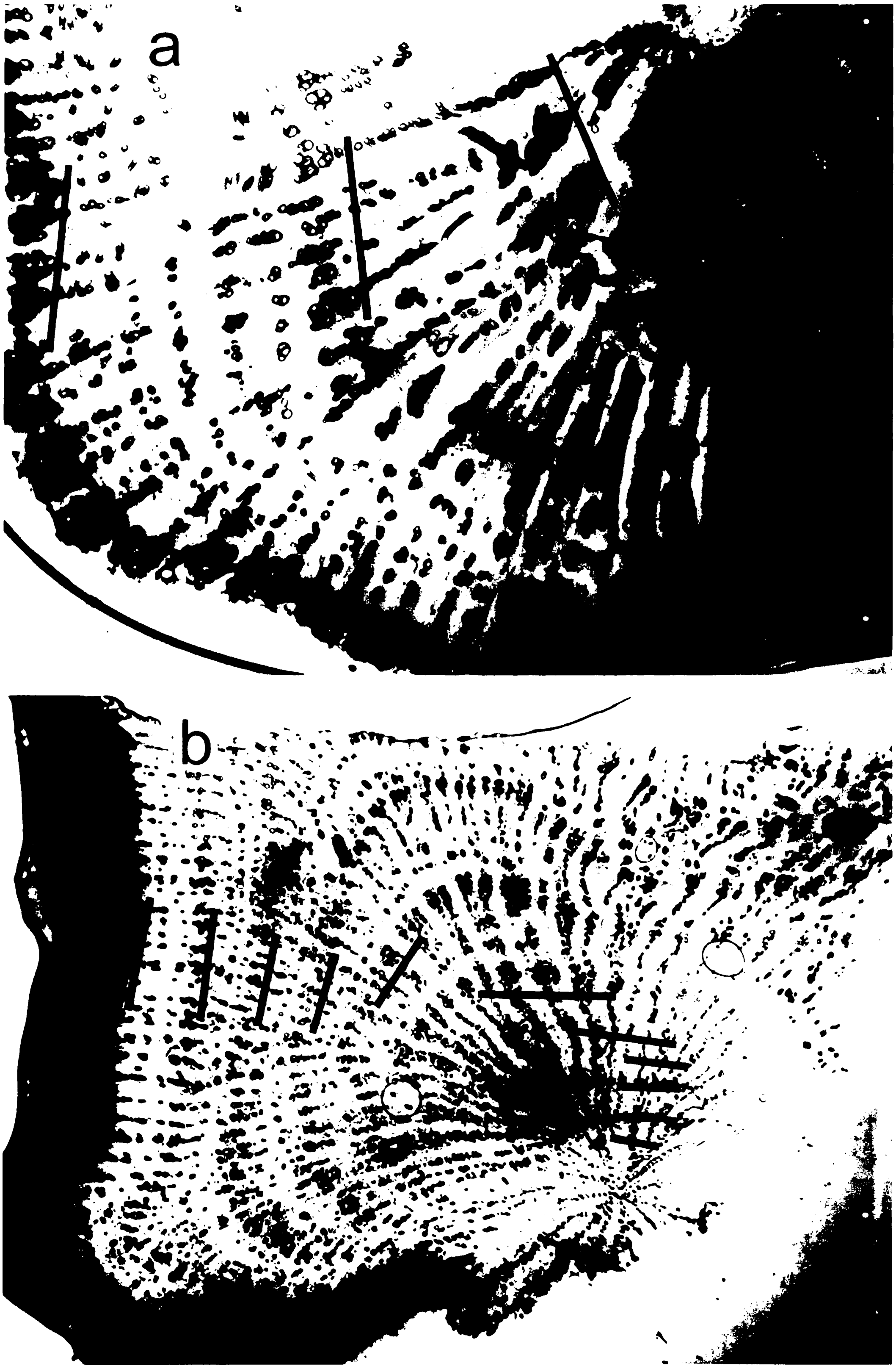
The effect of distribution range and habitat type on the proportion of flowering plants was tested using a two-way ANOVA. The proportion of flowering plants was calculated as their percentage of the total number of plants older than 1 year that were recorded within the sampling plot. Differen between frequency distributions of the ages at flowering were tested usi multiple G tests with Bonferroni's correction (Zar, 1999).

Only unmanaged sites were used to analyze the reproductive score flowering plants. Locality CZ3 was excluded from the analysis because missing information on the number of umbels on plants. Data were analyz using ANCOVA with site nested within distribution range and age of flower plants included as a covariable. The minimal adequate model for t reproductive score was determined by using stepwise selection from t maximal model based on the Akaike information criterion (AIC). This meth weighs the significance of a model by its complexity (Crawley, 2002).

For population density analyses, only individuals older than 1 year we used. Data were analyzed by two-way ANOVA with interactions, using t same set of populations as in the analysis on age at flowering. Distributi range and habitat type were included as fixed effects and the density vegetative plants and number of flowering plants within a sample plot we used as response variables.

RESULTS

Population density—In most habitats in both ranges, t mean population density of *H. mantegazzianum* varied betwe 4 and 5 plants/m^2 (Table 2). In managed sites in the introduce range, the mean population density was significantly high with 11 plants/m^2 (significant interaction between range an habitat type in their effect on population density; Table 3 an subsequent one-way ANOVA for each combination). Th variation in density between unmanaged sites was remarkabl high in the native area, ranging between 0.3 and 11 plants/m Population density was not significantly related to altitud (regression on pooled data: $F_{1,22} = 2.07$, $P = 0.16$).



Cross-sections of the root showing the annual rings in the secondary xylem of a (a) 4- and a (b) 12-yr-old individual. The markers indicate the between latewood of the previous year and the earlywood of the following year.

TABLE 2. Density of *Heracleum mantegazzianum* populations (individuals/m^2) and age of flowering plants in different habitat types of the native and invaded distribution range. Population density includes both flowering and vegetative plants older than 1 year.

		Population density (indiv/m^2)		Age (yr)	
Distribution range	Habitat type	Mean	SD	Median	Max
Native (Caucasus)	unmanaged	4.38	3.91	4	7
	managed	4.99	2.18	5	7
Invaded (Czech Republic)	unmanaged	4.58	1.86	3	4
	managed	11.17	2.37	5	7

Age of flowering plants—All 302 flowering plants of *H. mantegazzianum* that were aged were at least 3 years old. In unmanaged sites, the median age of flowering plants was 3 yr in the invaded and 4 yr in the native range, while in managed sites it was 5 yr, irrespective of the origin of the plants (Table 2). In unmanaged sites in both distribution ranges, relatively more plants flowered at the age of 3 yr than at any other age, and the number of flowering plants tailed off at increasingly higher ages. In managed sites, in contrast, the highest proportion of flowering plants was found among the 4- or 5-yr-old plants (Fig. 3). In unmanaged sites in the Czech Republic, the maximum age of flowering plants was 4 yr, while in managed sites in the Czech Republic as well as in both habitat types in Caucasus, it was 6 or 7 yr. The oldest flowering plant was 12 yr old, but it grew at the extremely dry, unmanaged locality in the Czech Republic (invaded range), which was not used in statistical analysis. The population in this site was clearly an outlier because the majority of plants flowered between the 5th and 8th year, in remarkable contrast to other unmanaged populations from the invaded range.

Because the interaction between habitats and ranges was significant (Table 3), the analysis was done separately for each habitat and range combination. Plants from unmanaged habitats in the native Caucasus region tended to flower at a later age than those growing in the corresponding habitats in the Czech Republic (subsequent one way ANOVA; $F_{1,10} = 8.74$, $P = 0.014$; Tables 2 and 3). Plants growing in the managed habitats in the invaded range lived longer, i.e., they flowered later than those in unmanaged habitats in the same range ($F_{1,10} = 24.06$, $P < 0.001$; Tables 2 and 3). There were no differences between unmanaged and managed habitats in the native distribution range ($F_{1,10} = 0.50$; $P = 0.50$), and managed habitats did not differ between ranges ($F_{1,10} = 0.0001$; $P = 0.99$). The difference in unmanaged habitats between distribution ranges was mediated through altitude because it disappeared once th altitude was filtered out. In this model, the habitat–rang interaction became nonsignificant and so did distribution rang ($P = 0.67$), while the significance level of habitat increased (P 0.001; Table 3). This is an evidence for a strong effect of altitu on the age at flowering, although it was not possible to test th relationship directly because of a limited number of sampl within groups (native sites are located at higher altitude and sit at comparable altitudes do not exist in the invaded range).

Age at flowering was not significantly related to populatio density as indicated by a regression ($F_{1,22} = 0.613$, $P = 0.44$

The frequency distribution of age at flowering indicates th in managed sites the highest proportion of flowering plan occur at intermediate age (Fig. 3). In unmanaged sites, on t contrary, the proportion of flowering plants decreased wi increasing age across the whole range of age classes. This hol for both distribution ranges, but the decrease is most profound unmanaged sites of the invaded range. Proportions of floweri plants were significantly different among habitats within rang as well as among ranges within habitats (all *G* tests were high significant; $P < 0.001$). The proportion of flowering plants the youngest age class in unmanaged sites in the Czech Repub and Caucasus was 89% and 31%, respectively.

Proportion of flowering plants—The percentage of flow ing individuals among all individuals older than 1 year w rather similar across distribution ranges and habitats (Fig. The mean values ranged from 16% in managed sites in t Czech Republic to 29% in managed sites in the Caucasus a were not significantly related to distribution range ($F_{1,20}$ 0.118), habitat type ($F_{1,20} = 0.434$), or their interaction ($F_{1,2}$ 1.970, $P = 0.176$).

The proportion of flowering plants in individual age clas (cohorts) increased with the age of the cohort (Fig. 4), and t pattern observed reflected the differences in the mean age flowering, with postponed flowering of plants in the nat range and managed habitats (Fig. 3). In the native range, nea half of the plants in a population flowered in the 4th year, a this proportion increased to 62–75% and 88–100% in subsequent age classes. The most remarkable differen between habitat types within the native range was in the year, with almost one third of plants in unmanaged si flowering but with only 10% flowering in managed habit Managed sites in the invaded range harbored a consisten lower proportion of flowering plants up to the 7th year wh the majority of plants in the population flowered. Unmanag habitats in the invaded range had a pattern remarkably disti from all other sites with flowering concentrated in the 3rd a 4th years when over a half of the plants flowered (Fig. 4).

TABLE 3. Summary of ANOVA showing the effect of distribution range and habitat type on the density of populations and age of flowering plant *Heracleum mantegazzianum*. The results for analysis of age cover the full model, and a model with altitude being held constant (see Materials methods/Statistical analysis for details on statistical treatment).

		Population density			Age of flowering					
					Full model			Altitude held constant		
Source of variation	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Habitat	1	90.13	10.37	0.004	0.0165	10.68	0.004	0.0262	23.06	<0.
Range	1	50.79	5.84	0.025	0.0069	4.43	0.048	0.0002	0.16	0.
Habitat × range	1	64.02	7.37	0.013	0.0067	4.35	0.050	0.0018	1.62	0.
Error	20	8.69			0.0015			0.0011		

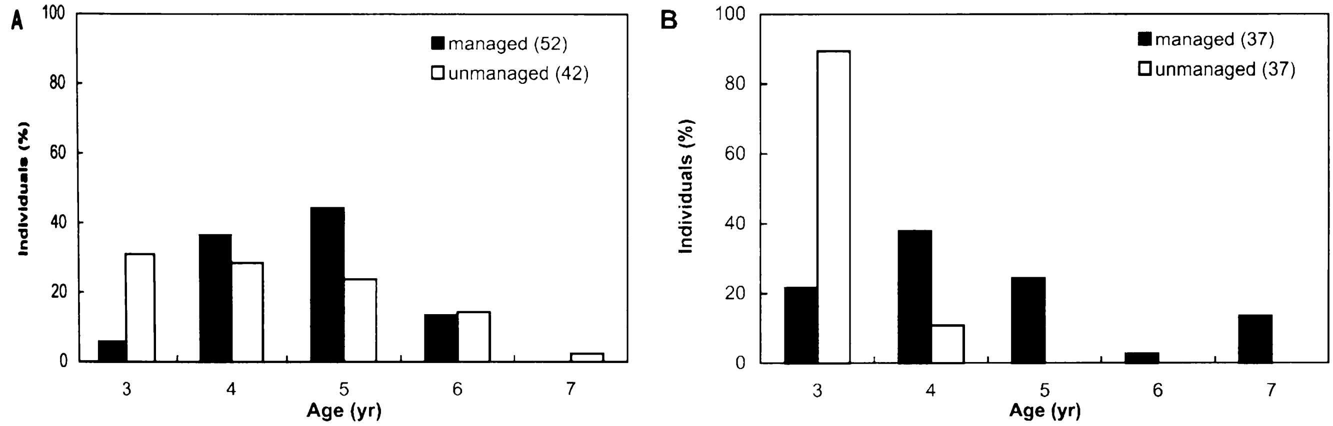


Fig. 3. Frequency distribution of age at flowering in managed and unmanaged habitats in the (A) native and the (B) invaded distribution range. Numbers in the key are sample sizes (number of individuals) at each site.

Variation in reproductive score with plant age—The reproductive scores of individual flowering plants in both distribution ranges varied between 9 and 15, corresponding to 10 000–25 000 seeds per plant. Selection toward the minimal adequate model (based on AIC) showed that reproductive score was not related to plant age. The reproductive scores differed significantly among sites within distribution ranges (ANOVA, $F_{9,94} = 4.81$, $P < 0.001$), but not between distribution ranges ($F_{1,9} = 0.26$, $P = 0.622$). The mean values (± SD) were very similar in unmanaged habitats in the native range (12.6 ± 2.9, $N = 60$) and in the invaded range (13.0 ± 1.65, $N = 45$).

DISCUSSION

Our study is significant in the context of current research on plant invasions (e.g., Richardson and Pyšek, 2006) in that it compares the population ecology of a problematic invasive plant between the native and the introduced range to gain understanding of the mechanisms underlying the invasion success of the species (Hierro et al., 2005). For analysis of the age structure and especially timing of reproduction, which is a key trait of a nonclonal monocarpic species like *H. mantegazzianum*, we used the relatively recent approach of herb-chronological dating. The method allows direct access to this important parameter without the need to perform multiyear surveys. A population with individuals at a younger age at reproduction introduces more seeds to the system. Therefore, our approach allowed us to efficiently investigate whether there is early flowering in invasive populations, probably favoring invasion.

Population structure and patterns of reproduction in Heracleum mantegazzianum—Our results provide the first information on the age structure in populations of *H. mantegazzianum* in its native and invaded distribution ranges. In different habitats in both regions, the species had relatively broad age distributions for a monocarpic perennial forb. The shape of the age structure was determined by the age at flowering because each plant dies after seed production. Under favorable site conditions, many monocarpic perennial forbs can flower in the second year of growth (e.g., Reinartz, 1984; De Jong et al., 1986). However, in *H. mantegazzianum* all plants sampled in the field flowered at the age of 3 years or later. Flowering in the second year was only observed in about one third of plants (22 out of 70) grown from seed under favorable conditions in a common garden (J. Pergl et al., unpublished data). Two-year-old flowering individuals were also reported from a common garden hybridization study on *H. mantegazzianum* and *H. sphondylium* in Scotland (Stewart and Grace, 1984). At the other end of the gradient, we found few individuals in this study and a previous pilot study that lived for more than 10 yr before entering the flowering stage. Such remarkable variation in the life span of *H. mantegazzianum* indicates rather high phenotypic plasticity in the timing of flowering in response to varying resource accumulation in distinct habitats (cf. Harper and White, 1974; Gross, 1981; De Jong et al., 1998).

There are reports on perennation of flowering individuals of *H. mantegazzianum* into the following year from both native and invaded distribution ranges (Tiley et al., 1996; Shumova, 1972; Morton, 1978; Tiley and Philp, 1997). However, surviving flowering plants were never observed in our study. Roots of flowering plants always died during mid summer, and by late summer their central parts were almost completely decayed. The strictly monocarpic life history of the species was further demonstrated in a common garden experiment in which none of the flowering plants survived into the following year, not even when all flowering umbels were removed before seed set (Pyšek et al., 2006). The reported survival of flowering plants into following years may be attributed to misinterpretation. Plants often grow in clumps, where a group of seedlings germinated in a safe site (sensu Harper, 1977), and vegetative plants that did not flower in the previous year sprout in close vicinity of the last year's dead stem. Without closer inspection, they may be considered as resprouting from the rootstock leading to the wrong conclusion that the species is polycarpic (Morton, 1978).

The general trend of flowering at a later age and a wider range of ages of flowering plants in the native Caucasus as compared to the Czech region in unmanaged sites can be related to the effect of altitude and associated differences in environmental conditions, in particular the length of the vegetation period, which is considerably shorter in the high mountains. However, in managed habitats, the age of flowering plants did not differ between distribution ranges, suggesting that management effects like pasturing are of greater

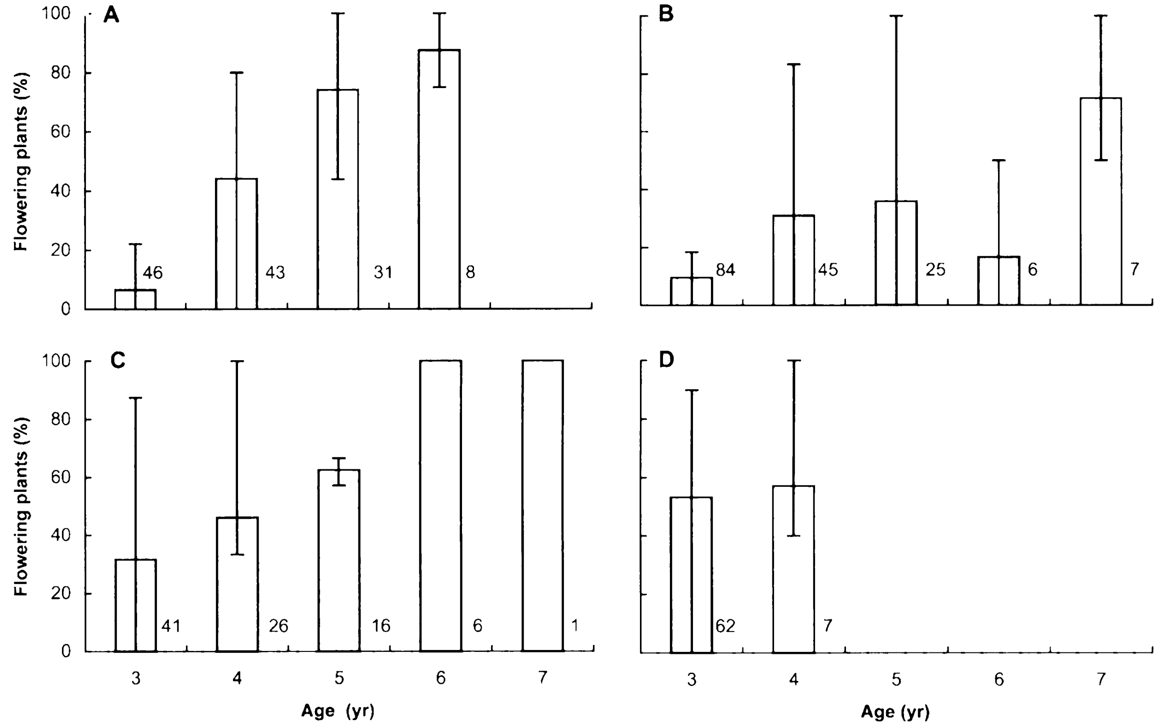


Fig. 4. The mean percentage of flowering plants of *Heracleum mantegazzianum* within individual age classes (cohorts), shown separately for differ distribution range–habitat combinations (A) native/managed, (B) invaded/managed, (C) native/unmanaged and (D) invaded/unmanaged. For th combinations, the values were averaged across study sites. Minimum and maximum proportions are indicated by the length of vertical lines. Sample si are shown next to each column.

importance for population development of *H. mantegazzianum* than climatic differences. Across distribution ranges, we found clear evidence that flowering of *H. mantegazzianum* was postponed to later ages in managed habitats, and this pattern became even more pronounced when altitude was held constant. Plants growing in pastures probably need more time for sufficient resource accumulation to start flowering because of repeated biomass removal and trampling, which may not only injure the plants directly but may also impair growth by soil compaction. Similar results indicating that the age of plants at or above a threshold probability of flowering increases with the adversity of site conditions were found for other perennial forbs (e.g., Werner, 1975; Dietz and Ullmann, 1998). Interestingly, the oldest plants were not found in a pasture but in an unmanaged site in the invaded range. In the latter, strong constraints on resource accumulation imposed by low water availability appear to have resulted in a very extended vegetative growth phase (note that the chemical composition of the soil was similar across distribution ranges and habitat types). This contrasts with other unmanaged sites in the Czech region where almost all plants flowered early compared to managed habitats or the native area.

The proportions of flowering plants within individual cohorts indicate a similar population structure in the native distribution range, regardless of the type of management, and in managed sites in the Czech Republic. Grazing in the invaded range results in more evenly distributed flowering across age classes, an effect similar to relatively severe climatic conditions in the native range of Caucasus. Plants in unmanaged sites in the invaded range seem to be less affected by these constraints, and favorable conditions appear to cause early flowering in t majority of individuals.

Reproductive output of *H. mantegazzianum* did not incre with the age of plants. This indicates the existence a threshold in the amount of resources needed to trig flowering as in other monocarpic species where age flowering is a function of the rate of resource accumulati (e.g., Harper, 1977; Crawley, 1997). Our snapshot analyses well- and long-established populations indicate that, indep dent of the presence or absence of habitat management or position in the distribution range, the reproductive output of *mantegazzianum* populations appears to be maintained o time by a stable proportion of flowering plants. Correspo ingly, in a previous study using longitudinal data from ae photographs spanning 40 yr of invasion, the percentage flowering individuals was rather stable since the beginning the invasion of a site (Müllerová et al., 2005). *Heracle mantegazzianum* thus appears to maintain high and sta reproductive output over both space and time in differ environmental settings.

We have no indication that the range of population densit observed in our study affected the age at flowering or reproductive vigor in *H. mantegazzianum*. Populations with highest density were found in managed sites in the inva range, probably due to higher grazing pressure compared a more extensive grazing in the Caucasus (lower rate of num of cattle per unit of area). Dispersal of *H. mantegazzian* seeds by the cattle, disturbances associated with grazing, a the regular removal of above-ground biomass minimizi

ific and intraspecific competition may have promoted
establishment at these sites.

·ations for invasion—The vigorous populations of *H.*
::ianum recorded in this study correspond to previous
vhich showed that the species was little constrained by
ıcteristics of the invaded environment (Moravcová et
: Müllerová et al., 2005). This broad ecological niche
ecies and its high plasticity in the timing of flowering
adds to its high invasiveness. But are there clear
es in population parameters between the native and
ranges, and what can be inferred from these with
the remarkable success of *H. mantegazzianum* as an
The early flowering in unmanaged habitats and a high
ɔn density in managed habitats indicate more rapid
ɔn development in the invaded area than in the native
ch might have contributed to the accelerated spread of
ies in the Czech region.
:ic matching between the native and the introduced
ch is of primary importance for a species' ability to set
the new region (Pauchard et al., 2004; Liška and
2004; Thuiller et al., 2005), is often crucial for suc-
ıvasion. Early flowering of *H. mantegazzianum* in the
ed sites in the Czech region may have been promoted
favorable climatic conditions than exist in the high
ıl belt of the native region of the Caucasus. The ability
ɔcies to accelerate its life cycle under these conditions
ve resulted in increased production of highly
ɔle seed (Moravcová et al., 2005), mainly in the early
f habitat colonization.
:h population densities, plant individuals may have
seed set, the principle underlying the law of constant
ırper, 1977). However, across the range of densities
in our study the reproductive score of *H. man-*
ıum individuals did not decline with density. Hence,
population densities observed in managed habitats in
ded area translate into higher seed output per area.
ɔn effects of this high seed production with the high
human activity, transport of biomass, and increased
f disturbances in managed habitats may have strongly
l the efficient spread of the species in the Czech

ns that the more favorable climatic conditions in the
gion, together with increased chances for dispersal in
colonized Central European landscape, resulted in
ive invasion. Interestingly, we observed a similar
non in habitats strongly influenced by humans at
itudes of the Caucasus where the species begins to
se stands resembling those in the Czech Republic (J.
l I. Perglová, personal observation). This suggests that
ıvasions in part may not be unique phenomena driven
ic conditions in the new area but may be paralleled by
ns of the same species in the native area as a result of
ctors such as climate change or changing land use.

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3

Historical regional dynamics assessed by aerial photographs

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Aerial photographs as a tool for assessing the regional dynamics of the invasive plant species *Heracleum mantegazzianum*

JANA MÜLLEROVÁ,* PETR PYŠEK,*† VOJTĚCH JAROŠÍK*† and JAN PERGL*

**Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice, Czech Republic; and*
†Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-128 01 Praha 2, Czech Republic

Summary

1. The initiation of an invasion event is rarely dated in studies of alien plants. Data from aerial photographs documenting the invasion from the outset facilitate the quantification of the rate of spread, allowing researchers to analyse species' population dynamics and providing a basis for management.

2. For 10 sites invaded by *Heracleum mantegazzianum* in the Slavkovský les, Czech Republic, aerial photographs from 11 sampling dates between 1947 (before invasion started) and 2000 were analysed. The area covered by the invader was measured digitally in a 60-ha section of landscape, and information obtained on invaded habitats, year of invasion, flowering intensity and structure of patches. Invaded area was regressed on residence time (time since the beginning of invasion) and regression slopes were used to measure the rate of spread. Data were analysed by ANCOVA, multiple regression and path analysis.

3. Pastures and fields contributed 84·7% to *Heracleum* total cover, forest and scrub 13·7% and human settlements 1·6% at the later stage of invasion. The direct effect of the rate of invasion on invaded area (0·82) was greater than that of residence time (0·22), but the total effect (direct and indirect) of residence time was only slightly less (0·79) than that of the rate of invasion (0·82). As invasion proceeded, the populations spread from linear habitats to the surrounding landscape. Mean rate of areal spread was 1261 m^2 year^{-1} and that of linear spread 10·8 m year^{-1}. Flowering intensity did not exhibit any significant trend over time.

4. *Synthesis and applications.* The strong effect of the rate of spread on the invaded area indicates that local environmental conditions hardly limit the spread of *Heracleum*. The species is easily detectable on aerial photographs taken at flowering and early fruiting times, from June to August. Knowledge gained from aerial photographs allows managers to identify dispersal foci and to focus control efforts on linear landscape structures with developing populations. Knowledge of the rate of spread and habitat vulnerability to invasion facilitates the identification of areas at highest risk of immediate invasion.

Key-words: alien plant, beginning of invasion, biological invasions, Czech Republic, historical dynamics, path analysis, population structure, rate of invasion, residence time

Journal of Applied Ecology (2005) **42**, 1042–1053
doi: 10.1111/j.1365-2664.2005.01092.x

Introduction

Invasive species (*sensu* Richardson *et al.* 2000; Pyšek *et al.* 2004) are characterized by remarkable dynamics of spread that allow them to colonize large areas in regions where they are not native. A primary question in invasion biology is: what will the rate of spread of an organism be after the initial establishment at a single location (Hastings 1996)? The issue of invasion dynamics also has a practical aspect: rate of spread has been long recognized as one of the parameters that we need to know if an alien weed is to be controlled, as alien taxa

Correspondence: P. Pyšek, Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice, Czech Republic (fax + 420 2 67750031; e-mail pysek@ibot.cas.cz).

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that exhibit high rates of spread are likely to become widely distributed and troublesome (Forcella 1985). Unfortunately, as the crucial aspect of recognizing an invasive species is the invasion itself (observable only after the event), plant invasions are mostly studied *post hoc* (Fuller & Boorman 1977; Pyšek & Prach 1993; Delisle *et al.* 2003) and studies rarely describe the whole process of invasion from its beginning (but see Robinson 1965; Richardson & Brown 1986; Lonsdale 1993).

Methods used to assess the dynamics of invasion in the past vary with respect to the aims of the study and provide different information, depending on scale (Hulme 2003). At regional to continental scales, herbarium records are informative (Weber 1998; Delisle *et al.* 2003; Petřík 2003; Mandák, Pyšek & Bímová 2004), but such data are usually not informative regarding the increase of area covered by the invader over time. However, the area occupied by an invasive population is a key dimension of an invasion (Higgins & Richardson 1996). Computer image analyses have been used recently to monitor invasive species (reviewed by Everitt *et al.* 1995). Aerial photographs are the most often used remote-sensing technique for detecting plant species. As they can provide area estimates of plant populations, they have been used as a tool for quantitative assessment of the infestation by alien plants (Everitt 1998; Higgins & Richardson 1999; McCormick 1999; Stow *et al.* 2000; Higgins, Richardson & Cowling 2001; Rouget *et al.* 2001, 2003) and the dynamics of their spread (Fuller & Boorman 1977; Mast, Veblen & Hodgson 1997).

The present study dealt with one of the most noxious European invaders, *Heracleum mantegazzianum* Sommier et Levier (Apiaceae) (Tiley, Dodd & Wade 1996), and analysed the dynamics of its invasion at the local scale by using aerial photographs. This invasion was captured since its very beginning, which made it possible to ask questions that can rarely be answered in invasion biology. (i) What is more important in determining the outcome of the invasion, its duration or the rate of spread? (ii) What are the spatial extent and dynamics of the invasion by the species? (iii) How do some parameters of the species' population dynamics change over 40 years of invasion?

Methods

STUDY SPECIES

Heracleum mantegazzianum is a perennial monocarpic herb, 200–500 cm tall, with leaves up to 250 cm in length. Flowers are insect-pollinated, arranged in numerous compound umbels, with the largest terminal up to 80 cm in diameter (Tiley, Dodd & Wade 1996). In the study area, the plants flower from late June to late July. A single plant is capable of producing from 5000 to more than 100 000 fruits (Pyšek *et al.* 1995; Tiley, Dodd & Wade 1996). The seeds exhibit a morphophysiological dormancy (Baskin & Baskin 1998), resulting in a short-term persistent seed bank (Krink 2005). Plants rapidly attain dominance in invad (Pyšek & Pyšek 1995). Disturbed habitats wit possibilities for the immigration of fruit by wat and human-dispersal are more easily invaded. species also invades semi-natural vegetation (P Pyšek 1995; Pyšek, Sádlo & Mandák 2002).

Heracleum mantegazzianum is the largest European forb, native to the western Ca (Mandenova 1950) and naturalized or invasi number of European countries (Tiley, Dodd & 1996; Collingham *et al.* 2000), Canada (Morto and the USA (Kartesz & Meacham 1999). It wa duced to the Czech Republic as a garden ornam the region studied here (Slavkovský les, west Bo in 1862. The species has spread from there t parts of the country (Pyšek 1991; Pyšek *et al.* 19 become invasive (Pyšek, Sádlo & Mandák 200

STUDY AREA

The study area was located in the Slavkovský l tected Landscape Area, west Bohemia, a region invaded by *H. mantegazzianum* (Pyšek & Pyšek The total size of the protected area is 617 km², alti range is 373–983 m a.s.l. (Kos & Maršáková minimum and maximum temperatures are for J −5·1° to −0·2 °C and for July 10·5–21·5 °C. The sum of precipitation is 1094 mm (Mariánské meteorological station, 50-year average). The vegetation of the area is mainly beech and forests, peat bogs, and pine forests on serp (Neuhäuslová & Moravec 1997). This vegetation only present in remnants, and has been replac much of its original extent by extensive wetlan a high diversity of flora, pastures and spruce plan that cover 53% of the area (Kos & Maršáková

Colonization of the region by humans starte end of the 13th century. After World War II, C inhabitants were displaced and part of the regio military area with restricted access until the 196 lack of appropriate landscape management ass with disturbances from military activities, as climatic conditions matching those in the native d tion area (Pyšek 1991), are probable reasons rapid spread of the species in the study area o study period.

Ten study sites with vegetation dominated b *cleum* were selected (Table 1). They were evenly uted across an area of 20 × 30 km to cover the r habitat conditions, and correspond to those in a detailed research on the population biolo ecology of the species is being carried out (Mor *et al.* 2005). Most localities represented open otherwise forested landscape or were separate the surroundings by forests and scrub.

The oldest herbarium specimen documentin certainty a spontaneous occurrence in the stud in close proximity to the introduction site, is fro

Table 1. Geographical location, altitude (m a.s.l.) and area covered by *Heracleum mantegazzianum* (in m^2) as inferred from aerial photographs in 60-ha sections surrounding each site. 0, species not present; –, data not available or not reliable. Note that the locality Rájov was not included into analyses because the species only appeared there recently. Areal rate of spread (m^2 year^{-1}) was calculated as the highest value of invaded area recorded over the study period divided by residence time (= years since the beginning of invasion). Linear rate of spread (m year^{-1}) was expressed as the distance between the location of the *Heracleum* population on the earliest date the species was recorded and the most distant point within the plot reached at the time when the highest value of invaded area was recorded, divided by the residence time. If there were several foci at the beginning, the distance was measured from the one closest to the most distant one on the recent photograph. Note that the mean rate of spread shown here is only a reference measure and was not used in statistical analyses (see the Methods)

				Area covered by *Heracleum* (m^2)								Mean rate of spread	
Locality	Latitude	Longitude	Altitude	1947	1957	1962	1973	1987	1991	1996	2000	Areal (m^2 year^{-1})	Linear (m year^{-1})
Arnoltov	50°06·801	12°36·147	575	0	0	0	966	13 744	11 139	27 251	47 170	1241	12·8
Dvorečky	50°05·982	12°34·137	506	0	0	0	1 074		18 018	24 817		730	17·4
Krásná Lípa II	50°06·306	12°38·393	596	0	0	0	0	5 078	3 324	9 454	7 945	350	3·8
Lískovec	49°59·156	12°38·721	541	0	0	0	0	68	2 755	8 174		355	26·7
Litrbachy	50°06·009	12°43·777	800	0	0	0	551	2 120	2 631	4 711		139	6·6
Potok	50°04·660	12°35·953	643	0	0	5 827	14 619	17 244	28 877	39 774		1020	8·2
Prameny	50°03·173	12°43·751	738	0	0	0	14 099	52 249	46 243	55 575		1635	5·8
Rájov	49°59·704	12°54·933	753	0	0	0	0	0	0	5 198		1040	
Žitný I	50°03·754	12°37·569	787	0	5938	16 413	28 068	113 236	101 701	99 121		2831*	8·0
Žitný II	50°03·837	12°37·304	734	0	0	13 780	35 284	90 902	111 351	–		3275*	8·2

*A conservative value, as in these sites the species may have invaded outside the plot limits in later stages of invasion.

(Holub 1997). However, after that date the species was not recorded again in the study area until 1947, when reports on the scattered occurrence of individual plants started to appear (Pyšek & Pyšek 1994). The absence of *H. mantegazzianum* on aerial photographs from 1947, confirmed by floristic data, allowed us to assume with reasonable certainty that the present study captured the invasion from its beginning. Although the presence of individual plants at the rosette stage cannot be completely excluded, as these would not have been detected on aerial photographs, they would not affect the rather robust results of the analysis of invasion dynamics. Moreover, plants usually flower in the third year (J. Pergl *et al.*, unpublished data) so failure to detect their presence would mean a negligible bias to the dates considered as the beginning of invasion in particular localities.

PHOTO-INTERPRETATION AND ANALYSIS OF AERIAL PHOTOGRAPHS

Aerial photographs of study sites (panchromatic, multispectral and orthophotographs; Table 2) were available from 1947 to 2000 (Table 1). Panchromatic photographs were provided by the Military Topographic Institute VTOPÚ, Dobruška, Czech Republic, and multispectral photographs by the Agency for Nature Conservation and Landscape Protection in Prague, Czech Republic. Orthophotographs at a final pixel resolution of 0·5 m were created by the Czech Office for Surveying, Mapping and Cadastre, Prague, Czech Republic, from scanned aerial panchromatic photographs at a scale of 1 : 22 500 with 60% overlap. A digital terrain model created by vectorization of topographic maps at 1 : 10 000 was used. Orientation points of images were identified by analytical aerotriangulation in the system ORIMA (Leica Geosystems, Geospatial Imaging, Norcross, Georgia, USA); orthorectification was performed on the digital photogrammetric station Leica-Helava DPW 770, module Mosaic (Leica Geosystems).

In each study site, a sector of 60-ha (750 × 800 m) surrounding the recently invaded area was selected and the presence of *Heracleum* within this area investigated. *Heracleum* stands and solitary plants were recognizable in the photographs. Flowering plants appeared as white dots (Fig. 1); on photographs taken in August plants were still recognizable because of the distinct structure of fruiting umbels. Critical examination of the sensitivity of the air photographs to detect single plants was beyond the scope of the current study. However, the very distinct morphological features of the study species (Fig. 1) indicate that the photo-interpretation was unbiased and, together with detailed information on population characteristics collated in the field (J. Pergl *et al.*, unpublished data), provided a reliable estimate of population size.

The process of photo-interpretation consisted of the following steps: (i) scanning of negatives (800 dpi); (ii) rectification using recent ortophotographs, with 40–60 ground control points distributed along the

Table 2. Technical parameters of aerial photographs used in the study

Year	Date	Scale	Type	Channels	Camera	Focal length (mm)	Film material
1947	Unknown	1 : 10 000	Panchromatic	–	RD 20/30	Unknown	AGFA
1957	15–16 June	1 : 12 500	Panchromatic	–	RD 20	210	AGFA
1962	25 June	1 : 12 000	Panchromatic		WILD 328	209·73	Unknown
1973	11–16 August	1 : 27 000	Panchromatic	–	WILD 328	114·36	Unknown
1987	21–23 August	1 : 25 000	Multispectral	0·48, 0·54, 0·66, 0·84 nm	MSK-4	125	FOMA (visible), I-840 (NIR)
1991	23 July	1 : 13 400	Panchromatic	–	LMK 269152B	152·2	FOMA
1996	10 June	1 : 26 500	Multispectral	0·54, 0·60, 0·66, 0·84 nm	MSK-4	125	Aviphot Pan 200PE1 (visible), Kodak Aerographic Film 2424 (NIR)

Fig. 1. Aerial photograph of the locality Žitný lon 23 July 1991 (scale 1 : 2000). Flowering umbels of *Heracleum* appear as white dots.

whole area of the rectified photograph, using the second order of transformation and nearest neighbour rectification method (Lillesand & Kiefer 1999); (iii) visualization of *Heracleum* plants on images (image enhancement, filtering; Jensen 1996) using Chips software (Chips Development Team 1998); (iv) on-screen digitizing of *Heracleum* stands and individual plants using CartaLinx software (Clark Laboratories 1998); (v) digital classification of flowering plants inside the previously defined polygons using Chips software (histogram slicing and Parallelpiped classification), with the number of flowering plants assessed by dividing the total area covered by *Heracleum* by the average size of an individual flowering plant, estimated on the basis of field data (J. Pergl *et al.*, unpublished data); (vi) on-screen digitizing of land-use types using CartaLinx software. The following habitats were distinguished and the area covered by each of them was measured: (i) forests and scrub; (ii) treeless area consisting of pastures, meadows and fields; (iii) urban areas; (iv) linear features (water courses, paths and roads, railways). For each land-use type, the proportion of its total area invaded by *Heracleum* was identified in a GIS using ArcView software (Environmental System Research Institute 1996).

The following parameters were recorded to characterize *Heracleum* invasion at each site: (i) the beginning of invasion, expressed as the earliest date at which the species was not recorded in the site; (ii) the area invaded (total area covered by *Heracleum*) in each sampled year (Table 1); (iii) the area covered by flowering plants; (iv) the estimated number of flowering plants; (v) the number and size of *Heracleum* patches, a patch being defined as an isolated area of minimum size 3 m^2 covered by *Heracleum* plants; (vi) affiliation of *Heracleum* to linear features expressed as the proportion of the total *Heracleum* cover accounted for by stands within 20 m of water courses, path, roads and railways (linear stands).

STATISTICAL ANALYSIS

To evaluate (i) the contribution of the linear stands to invaded area, (ii) trends in the number and size of *Heracleum* patches in the course of invasion and (iii) the relationship between flowering intensity and *Heracleum* residence time (defined as how long the species has been present in a site; Rejmánek 2000; Pyšek & Jarošík 2005), the data were analysed by ANCOVA. Proportion of linear stands, patch number, patch size and the proportional area covered by flowering plants were response variables, sites were a factor, and residence time was a covariate. The modelling of ANCOVAS started with fitting models in which each site was regressed on residence time with a different intercept and a different slope. The parameters of these models were inspected, and the least significant term was removed in a deletion test. If the deletion caused an insignificant increase in deviance, the term was removed. Deletion tests were repeated until minimal adequate models were established. In these minimal adequate models, all non-significant parameters were removed, and all the remaining parameters were significantly ($P < 0{\cdot}05$) different from zero and from one another (Crawley 1993).

The most appropriate transformations of the ANCOVA models were ascertained by plotting the response variables against the covariate, by comparing residual variance and the explained variance of the fitted models, by plotting standardized residuals against fitted values, and by normal probability plots (Crawley 1993). To test for additional 'domed' non-linear components in the models, the square power of the covariate was calculated and added to the models. If the addition caused a significant increase in explained variance, the power was kept in the model (Sokal & Rohlf 1995). To check for outliers, the points with the largest influence on minimal adequate models were assessed by Cook's distances (Cook 1977). Data points with the largest Cook's distances were sorted in a descending order and weighted out of the analysis one after another. The models were refitted after weighting out each data point, and the points causing a significant change in deviance were considered as outliers (Gilchrist & Green 1994).

To evaluate the mean rate of spread in particular sites, the area invaded by *Heracleum* at each site (response variable) was plotted against residence time (explanatory variable). The plotted curves were analysed by specifying binomial errors and a logit link function. The logit link function had as its numerator the cumulative invaded area to a specific date, while the total area invaded at the end of the observation was the denominator (Pyšek, Jarošík & Kučera 2003). Because the binomial errors were overdispersed, Williams' adjustment for unequal binomial denominators was applied (Crawley 1993). Curvilinearity was determined by stepwise adding of power terms to the explanatory variable and by checking if the addition caused a significant reduction in deviance. To compare the mean rate of spread in particular sites, the estimated time of 50% of the total area invaded, t_{50}, with 95% confidence intervals (CI), was calculated for each statistically significant curve using Fieller's theorem (Collet 1991; Crawley 1993). When the t_{50} of mean rates overlapped in CI (lower limit – upper limit), the curves did not differ significantly in the mean rate of invasion. All calculations were made in GLIM® version 4 (Francis, Green & Payne 1994).

To evaluate the relationship between invaded area, rate of spread and residence time, the area invaded by *Heracleum* (using the highest recorded value in each site; Table 1) was regressed on residence time using the ordinary least-square regression, and the slope of the regression line was used as a measure of the rate of spread. Path analysis (Sokal & Rohlf 1995) was used to explore the interrelationship between the invaded area, residence time and rate of spread. The path analysis enabled an assessment of relative direct and indirect effects by which the residence time contributed to invaded area both directly and indirectly, through the rate of spread. An appropriate path model was suggested by the regression analysis of invaded area, residence time and rate of spread. To achieve a comparable influence in absolute values, each parameter was standardized to have a zero mean and variance of one.

Results

On average, 7·0% of the landscape was covered by *Heracleum* in the localities studied at the later stage of invasion, ranging from 0·8 to 18·9% (Table 3). Of the land-use types, treeless areas were most suitable for *Heracleum* invasion; their mean contribution to the total cover of *Heracleum* in a site was 83·4%, while that of forested landscape and settlement areas were 15·1% and 1·5%, respectively. On average 10·1% of the total cover of treeless areas, 7·7% of urban areas and 3·0% of forests and scrub were invaded by *Heracleum* (Table 3).

The percentage of invaded area contributed by linear stands significantly decreased as the invasion continued (effect of the percentage of linear stands = 46·36 – 0·88 residence time; $F_{1,22} = 14{\cdot}49$, $P < 0{\cdot}001$, $r^2 = 0{\cdot}397$). The contribution of linear stands to total invaded area varied significantly among sites (deletion test for the same contribution of all sites: $F_{12,22} = 10{\cdot}53$, $P < 0{\cdot}001$), with significant effects at sites Žitný I, Žitný II and Litrbachy (Fig. 2).

RATE OF SPREAD

Mean rate of areal spread was 1261 ± 1052 m^2 year^{-1} (mean ± SD, $n = 10$). These values, calculated as the ratio between the highest recorded value of invaded area at a locality and the residence time needed to achieve this area, ranged from 139 to 3275 m^2 year^{-1} (Table 1).

Table 3. Characteristics of invasion in particular sites and its extent shown for land-use types. Invaded area relates to the year in which the largest area covered by *Heracleum* was recorded (indicated in the Year column). Relative invaded area is the percentage of the 60-ha landscape sector that was covered by *Heracleum* in that year. Contribution to the invaded area is the proportion of invaded area accounted for by each land-use type. Flowering intensity is expressed as the proportion of invaded area covered by flowering plants in the year when the largest invaded area was recorded; proportion of land-use invaded is the percentage of the land-use area that was covered by *Heracleum* in that year

						Contribution to the invaded area (%)			Proportion of land-use type invaded (%)		
Locality	Invaded area (m^2)	Relative invaded area (%)	Flowering intensity (%)	Beginning of invasion	Year	Forest	Treeless	Urban	Forest	Treeless	Urban
Arnoltov	47 170	7·9	57·7	1973	2000	9·3	90·5	0·2	1·9	11·7	1·5
Dvorečky	24 817	4·1	68·1	1973	1996	27·8	71·6	0·6	1·9	7·8	1·1
Krásná Lípa II	9 454	1·6	43·9	1987	1996	15·6	83·1	1·3	0·8	2·1	0·0
Liskovec	8 174	1·4	47·3	1987	1996	0·7	99·2	0·1	0·0	1·9	0·0
Litrbachy	4 711	0·8	42·2	1973	1996	17·2	82·7	0·0	0·9	0·8	0·0
Potok	39 774	6·6	52·7	1962	1996	50·7	49·0	0·3	4·6	12·4	1·6
Prameny	55 575	9·3	69·2	1973	1996	8·0	86·7	5·3	8·9	9·4	7·7
Rájov	5 198	0·9	39·3	1996	1996	0·0	100·0	0·0	0·0	1·0	0·0
Žitný I	113 236	18·9	52·5	1957	1987	10·1	86·0	3·9	5·8	24·9	32·7

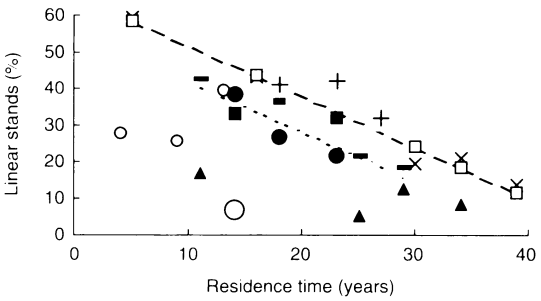

Fig. 2. Changes in the importance of linear stands (defined as the proportion of the total invaded area accounted for by stands up to 20 m from the axis of a linear habitat) for *Heracleum* invasion. Fitted lines show significant slopes for Žitný I (percentage of linear stands = 65·57 1·38 residence time), Žitný II and Litrbachy (common slope: percentage of linear stands = –4·78 + 1·72 residence time). Overall significance of the minimal adequate model: $F_{4,19} = 41{\cdot}56$, $P < 0{\cdot}001$, $R^2 =$ 89·7%. The enlarged white point (site Arnoltov) is an outlier not included in the analysis. Black squares, Prameny; white squares, Žitný I; black triangles, Potok; crosses, Arnoltov; black circles, Litrbachy; white circles, Krásná Lípa II; dash, Žitný II. Fitted lines: large dashes, Žitný I; small dashes, Žitný II and Litrbachy.

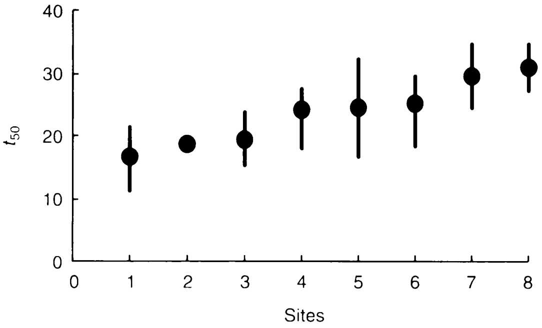

Fig. 3. Mean rates of spread (with 95% confidence intervals) expressed as t_{50}, the estimated time to 50% of the total area invaded. Means at individual sites, ranked in ascending order, whose confidence intervals do not overlap, are significantly different. 1, Prameny; 2, Lískovec; 3, Žitný II; 4, Dvorečky; 5, Potok; 6, Litrbachy; 7, Žitný I; 8, Arnoltov.

When evaluated statistically, mean rate of areal spread, expressed as the estimated time of 50% of the total invaded area (t_{50}), ranged between 17 and 31 years, and differed significantly among sites, being faster at Žitný I and Arnoltov than at Prameny and Lískovec (Fig. 3).

Mean rate of linear spread, expressed as the maximum distance the population reached from the primary invasion focus divided by the residence time, was 10·8 ± 7·2 m year^{-1} (mean ± SD, $n = 9$) and ranged from 3·8 to 26·7 m year^{-1} (Table 1).

RELATIONSHIP BETWEEN INVADED AREA, RATE OF SPREAD AND RESIDENCE TIME

Significant pairwise relationships between invaded area, rate of spread and residence time were found. The rate of spread positively affected invaded area and was its strongest pairwise predictor (invaded area = 255·8 + 37·8 rate of spread; $F_{1,7} = 138{\cdot}90$, $P < 0{\cdot}001$, $r^2 = 0{\cdot}952$). At the same time, the invaded area was significantly lower in sites where invasion started later (invaded area = −111 626 + 4113 residence time; $F_{1,7} = 11{\cdot}94$, $P < 0{\cdot}05$, $r^2 = 0{\cdot}631$). Residence time also exerted a positive effect on the rate of spread (rate of spread = −2348 + 92·84 residence time; $F_{1,7} = 6{\cdot}52$, $P < 0{\cdot}05$).

Multiple regression relating the invaded area to both rate of spread and residence time yielded the following relationship:

$$\text{invaded area} = -37\,097 + 1166\ \text{residence time} + 31{\cdot}74\ \text{rate of spread}$$

The regression was highly significant ($F_{2,6} = 134{\cdot}9$, $P < 0{\cdot}001$), explaining 97·8% of the variance. Both explanatory variables, i.e. residence time ($F_{1,7} = 7{\cdot}23$, $P < 0{\cdot}05$, $r^2 = 0{\cdot}026$) and the rate of spread ($F_{1,7} = 95{\cdot}92$, $P < 0{\cdot}001$, $r^2 = 0{\cdot}348$), were significant.

Based on the significance of the two terms in the multiple regression, it was evident that both residence time and rate of spread contributed to invaded area. The direct effect of residence time on invaded area was less than half (0·22) its indirect effect (0·57). The direct effect of the rate of spread on invaded area (0·82) was nearly four times larger than the direct effect of residence time (0·22), but the combined direct and indirect effect of residence time was only slightly less (0·79) than the effect of the rate of spread (0·82) (Table 4).

CHANGES IN POPULATION CHARACTERISTICS DURING INVASION

Flowering intensity varied between 30% and 70% over time and did not exhibit any significant trend over the

Table 4. Path and effect coefficients of the path model of invaded area as a function of the residence time and the rate of spread. Path coefficients a_1, b_1 and b_2 represent direct effects: a_1 is the regression slope for the standardized variables rate of spread and residence time; b_1 and b_2 are standardized regression slopes from multiple regression of invaded area as a function of residence time and the rate of spread. Indirect effects are calculated as a product of path coefficients along the links between causal variables and the response variable through other causal variables. Effect coefficients are the sum of direct and indirect effects

Path coefficients	
a_1, effect of residence time on the rate of spread (direct)	0·69
b_1, effect of rate of spread on invaded area (direct)	0·82
b_2, effect of residence time on invaded area (direct)	0·22
a_1b_1, effect of residence time on invaded area (indirect)	0·57
Effect coefficients	
$b_2 + a_1b_1$, residence time effect on invaded area (total)	0·79
b_1, rate of spread effect on invaded area (total)	0·82

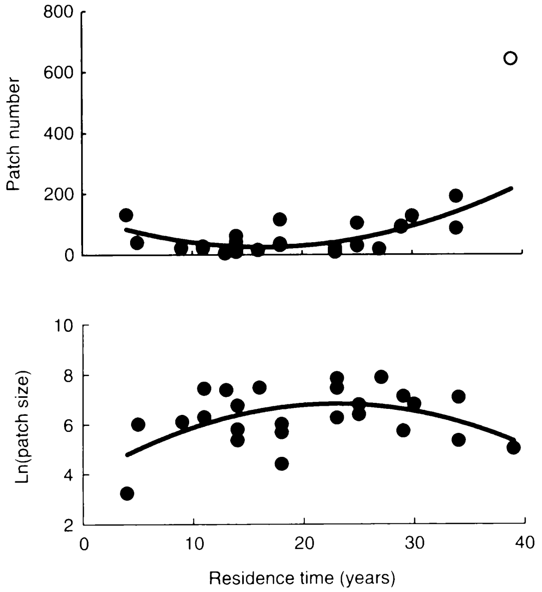

Fig. 4. Trends in the number and size of *Heracleum* patches (defined as an isolated area of minimum size 3 m^2 covered by *Heracleum* plants) in the course of invasion. Patch number = 127 – 12·34 residence time + 0·37 (residence time)^2. $F_{2,21}$ = 9·77, $P < 0·01$, R^2 = 48·2%; the enlarged white point (site Žitný I) is an outlier not included in the regression. Ln(patch size) = 3·84 + 0·26 (residence time) – 0·0057 (residence time)^2. $F_{2,22}$ = 3·84, $P < 0·05$, R^2 = 25·9%.

40 years of invasion. The number of isolated *Heracleum* patches initially decreased from the beginning of the invasion; this trend reversed after *c*. 20 years when the number of patches started to increase. Patch size was largest at the intermediate course of invasion (Fig. 4). Both patterns were consistent over sites (deletion test for patch number, effect of varying quadratic terms, $F_{6,9}$ = 1·74, NS; linear terms, $F_{6,15}$ = 1·17, NS; intercepts, $F_{6,21}$ = 0·79, NS; deletion test for patch size, effect of varying quadratic terms, $F_{6,10}$ = 2·23, NS; linear terms, $F_{6,16}$ = 2·64, NS; intercepts, $F_{6,22}$ = 2·37, NS).

Discussion

The rate of linear spread found for *Heracleum* in our study (average 10·8 m year^{-1}, site maximum 26·7 m year^{-1}) is of the same order as values reported for some of the world's most dramatic invasions (for a review of rates of spread see Pyšek & Hulme 2005). Comparing the value of areal spread recorded in the present study (1261 m^2 year^{-1}, site maximum 3275 m^2 year^{-1}) with data from the literature is difficult because the values must be related to the size of the monitored area and different source population sizes, which differ among studies (Pyšek & Hulme 2005).

By selecting the study sites *post hoc* using knowledge of present-day infestation, we could select areas where it could be assumed populations had not spread outside the study plots. The majority of study sites were located in isolated open areas within otherwise mostly forested landscape, and invading popul
located in the central parts of these areas. I
fore be assumed that the invaded area recor
resulted from the foci identified on the ear
graphs. The penetration of invading plant
side analysed plots cannot be completely ex
the data indicate that if this occurred it w
importance. Such occurrence would ma
mated values of spread more conservative. C
hand, the maximum values found at the Žit
sites (Table 1) represent a good estimate
potential because they are located in a l
area of former pastures and meadows, surr
abandoned village, with low representatio
and scrub patches that could represent ph
straints to the invasion. In these two sites,
invaded 18·6% and 18·9% of the available
40 years (Table 3 and Fig. 1). Field researc
firmed and previous study (Pyšek & Pyšek
demonstrated that forests indeed represe
to invasion by *Heracleum*. *Heracleum* inva
margins but only very rarely are solitary pl
in forest interior.

An absence of correlation between linear
measures of spread (Table 3; $F_{1,7}$ = 0·57, P =
cates that *Heracleum* populations do not sp
advancing front but that long-distance disper
the scale involved in the study) plays an imp
in the invasion process (Higgins & Richard
Hulme 2003).

The analyses presented make several ass
(i) Photographs were taken when *Heracleum* w
ing or fruiting and plants are easy to distin
that the invaded area could have been iden
measured. The largest invaded area recorde
over the study period was used, rather than
recent value recorded, because in two sites (Ta
total invaded area decreased slightly between
recent dates. This was probably the result of o
unsuccessful small-scale control efforts and/
graph quality varying between samples. (ii)
were regularly distributed over the 40 years of i
allowing us to measure the rate of invasion. (i
itoring had started before the onset of invasi
was possible to determine the start with reason
cision given the intervals between monitoring

These data allowed us to explore the relativ
the two determinants of invaded area. Both t
ence time and rate of spread significantly co
to the invaded, area with the direct effect of t
being much larger than that of the former. Ho
the residence time also had a significant effec
rate of spread (the invasion proceeded faster
where *Heracleum* was introduced earlier), t
effects of the residence time and rate of spread
comparable importance. If the invaded area w
mined only by the year a site was invaded, t
of invasion would be the same in each locality
species would have spread regardless of spec

conditions. As the year of invasion was determined mainly by dispersal opportunities, the current pattern of *Heracleum* occurrence in the study area would be primarily determined by the fact that the species' propagules reached the sites at different times. However, the significant differences in the rate of invasion among sites indicate that, despite *Heracleum* being an extremely successful invader (Moravcová *et al.* 2005) and the study region being climatically suitable (Pyšek 1991; Pyšek *et al.* 1998), there are constraints to invasion that vary among sites. That the sites are not equally suited for colonization by *Heracleum* is determined by variation in environmental conditions such as soil nutrients and moisture, character of resident vegetation and site history (Rouget & Richardson 2003; Rickey & Anderson 2004; Barney, DiTommaso & Weston 2005). These features affect the species' population biology and ecology and act in concert with landscape determinants of invasion. The importance of environmental heterogeneity in influencing invasions has been highlighted (Davis, Grime & Thompson 2000). As environments differ in their spatial and temporal patterns of resource supply, the opportunities they provide for recruitment and spread differ (Higgins & Richardson 1996).

Distribution of invasive species has been reported to depend on the rate of spread in a study of alien weeds in Australia (Forcella 1985). The present results suggest that the residence time is of the same importance.

Inferring population characteristics from aerial photographs is limited by the quality of the photographs; however, some robust patterns over the 40 years of invasion could be identified. The proportion of plants that flowered did not change over time. This indicates that the study region is climatically suitable for this species of Caucasian origin, unlike warmer parts of the Czech Republic where the warm January temperatures are probably suboptimal (Pyšek *et al.* 1998). A stable proportion of flowering plants was also recorded by sampling permanent plots in the field (J. Pergl *et al.*, unpublished data).

The spatial structure of *Heracleum* populations changed during the course of invasion. The number of isolated patches decreased in the initial 10–15 years and at the same time their mean size increased. This suggests that during the process of establishment at a site there is a period of enlargement of individual patches that merge with each other, and hence their total number decreases. After 20–25 years, patch number started to increase, indicating colonization of more distance places within a site. At the same time patch size started to decrease, suggesting dynamic spread associated with forming a large number of small colonizing patches.

Linear landscape features such as paths, roads and streams provide good possibilities for dispersal by humans and water, and proved to be important drivers of invasion. At the beginning, a large proportion of *Heracleum* stands was associated with these habitats, but their importance gradually decreased as invasion proceeded and populations invaded more distant places. The pattern found at the local scale is mimicked at the geographical scale of the Czech Republic. *Heracleum* was reported to spread first along large rivers, acting as migration corridors, and only later invaded landscapes distant from water streams (Pyšek 1991, 1994).

Aerial photographs are used for detecting invasive plant species because estimates of invaded area make it possible to monitor their spread over time (Higgins & Richardson 1999; McCormick 1999; Stow *et al.* 2000; Higgins, Richardson & Cowling 2001). Examples where this method has been applied for the study of alien plant invasions include *Tamarix ramosissima* (Robinson 1965), *Rhododendron ponticum* (Fuller & Boorman 1977), *Pinus radiata* (Richardson & Brown 1986), *Pinus halepensis* (Rouget *et al.* 2001) and *Ammophila arenaria* (Buell, Pickart & Stuart 1995). The cost of repeated coverage to detect changes must be borne in mind but, given the costs associated with the impact of alien plants (Zavaleta, Hobbs & Mooney 2001), the benefits prevail if repeated monitoring is followed by the design of an appropriate control strategy (Bakker & Wilson 2004; Paynter & Flanagan 2004; Perry, Galatowitsch & Rosen 2004; Taylor & Hastings 2004). It should be noted that the examples mentioned above are invasions by a different life form, not present in the invaded community before; this makes their detection by aerial photographs easier. The potential to study invasions by herbaceous plants at such large scales is in general very limited; *Heracleum* is an exception to this rule.

On earlier sampling dates, the photographs of our study area were taken for military purposes and kept classified. From the 1990s, sampling was initiated by the Protected Landscape Area authorities for the purpose of monitoring the extent of *Heracleum* invasion. Although infestation maps were created they have not been used efficiently in practice up to now, and the control efforts remain largely unsystematic and the selection of stands for control is quite random. The present study has shown that aerial photography is appropriate for monitoring the distribution of *Heracleum* and the method benefits from the invader having a very different appearance from native dominants (Rouget *et al.* 2003). The results of our study could facilitate the development of a control strategy that could not have been devised without this information (Wadsworth *et al.* 2000). There are four important aspects that can be incorporated directly into an appropriate control strategy. (i) *Heracleum* is easily detected from aerial photographs taken not only at flowering but also at early fruiting time, which extends the potential sampling period until late August. A detailed inspection of photographs allows detection of even single plants. These should be targeted for immediate removal to prevent further spread. As demonstrated by Moody & Mack (1988), effectiveness of control measures is greatly improved by concentrating on satellite isolated populations instead of on large expanding stands. Unlike in other herb species that are less easy to recognize, the control programmes could profit from the level of recording detail that can be achieved in monitoring *Heracleum*.

(ii) Linear landscape structures such as paths, roads and streams play an important role at the beginning of *Heracleum* invasion. The role of these linear corridors in the spread of alien plants has been documented (Thébaud & Debussche 1991; Pyšek & Prach 1993; Planty-Tabacchi *et al.* 1996; Hood & Naiman 2000) but the present study highlights that they should be targeted in the early stages of invasions, when control measures can be applied more efficiently than later on. Therefore the utmost attention should be paid to the occurrence of *Heracleum* along these corridors in sections of landscape where the invasion starts.

(iii) By employing longitudinal data, the present study allowed us to measure the actual rate of spread. Its strong effect on the extent of invaded area indicates that the species is not limited much by local site conditions. This should be taken as a warning that the entire area, including habitats currently less prone to the invasion, must be included in control programmes. On the other hand, knowing how fast the invader is able to spread locally and which of the habitats are particularly prone to the invasion makes it possible to identify localities that are at highest risk of immediate infestation.

(iv) Results of the present study can be applied to predict the occurrence of *Heracleum* in unsampled sites (N. Nehrbass *et al.*, unpublished). A clear indication of where invasion is most likely to occur in the future would be the most valuable message for managers (Hulme 2003).

Acknowledgements

We thank Phil Hulme and three anonymous referees for valuable comments on the manuscript. Our thanks also go to Irena Perglová and Václav Procházka for logistics support. The study was supported by the project 'Giant Hogweed (*Heracleum mantegazzianum*) a pernicious invasive weed: developing a sustainable strategy for alien invasive plant management in Europe', funded within the 'Energy, environment and sustainable development programme' (grant no. EVK2-CT-2001-00128) of the European Union 5th Framework Programme, by the long-term institutional research plan no. AV0Z60050516 funded by the Academy of Sciences of the Czech Republic, and MSMT project no. 0021620828 from the Ministry of Education of the Czech Republic.

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Received 25 April 2005; final copy received 15 July
Editor: Phil Hulme

4

The role of long-distance dispersal determined by simulation model of invasion

A simulation model of invasion by *Heracleum mantegazzianum* based on historical aerial photographs and field data: long-distance dispersal determines the course of invasion

Nehrbass N., Winkler E., Müllerová J., Pergl J., Pyšek P. & Perglová I.
Biological Invasions (in press)

Abstract

Mechanisms and consequences of biological invasions are a global issue. Yet, one of the key aspects, the initial phase of invasion, is rarely observed in detail. Data from aerial photographs covering the spread of *Heracleum mantegazzianum* (Apiaceae, native to Caucasus) on a local scale of hectares in the Czech Republic from the beginning of invasion were used as an input for an individual-based model (IBM), based on small-scale and short-time data. To capture the population development inferred from the photographs, long-distance seed dispersal, changes in landscape structures and suitability of landscape elements to invasion by *H. mantegazzianum* were implemented in the model. The model was used to address (1) the role of long-distance dispersal in regional invasion dynamics, and (2) the effect of land-use changes on the progress of the invasion. Simulations showed that already small fractions of seed subjected to long-distance dispersal, as determined by systematic comparison of field data and modelling results, had an over-proportional effect on the spread of this species. The effect of land-use changes on the simulated course of invasion depends on the actual level of habitat saturation; it is larger for populations covering a high proportion of available habitat area than for those in the initial phase of invasion. Our results indicate how empirical field data and model outputs can be linked more closely with each other to improve the understanding of invasion dynamics. The multi-level, but nevertheless simple structure of our model suggests that it can be used for studying the spread of similar species invading in comparable landscapes.

Introduction

Invasive species (sensu Richardson et al. 2000; Pyšek et al. 2004) are characterized by remarkable dynamics of spread that allow them to colonize large areas in regions where they are not native, and occupy a wide range of habitats (Chytrý et al. 2005). Biological invasions have become a global issue, attractive from the scientific point of view, and require urgent solutions (Mooney and Hofgaard 1999; Davis 2003; Weber 2003). As other ecological processes, invasions occur on temporal and spatial scales which are difficult to monitor in empirical studies. To overcome this limitation, models are used to capture key processes of ecological systems and describe scales beyond empirical reach (Grimm et al. 1996). The results of such models are more powerful if validated and supported by empirical observations. Invasions by plants and animals represent a unique opportunity to study spatiotemporal dynamics on various scales, because they occur at a rate and extent of spread currently unparalleled by other species (Pyšek and Hulme 2005; Williamson et al. 2005).

Unfortunately, individual invasion events are rarely captured from the very beginning (but see Robinson 1965; Richardson and Brown 1986; Lonsdale 1993; Müllerová et al. 2005). As the crucial aspect of recognizing an invasive species is the invasion itself, plant invasions are in majority of cases studied post hoc (e.g. Fuller and Boorman 1977; Perrins et al. 1993; Pyšek and Prach 1993; Delisle et al. 2003), mostly using floristic records (Weber 1998; Mandák et al. 2004; Williamson et al. 2005). However, floristic data do not provide information on the actual increase in area covered by the invader over time, i.e. the dynamics of an invasion (Higgins and Richardson 1996). In the last decade, computer image analyses were used to monitor invasive species (see Everitt et al. 1995 for a review); among them, aerial photographs are the most convenient remote sensing technique. As they provide information about spatial extension, they are used for quantitative assessment of infestation by alien plant species (Everitt 1998; Stow et al. 2000; Higgins et al. 2001; Rouget et al. 2003; Müllerová et al. 2005). In areas where repeated aerial photographs were taken over time, records from before the invasion might be available and the initial phase of the process captured. This is the case with the invasive species *Heracleum mantegazzianum* in the Czech Republic. This species has white flowers arranged in large conspicuous umbels, which allow the identification of flowering individuals on aerial photographs (Müllerová et al. 2005).

This study compares historical development of an invading population of *H. mantegazzianum*, reconstructed from aerial photographs, with modelled dynamics of invasion. A time series of more than 40 years (1957–2000) made it possible to quantify the spatial extension of an invading population from the founding individuals (Müllerová et al. 2005). This invasion process was reproduced by a spatially-explicit individual-based simulation model. The model started from a population-dynamic core model designed, parameterized, and validated by using data from recent local censuses, carried out in the same study area (Nehrbass et al. 2006). As the data used for parameterization were only from a homogeneous habitat in the central parts of *H. mantegazzianum* populations, changes in the structure of landscape that occurred in the course of invasion were implemented in the model and so was the response of the invading species to these changes. By conducting experiments in the virtual environment we addressed the topics, which are difficult to evaluate in a purely empirical context: (1) the role of long-distance dispersal in regional invasion dynamics, and (2) the effect of land-use changes on the progress of invasion.

Methods

Study species

Heracleum mantegazzianum Sommier et Levier (Giant hogweed, Apiaceae) is native to the western part of the Greater Caucasus and invasive in Europe, North America and New Zealand (Weber 2003; Nielsen et al. 2005). In its invaded range, *H. mantegazzianum* is a problem species, because it forms stands with a high cover, replaces resident vegetation, and produces photosensitive sap that is toxic for humans (Tiley et al. 1996). The rapid invasion of this species in Europe was encouraged by its planting as a garden ornamental. In the study area (Slavkovský les, W Bohemia, Czech Republic) the plant was introduced as a garden ornamental in 1862 and was first recorded in the wild in 1877 (Holub 1997). From this region of introduction the species rapidly spread to other parts of the country (Pyšek 1991). Seeds are dispersed mainly by water and humans, through planting and transport of contaminated soil; the species spreads effectively along linear corridors such as roads and waterways (Collingham et al. 2000; Pyšek et al. 2002).

Heracleum mantegazzianum is the tallest herbaceous plant in Europe; flowering plants can reach a height of up to 500 cm. It is a monocarpic perennial, which usually flowers in the third year; the lifespan, however, depends on habitat conditions and can be extended to more than 10 years (Pergl et al. 2006). White flowers are arranged in compound umbels with a terminal umbel of up to 80 cm in diameter (Tiley et al. 1996). In the study area the plants flower from late June to late July (Müllerová et al. 2005) and a single plant can produce on average 20,500 fruits with a maximum of 46,500 (Perglová et al. 2007). Seeds germinate to high percentages after the morpho-physiological dormancy has been broken during the period of cold stratification (Moravcová et al. 2005). The species forms a short-term persistent seed bank (Krinke et al. 2005) and little fraction of viable seed persist in soil for at least three years (Moravcová et al. 2007).

Study area

The study area was located in the Slavkovský les Protected Landscape Area, W Bohemia, Czech Republic, where the species was first introduced to the country. After World War 2, inhabitants were transferred from the area which became a military zone with restricted access until the 1960s. The absence of regular land use, combined with disturbances caused by military activities increased the suitability of the landscape to the invasion by *H. mantegazzianum* (Pyšek 1991). As a result, the region is heavily invaded by *H. mantegazzianum* (Pyšek 1991; Pyšek and Pyšek 1995; Müllerová et al. 2005). The natural vegetation consisted of beech and spruce forests, peat bogs and pine forests on serpentine, which have been replaced by managed wetlands with a high diversity of flora, as well as by pastures and spruce plantations (Kos and Maršáková 1997).

Analysis and interpretation of aerial photographs

From aerial photographs available for 10 sites in the study area (see Müllerová et al. 2005 for detailed characteristics), the site Arnoltov was chosen for the analysis in the present study. Five observations (panchromatic, multi-spectral and ortho-photographs) from 1953 to 2000 were available for this site. Panchromatic photographs (1957, 1973, and 1991) were provided by the Military Topographic Institute, Dobruška, multi-spectral (1987) by the Agency for Nature Conservation and Landscape Protection, Prague, and ortho-photographs (2000) by Czech Office for Surveying, Mapping and Cadastre. Images were created from scanned aerial panchromatic photographs of the scale 1:22 500 with 60% overlap, using a digital terrain model gained by vectorization of topographic maps 1:10 000. Orientation points of images were identified by analytical aero-triangulation in system ORIMA; ortho-rectification was performed on digital photogrammetric station Leica-Helava DPW 770, module Mosaic, final pixel resolution 0.5 m (see Müllerová et al. 2005 for more details).

Table 1. Land-use categories identified on aerial photographs and their suitability for invading *Heracleum mantegazzianum*, based on its presence or absence in individual categories.

Category	Land-use type	Suitability
1	Forest	no
2	Individual trees	yes
3	Buildings	no
4	Grazed and mown after grazing	yes
5	Meadows	yes
6	Arable fields	no
7	Pastures	yes
8	Road or railway and its surroundings	yes
9	Planted trees (saplings)	yes
10	Open or young forest	yes
11	Water body	no
12	Forest clearing	yes
13	Surrounding of buildings	yes
14	Surrounding of roads and other disturbed areas	yes
15	Pastures - buffers 5 m along forest categories (1, 2, 9, 10, 12)	yes
16	Unmanaged	yes
17	Pastures - buffers 5 m along meadows (cat. 5)	yes
18	Pastures - buffers 5 m along roads, buildings, etc. (cat. 3, 8, 13, 14)	yes

Each photograph covered an area of 710 × 710 m around the nascent focus, defined as the place where the plants of *H. mantegazzianum* were earliest recorded. We distinguished eighteen different habitat types and classified them as suitable or unsuitable for *H. mantegazzianum*, based on the empirically observed habitat preferences in the study area (Tab. 1). The analysis and interpretation of aerial photographs allowed us to identify stands as well as solitary individuals of flowering *H. mantegazzianum* and their precise position. The process of photo-interpretation (Müllerová et al. 2005), consisted of: (i) scanning of negatives 20 in resolution 800 dpi; (ii) rectification using orto-photographs (40–60 ground control points distributed along the rectified photograph, 2nd order of transformation and nearest neighbour rectification method; Lillesand and Kiefer 1999); (iii) visualisation of Heracleum plants on images (image enhancement, filtering; Jensen 1996) using Chips software (Chips Development Team 1998); and (iv) on-screen digitizing of *Heracleum* stands and individual plants using CartaLinx software (Clark Labs 1998).

Area covered by flowering plants was extrapolated to give the cover of *H. mantegazzianum* in the respective year, expressed by the number of occupied cells. This measure was used for comparison with simulation results.

Empirical field data

Biology and ecology of *H. mantegazzianum* (Moravcová et al. 2005; Krinke et al. 2005; Pergl et al. 2007) and the history of invasion in the study region (Müllerová et al. 2005) are intensively studied. The data on population dynamics, used in this study, were obtained from observations in permanent plots at 11 sites in 2002–2005 (Pergl et al. 2007). The plots 10 × 1 m in size were sampled twice a year (in spring and autumn) and the characteristics of individual plants were recorded: position, size and life stage. In the present study only data from the autumn monitoring are used.

Model

To describe local population dynamics of *H. mantegazzianum* a stochastic, spatially-explicit, individual-based model (IBM) was developed. Life-history rules, their parameterization and validation were described in detail by Nehrbass et al. (2006).

Habitat: From the original landscape a square of 700 x 700 m was used in the model. Landscape was divided into grid cells of 25 m^2 (19,600 cells of 5 × 5 m). Within a grid cell habitat conditions were assumed to be homogeneous for the species. Each cell represented either a suitable or an unsuitable habitat. Classification of grid cell as suitable or unsuitable was based on the occurrence of *H. mantegazzianum* as recorded on aerial photographs; habitats in which the species occurred were classified as suitable, those from which it was absent as unsuitable (Müllerová et al. 2005; Table 1). Changes in habitat structure over time were inferred from aerial photographs and were implemented in the year when first recorded. Suitable cells had an empirically suggested maximum carrying capacity of $K = 200$ individuals; for unsuitable cells we set $K = 0$. The effect of carrying capacity was implemented by a ceiling rule (Akcakaya et al. 1999): seedling recruitment was only possible when maximum capacity of the cell was not reached.

Time: The model was discrete in time. One time step represented the interval from one flowering period (autumn) to the next (one year).

Life history of plants: Plants were modelled as individuals. Thus, demographic stochasticity was included in the model. Each plant was characterized by the following set of traits: age, number of leaves, and the length of the largest leaf. In a complete life-cycle the plant grew for several years, flowered, produced offspring and died (Fig. 1). Growth of an individual plant depended on its size in the previous year. The increase in leaf number followed probabilities derived from empirical values (see Nehrbass et al. 2006 for details) and changes in the length of the largest leaf followed rules that depended on the number of leaves.

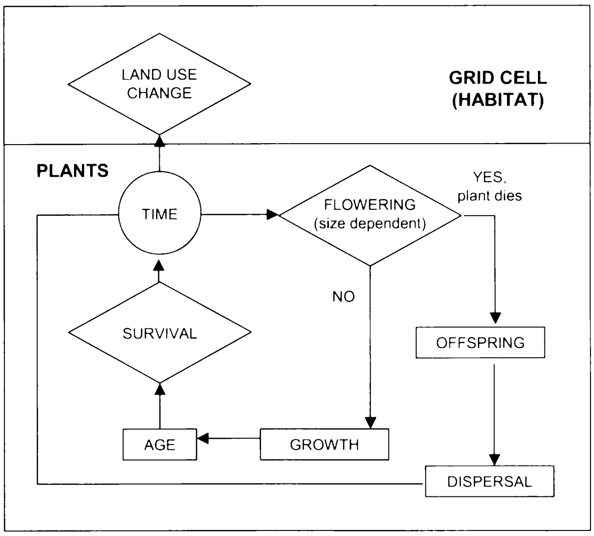

Fig. 1. Flow chart of the individual-based model of *Heracleum mantegazzianum*. Within one time-step (year) different probabilities determine the fate of an individual plant. Changes in landscape structure (i.e., if one land-use type changed into another) were incorporated in the model in the year when observed on aerial photographs. Rhombs represent decisions, boxes are mandatory developments.

As a monocarpic perennial plant *H. mantegazzianum* flowers at earliest in its second year (Tiley et al. 1996; Holub et al. 1997; Pergl et al. 2006), the model thus considered plants two years and older as capable of flowering. Flowering probability was not only agedependent, but also determined by a combination of two size attributes, i.e. the number of leaves and the length of the largest leaf. The number of offspring produced by a flowering plant was not correlated with any trait of the maternal plant (J. Pergl et al., unpublished). Seedling production per flowering individual as a product of seed production and establishment probability followed a fat-tailed probability function with a mean value of $M = 2.57$ (derived from empirical data). This basic value held for a situation without any establishment restriction in the target cell after dispersal (see below). When the carrying capacity of a cell was reached seedlings did not establish. Additionally establishment failed when the seedling met a cell within unsuitable habitat. New plants were assigned randomly chosen numbers of leaves, which in turn determined the length of the largest leaf using empirically retrieved values.

Flowering individuals died after setting seeds; the survival probability of nonflowering individuals depended on their size. Those individuals that had reached a maximum age (7 years) died without reproduction. As the underlying empirical data indicated that the sampled populations are currently at the stage of stagnation and the model parameterized with such data would give a population-increase rate of $R_P \approx 1$ we tentatively reconstructed the historical invasion with a rate of $R_P > 1$ by reducing mortality to a size-independent value of 0.2 for all individuals. As a result, the mean rate of population increase in the model was $R_P = 1.12$. This gross value was subsequently reduced by capacity control and habitat properties.

Dispersal: Seedlings were placed in the cell of origin (fraction f_H of the seedlings) or in neighbouring cells (fraction f_N). Due to a large cell size, this neighbourhood dispersal was limited to eight immediately adjacent cells (Moore neighbourhood; Czárán 1998). All cells within this radius were considered to have an equal probability of new plants to become established. Additionally, we incorporated dispersal at random (with uniform probability) over the whole simulation grid ("long-distance dispersal", fraction f_L). Directed dispersal along linear landscape elements (e.g. field margins) was not considered.

Simulations

The aerial photographs covered the period 1953–2000. The first observations of *H. mantegazzianum* on the photographs were for 1973. Hence, the simulation started in 1973 (t = 0) and ran for 37 time steps, ending with a projection of the population in 2010. The scenarios started with 10 vegetative plants, which were to flower in that year, in each cell that was recognized from aerial photographs as occupied in 1973. Then the population developed according to the assumptions on population dynamics, dispersal, and landscape changes of the scenario. For each scenario, 50 repetitions were calculated. The number of grid cells occupied by *H. mantegazzianum* in the course of simulated invasion was used to compare the scenarios with each other and with real historical development.

Scenarios

(1) Standard scenario: The population developed following standard model rules as described above. Landscape (habitat suitability of the cells) was altered according to the historical observations. Changes in landscape characteristics were considered from the year when they were first recorded: 1987 (t = 14), 1991 (t = 18), and 2000 (t = 27). Thus, landscape in the model did not transform continuously, but in discrete steps. Numbers of suitable habitat cells and their changes are given in Table 2. If the land-use type in a cell changed from suitable to unsuitable all plants were immediately deleted ("died") and the cell could not be re-occupied. The cells transformed from "unsuitable" to "suitable" were made available for invasion following the dispersal rules of the model. In the standard scenario a seedling had a probability of f_L = 2.5% to be randomly dispersed (see below for justification of this value). For the other seedlings it was assumed that 80% of them remained in the cell

of origin, giving fraction f_H, and 20% distributed into the immediate neighbourhood (fraction f_N).

(2) "Long-distance dispersal scenario": To estimate the effect of random (longdistance) dispersal on the rate of invasion, different fractions of random dispersal f_L (0 ...100%) were assumed, accompanied by changes in local (f_H) and near-neighbourhood dispersal (f_N) according to

$f_H = (1 - f_L) * 0.8$ and $f_N = (1 - f_L) * 0.2$. Land-use changes followed the standard scenario.

(3) "Land-use change scenario": The effect of land-use changes on the invasion was tested by retaining the original land-use structure from 1973 over the whole simulation period without any changes.

Table 2. Comparison between actual occupation data and modelled spread of *Heracleum mantegazzianum* (standard scenario). The first two rows of the table present data from the analysis of aerial photographs, which were used to reveal suitable habitat (number of grid cells, with percentages of the total number, and gross changes) and identify the number of cells in which the species was observed. In the next two rows, simulation results are presented: mean values for the number of occupied cells with standard deviation, calculated from 50 simulation runs, and percentages P_M of the cells, which were occupied on both aerial photographs and by simulation. For comparison, the last row gives matching probabilities for a uniform random distribution of simulated occupied cells. The study area covered 490 000 m² (19,600 grid cells of 5 × 5 m²).

	Year (Simulation)				
Characteristic	1957 (not incl.)	1973 (*t* – 0)	1987 (*t* – 14)	1991 (*t* – 18)	2000 (*t* – 27)
Suitable habitat	3402 (17.36)	3454 (17.62) **+52**	3405 (17.37) **-47**	13 866 (70.74) **+10461**	13 210 (67.39) **-656**
Occupied habitat (aerial photographs)	0	49 (0.25)	778 (3.97)	792 (4.04)	2240 (11.43)
Occupied habitats (simulation results)	0	49±0	592±34	1054±48	2903±132
Percentage P_M of correct matches for occupied cells (%)	0	100	16.67±1.4	21.49±1.7	27.00±3.0
Percentage P_R of correct matches for occupied cells (%) with random distribution of simulated occupation cells	0	1.4	17.4	7.6	22.0

Results

Historical data and model prediction (standard scenario)

Historical data on habitat occupation by *H. mantegazzianum* inferred from aerial photographs show a marked increase from 1973 to 2000: the number of occupied cells increased by a factor 45 (Table 2). The average rate of increase in habitat occupation was $R_C = 1.15$, with clearly distinguishable periods. From 1973 until

1987 average rate was 1.22, followed by a period of stagnation (1987 until 1991 with an average rate of only 1.01), again followed by a period of increase (R_C = 1.12). These periods are characterized by changes in land use. The stagnation period is associated with (but probably not fully explained by) a slight reduction of the number of suitable habitat. The opening of new suitable habitat in 1991, accounting for an increase from 17 to 71% of the total area, resulted in a re-start of population spread, but with a reduced rate compared with the initial period.

In the simulation of population development habitat cover increased with nearly the same average rate of increase of R_C = 1.16 for the whole period. This value was adjusted by the choice of a value for the percentage of long-distance dispersal f_L (see below). The simulation showed an average decrease of the rate of spread: with R_C = 1.19, 1.16, and 1.12, respectively, for the three periods denoted above. This decrease in R_C may reflect the effect of local saturation of habitats. The stagnation in the second period is hidden in this overall decrease of R_C, corresponding to only slight reduction in the number of occupied cells in 1987. The snapshots of Fig. 2 give an impression of the historical development, together with the result of a simulation run. In both cases there was a patchy spread, with some new populations arising over the years that are clearly distinct from those located in the centre of the plane in 1973. It should be mentioned that in Fig. 2 the simulated cover does not fully correspond to the data from Table 3 as in Fig. 2 only cells are shown in which at least two individuals occurred.

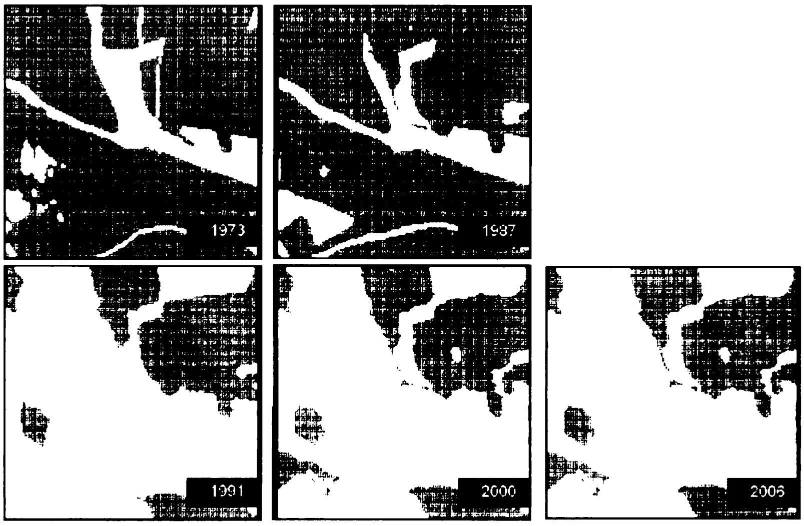

Fig. 2. Exemplary model simulation of the population development of *Heracleum mantegazzianum* in the study site Arnoltov (710 × 710 m, pixel size 25 m^2). White area represents suitable habitat, dark-grey area is the matrix of unsuitable landscape (see Tab. 1). Population spread as derived from aerial photographs (light grey) was compared with simulated spread (grey; only cells with more than 1 individual). Overlapping areas are indicated in a medium grey tone. The series illustrates the original setting in 1973, incorporated landscape changes in 1987, 1991 and 2000, and projected development for 2006.

Table 2 gives average percentages of correct matching PM of historically occupied cells by the simulated population. This percentage at first decreased from its initial value of 100% to less than 17%, but then increased again. The values can be compared with a null measure, with the probabilities for a really occupied cell to be "hit" by an occupied cell in the simulations if these cells were distributed fully at random. Such values P_R are equal to the percentages of occupied cells in the simulation and are given in Table 2. The P_R-values show that even under completely random dispersal there will be a considerable degree of matching. But, in 1991 the value P_M resulting from our model simulations is much lower and reflects the situation after the sudden opening of suitable area. In 2000 P_M was almost equal to the "random" value P_R. The results in Table 2 shed some light on the long-term effects of historical settings on the population development in the landscape studied, but a detailed interpretation is somewhat blurred by methodical problems associated with comparison of field data with simulated results.

Effect of long-distance dispersal (scenario 2)

Long-distance dispersal is the driving force of the invasion. The higher was the probability f_L for new plants to disperse randomly over a long distance, the faster the population of *H. mantegazzianum* covered entire area of suitable habitats (Fig. 3). From Fig. 3 the value f_L = 2.5% was adopted, which gave visually the best fit to the observed occupation values.

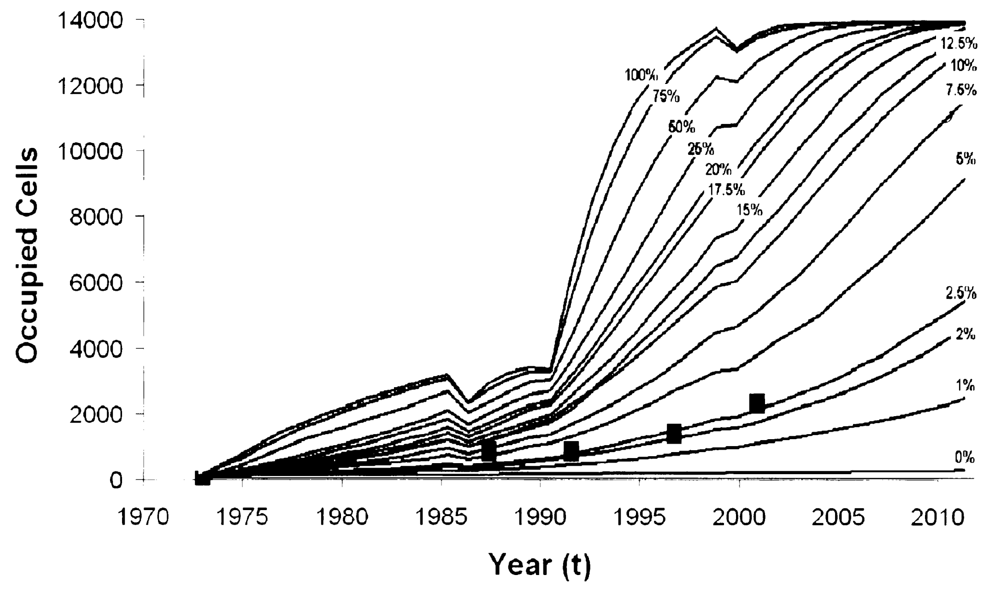

Fig. 3. Effect of long-distance dispersal on invasion in exemplary simulation runs in the standard landscape scenario. The categories of long-distance dispersal are based on the percentage of the total number of offspring involved in long-distance dispersal events. The changes in land-use structure at t = 1987, 1991, 1996, and 2000 are reflected indicated by abrupt changes in the displayed trends. Squares indicate historical development observed on aerial photographs.

With neighbourhood dispersal only, the rate of invasion did not accelerate with time and the area occupied by the species reached only 14% of that recorded by historical data from aerial photographs (Fig. 4). Already small percentages of long-distance dispersal had a marked effect on population increase (Fig. 5). The long-distance dispersal created new foci for satellite populations which again vigorously increased due to neighbourhood dispersal. The effect of higher f_L-values was less remarkable and vanished in the course of population development due to saturation in the closed simulation habitat.

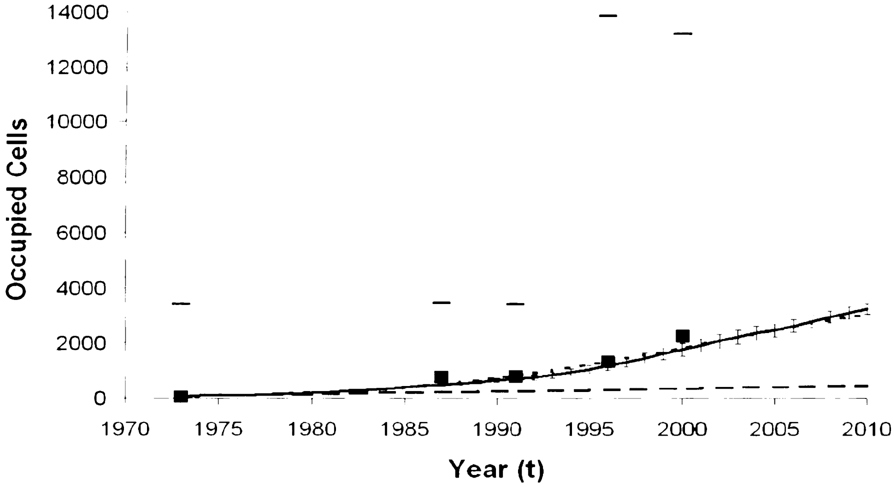

Fig. 4. Number of all occupied grid cells (5 × 5 m) in the simulation model of *Heracleum mantegazzianum* (line with SD). Land-use changes occurred in the years t = 1987, 1991, 1996, and 2000. Horizontal lines indicate the maximum number of grid cells that can be occupied at those times (except for scenario 3 where max. number remains constant at the level of 1973). Observed spread (squares) lies slightly above the values for the standard scenario (scenario 1, full line). The populations without long-distance dispersal (scenario 2, long broken line) only exhibit moderate increase. Populations in non-changing landscapes are showing the same increase in number of occupied cells as those in a shifting scenario (scenario 3, short broken line). Detailed values for the historical data are presented in Table 3.

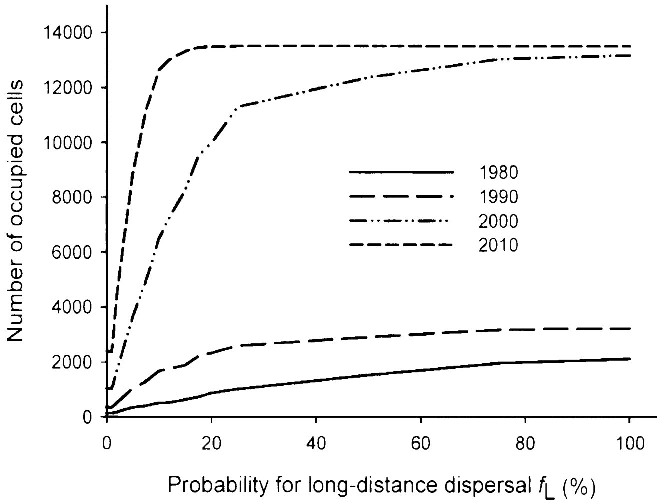

Fig. 5. Number of occupied cells for 1980, 1990, 2000, and 2010 in relation to the implemented probability for long-distance dispersal (f_L). Lower probabilities have over-proportionally higher effect on cell occupation than high probabilities.

Effects of land-use changes (scenario 3)

In the standard scenario the effect of changes in landscape suitability was hidden in the overall increase of habitat occupation, which was far from saturation. Fig. 4 shows that under the time-independent landscape the occupancy of grid cells was comparable to the scenario with implemented changes in habitat suitability. However, with increasing percentage of long-distance dispersal and hence higher habitat cover development periods following landscape changes differed markedly (Fig. 3). Habitat destruction in 1987 affected parts of the already occupied cells. Opening of new habitat in 1991 offered opportunities for population spread, until habitat limits were reached. This development was interrupted again by a reduction of suitable habitat in 2000. Thus, the effect of habitat changes was a function of actual habitat saturation and hence of the percentage of long-distance dispersal.

Discussion

Invasion as a multilevel process in landscape and the importance of long-distance dispersal

Invasion of a species into areas where it was not present before is a process with various temporal and spatial facets (Heger 2004). The combination of observations on different time and spatial scales with the reconstruction of these processes by computer simulation is a powerful tool for studying the dynamics of plant invasions (Higgins and Richardson 1999; Higgins et al. 2000; Buckley et al. 2003a). Whereas the initial phase of the invasion process is shaped by processes on a local scale, further spread of a species is governed by the possibility for long-distance dispersal, again accompanied by population increase into neighbourhood. Hence, the invasion process is a mixture of multiplication and dispersal, but also of stagnation and temporary decline.

Our study of the spread of *H. mantegazzianum* offered an opportunity to start from short-time investigations (3 years) on a scale of 10 m^2, focussing on the fate of individuals, and continue with data capturing more than 27 years, based on presence or absence of the species in plots of 25 m^2 covering the area total of approx. 0.5 km^2. The latter data were obtained from aerial photographs, which captured the historical development of land-use. Our model was also developed in two steps. The basic small-scale model that described the development of individuals as a multi-stage process was parameterized and verified along the short-time data set (Nehrbass et a. 2006). It was able to reproduce essentials of population structure: the proportion of flowering plants in the population, size distribution and the distribution of leaf numbers of individual plants. The next modelling step extended the basic model by two essential features; this was preceded by a small adaptation of life-history characteristics (reduction of mortality) in order to meet the requirements of a population in a growth phase. Besides the dispersal of seeds into the neighbourhood of the parent plant (approx. 10 m), long-distance dispersal over 10–500 m was introduced for a given percentage of seeds, and heterogeneous and temporally changing landscape was considered.

After adjustment of only one parameter, the fraction f_L of long-dispersed seeds, the model reproduced well the temporal dynamics of cell occupation as observed on aerial photographs. The fitted value for this percentage, 2.5%, is in line with generally recognized importance of multilevel dispersal processes for the dynamics of spreading populations (Levin et al. 2003, Pyšek and Hulme, 2005). Although the overwhelming majority of seeds remained in the neighbourhood of the mother plant, this small fraction was much more effective in spreading the population over distances 1–2 orders of magnitude larger than neighbourhood distances alone. This marked effect of small fractions of long-dispersed seeds on the filling of available area is due to a combined action of both dispersal modes by which plants growing far from their mother plant establish new (sub-) populations that will spread again into neighbourhood.

The extended model had also the potential to reproduce the effect of landscape structure on population development. The degree to which the simulated population responded to the changes in landscape structure, i.e. to changes in habitat suitability, depended on the actual level of habitat occupation, which in turn was a function of long-distance dispersal. As long as only small parts of suitable habitat were already covered, the opening of new habitat was of minor importance, but this importance was increasing with saturation level. A reduction of suitable habitat could, although not necessarily, affect parts of the population, depending on the actual spatial situation.

Some open problems

A complex endeavour, such as the analysis of the spread of an invasive species in a real landscape by a combination of different methods, inevitably brings about some methodological problems.

Our adaptation of the life-history model to the requirements of growing populations is based on some assumptions (e.g., density dependence of rates), which should be paid more detailed attention. This adaptation resulted in a certain value of the rate of population increase larger than one (R_P = 1.12), but the sensitivity of simulation results to the changes of this value has not been yet investigated. There may be an interference with the effect of the fraction of long-distance dispersal on landscape occupation.

Dispersal is a crucial element of the analysis. In the present model all the seeds dispersed over long distances were distributed at random with uniform probability over the whole area, and none were lost due to crossing the boundaries of the simulation area. For the initial state of population spread, as in our case, this simplified assumption about long-distance dispersal may be justified. Nevertheless, stratified dispersal (e.g., a combination of two exponential functions in the dispersal kernel) with components that reflect different dispersal mechanisms with different mean distances need to be introduced to make the model more satisfactory (Bullock et al. 2002, Clark et al. 2003). Formally, stratified dispersal needs at least one more parameter, implementation of which is inevitable to capture the population spread in a structured landscape in a more realistic manner, especially in landscapes with different degrees of fragmentation. Directed transport, preferential transport along rivers, roads and field margins, or transport towards certain targets should be included, because linear structures enhance directional dispersal (Collingham et al. 2000, Buckley et al. 2003b; Hansen and Clevenger 2005). However, our empirical findings did not prompt us to such a model extension which would lead to some ad hoc-rules. These again would diminish the general character of the modelling approach as they are unlikely to be easily transferable to other scenarios (but see Lonsdale 1993).

The special character of data acquired from aerial photographs brings about another special problem. The use of aerial photographs to reconstruct invasions of herbaceous plants is a recent achievement, encouraged by the development of powerful computer tools (Everitt et al. 1996; Stow et al. 2000; Müllerová et al. 2005). Although *Heracleum mantegazzianum* is a plant with a prominent appearance, only flowering and early fruiting individuals can be safely recognized on aerial photographs (Müllerová et al. 2005); the total number of cells occupied by flowering or non-flowering individuals was extrapolated by computation procedures. However, our model simulations of population spread suggest that many cells harbour individuals in vegetative stage but no flowering plants. The model was based on the assumption that most of these cells were at the edges of fully developed stands and covered by the extrapolation procedure. However, solitary plants apart from closed stands were not detected by aerial photographs. Such plants may form only ephemeral but also new permanent stands. In the latter case they essentially contribute to the spread, even if their absolute number may be low as suggested by the low proportion of seed that are dispersed to long distances. A detailed evaluation of the results provided by the model can help to quantify this "detection" problem and indicates two possible solutions. From the field perspective, it is systematic ground-truthing of photographic results. From the modelling perspective, the output needs to be designed so that it mimics more closely the procedure of extrapolation from flowering individuals to complete stands, as used in the analyses of aerial photographs. Such an output is to be used for all direct comparisons of the model performance with data from aerial photographs, especially for parameterization and model validation. The simulation using all occupied cells, especially with focus on the dynamics of emerging stands, provides information beyond the possibilities of empirical field research. Improvement of the correspondence between aerial-photograph data and simulation outputs would make it possible to extend the model and precise the present analysis of the coincidence between occupied cells observed in the field and simulated by the model.

Conclusions

The reconstruction and analysis of invasion processes is often hampered by the fact that information about past events is scarce. The series of aerial photographs provided unique insight into the local dynamics of spread of *H. mantegazzianum* over the whole course of invasion on a time scale of decades. A simulation model consisting of only a few components: population dynamics; neighbourhood dispersal; long-distance dispersal; and dynamic landscape structure, and combined with empirical field data proved to be a convenient tool for analysing such long-term longitudinal data. It allowed to quantify what is the role of long-distance dispersal and changing landscape in shaping the spread of invading populations.

The model included some aspects of reality in a very crude manner. However, even this simple design can be applied to the invasion of *H. mantegazzianum* in similar situations. More importantly, after some modifications and re-parameterization, it could also be used to study other species. Prominent candidates for a combination of aerial photography and modelling are species with prominent features and growing in dense stands (e.g., *Rhododendron ponticum* or *Pueraria montana*; Weber, 2003). The present study demonstrates how studies on population dynamic can contribute to understanding large-scale processes of plant invasions.

Acknowledgements

We thank the Giant Alien Project of the 5th European Union framework programme (EVK2- 20 CT-2001-00128) for financially supporting this work. Czech team was supported by institutional long-term research plans no. AV0Z60050516 from the Academy of Sciences of the Czech Republic, and no. 0021620828 from MŠMT CR. We also thank our reviewers for their extensive comments on previous versions of the article.

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Matrix vs. individual-based model

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Perspectives in Plant Ecology, Evolution and Systematics 7 (2006) 253–262
Perspectives in Plant Ecology, Evolution and Systematics
www.elsevier.de/ppees

npirical and virtual investigation of the population dynamics of an en plant under the constraints of local carrying capacity: *eracleum mantegazzianum* in the Czech Republic

na Nehrbass[a,*], Eckart Winkler[a], Jan Pergl[b], Irena Perglová[b], Petr Pyšek[b,c]

itre for Environmental Research (UFZ) Leipzig, Modelling, PO Box 500135, 04301 Leipzig, Germany
titute of Botany, Academy of Sciences of the Czech Republic, 252 43 Průhonice, Czech Republic
artment of Ecology, Faculty of Science, Charles University, Viničná 7, 128 01, Praha 2, Czech Republic

eived 16 August 2005; received in revised form 4 November 2005; accepted 9 November 2005

tract

uring the last decades, invasive alien species have become a global concern because of their ecological and iomic impact. *Heracleum mantegazzianum* (Apiaceae), is a tall monocarpic perennial native to Caucasus and sive in Europe since the 1950s. Within an interdisciplinary EU project aimed at assessing suitable management egy, we analysed the demography and ecology of this species in its invasive range. The monitoring of population imics in the Czech Republic led to the result that in the observed sites the species showed decreasing populations. ind an explanation for this unexpected result, two types of models were parameterized, based on the empirical : (1) a stage-based transition matrix model, which projected a continuous negative development, and (2) a spatially icit individual-based model (IBM), including individual variation. This second model was able to create a ilation with steady individual numbers. Analyses of the simulation showed that in more than 54% of the simulated s ($n = 5000$) the growth rate was smaller than one. Still, population increase in the remaining years was sufficient ustain a population. Nevertheless long-term observations document an invasive behaviour of the observed ilations. Hence, we could assume temporal changes in the course of an invasion and thus wanted to evaluate the ability of sampling negative growth in dependence of time since first invasion. By using a method from 'Virtual ogy', we approached the question: first we create an invasive population, based on the empirical data of *H. egazzianum* and second empirical sampling techniques were mimicked using the Virtual Ecologist approach. The ts demonstrate how the probability of sampling negative growth increases with time since first invasion. Hence, we me that the studied populations have already reached a maximum of their local invasive potential and thus iate in their size.

ords: Demography; IBM; Individual-based modelling; Invasion; Virtual Ecologist; Matrix model

Introduction

Biological invasions have been receiving increasing attention and become a global concern in the last decades (Davis, 2003; Weber, 2003). Of special ecological

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orresponding author.
mail address: nana.nehrbass@ufz.de (N. Nehrbass).

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.1016 j.ppees.2005.11.001

and economical interest are those species, which have been introduced by humans and rapidly spread in their new environment (see Richardson et al., 2000 for definitions of invasive species). Those alien invaders represent an appealing study subject because of their unprecedented dynamics (Pyšek and Hulme, 2005) and the high relevance of their demography for practical implications in controlling them. Some invasive species threaten biodiversity in natural habitats by displacement of native biota through competition, hybridization or predation (Cox, 2004) and the effects invasive species have are not only ecological but also economic (Zavaleta, 2000; Pimentel et al., 2005). One of the plant species posing such a threat to common goods in Europe is the Giant Hogweed (*Heracleum mantegazzianum* Sommier et Levier, Apiaceae; Tiley et al., 1996; Pyšek, 1991; Otte and Franke, 1998; Willis and Hulme, 2002). An interdisciplinary EU project ('Giant Alien') aimed at developing an integrated pest management for invasive plants, used *H. mantegazzianum* as a model species. To identify life history stages that make a species vulnerable in terms of the population dynamics and at which the control efforts could be targeted, a detailed knowledge of the plant's demography and ecology is necessary (Hobbs and Humphries, 1995). To obtain this information, empirical studies of local populations were conducted over a 3 years period in the Czech Republic. These data were analysed using stage-based transition matrix models (Caswell, 2001).

The empirical data and their analysis by matrix models led to surprising results: (1) instead of expected expansion the majority of populations showed decreasing individual numbers, and (2) the intrinsic growth rates λ of the matrix models also projected population decline. This contradicted conventional wisdom on the behaviour of *H. mantegazzianum* and the knowledge about the sites' history. From long-term observations in the study area a steady increase in the size of invading populations was documented for the last 40 years (Müllerová et al., 2005). Marked invasion dynamics were also reported for the geographical scale of the entire country: the number of reported localities of *H. mantegazzianum* has been increasing exponentially since the 1940s (Pyšek, 1991; Pyšek and Prach, 1993).

To resolve the contradiction between short-term empirical studies and matrix modelling on the one hand and long-term observations on the other hand a spatially explicit individual-based model (IBM) was built, based on the same data as the original matrix models. This individual-based approach allowed to incorporate rules that retained individual variation in growth behaviour. We also applied the 'Virtual Ecologist' (VEco) approach to analyse possible consequences of sampling on the empirically found results. The VEco tool mimics empirical sampling behaviour in a model environment (e.g. Berger et al., 1999; Tyre et al., 2001). It was applied in an altered model version, which was parameterized to show clearly invasive behaviour of a population.

To disentangle the puzzle of an invasive population apparently being declining we:

1. Compared results from a deterministic matrix model and an individual-based simulation model with each other, with data from short-term observations and with long-term knowledge.
2. Studied the effect of local population behaviour on the sampled growth rates with the method of Virtu Ecology.

Materials and methods

Study species

Heracleum mantegazzianum (Apiaceae) is the talle forb in Europe, flowering individuals can reach up 5 m of height. The plant is a monocarpic perennial a reproduces exclusively by seed. An average plant bea about 20,000 seeds (I. Perglová et al., unpubl. data), b individuals with over 100,000 seeds have been reported (Tiley et al., 1996). The species forms a short-term persistent seed bank (Krinke et al., 2005), with a small proportion of seed persisting dormant for at least years (L. Moravcová et al., unpubl. data). Seeds germinate to high percentages (90% on average) once the morphophysiological dormancy is broken (Moravcová et al., 2005). The plant is capable of self-fertilization (I. Perglová et al., unpubl. data) which enables it to invade new habitats following a single long-distance dispersal event. *Heracleum mantegazzianum* is native to the W-Caucasus and the first record of its introduction is from Kew Botanic Gardens in Great Britain in 1817. Ever since, it has been popular as an ornamental plant in gardens throughout Europe. From such nascent foci the plant continuously spread into the wild. In the Czech Republic, there is a detailed knowledge of the history of invasion both at the national (Pyšek, 1991, Pyšek and Prach, 1993) and regional scales (Müllerová et al., 2005), the latter from the region of the first introduction to the country in 1862. Nowadays, there are 603 localities reported from the Czech Republic (P. Pyšek and K. Prach, unpubl. data) and the species is considered invasive in this country (Pyšek et al., 2002). Within its new range, *H. mantegazzianum* is a problem species due to its tendency to form mono-specific stands and its phototoxic sap causing human injuries (Tiley et al., 1996).

Study sites and empirical methods

The study sites were situated around the earliest introduction known in the Czech Republic (Pyšek

91), in the Slavkovský Les Protected Landscape Area, -Bohemia. Within the study area there are extensive etlands with a high diversity of flora and pastures here *H. mantegazzianum* occurs. In the years following e end of the 2nd World War, the change of land use ith lack of appropriate management and abandoning the area lead to the rapid spread of the Giant ogweed and the consequent heavy infestation. To ver the range of various habitat conditions, 11 sites ere chosen and in each one permanent plot (1 × 10 m^2) th dominance of *H. mantegazzianum* was established 2002. For these sites additional detailed studies were rried out on the biology and ecology of studied species rinke et al., 2005; Moravcová et al., 2005; Müllerová al., 2005).

Within each of the plots position of all *H. mantezzianum* plants with leaves larger than 7 cm was apped and their size characteristics were recorded. ence, the fate of each individual in the plot could followed throughout the survey period of 3 years. characterize size for each plant the following tributes were measured: number of leaves, length of e longest leaf, height of flowering stem and number of anches.

The first two were correlated with flowering and rvival probability and thus were used (1) to categorize e plants for the matrix model, and (2) to characterize ants in the IBM. For the models data from the annual nsus in late summer was used. The data set is based on ore than 1000 individuals.

ransition matrix model

Matrix models describe population dynamics by ansition probabilities between categories (age or age). In the presented study a stage-based approach as chosen and the plant's life cycle divided into: edling, small plant, vegetative adult plant, and flowerg plant (Fig. 1). During sampling plants in vegetative age were sorted into three classes (seedling, juvenile, sette) and later were reclassified according to their size umber and length of largest leaf) to make the stage asses comparable and filter out subjectivity. Thus we stinguished seedlings with 1–3 leaves and leaf length 70 cm, juveniles with <5 leaves and leaf length 140 cm and rosettes having $\geqslant 5$ leaves and leaf length 140 cm). For *H. mantegazzianum* the observed transions were growth (G), survival/longevity (L), retroression (R), and sexual reproduction/fecundity (F). In ses where data were missing, data for matrix entries ere pooled across years and populations.

The model uses discrete time-steps. Chosen model terval was one year from flowering to flowering. The quation

$$(t+1) = A\,n(t) \tag{1}$$

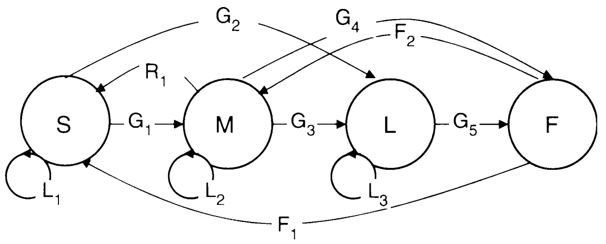


Fig. 1. Life-cycle diagram of the implemented plant species. Small (S), medium (M) and large (L) vegetative plants can grow or remain in the same category. Flowering individuals (F) die after flowering. The transitions mark survival (longevity L), growth (G), regression (R), and reproduction (fecundity F). The plant has no vegetative reproduction. A possible seed-bank is neglected in the model.

projects the population at time $t+1$, where A is the transition matrix (cf. Fig. 1)

$$A = \begin{pmatrix} L_1 & R_1 & 0 & F_1 \\ G_1 & L_2 & 0 & F_2 \\ G_2 & G_3 & L_3 & 0 \\ 0 & G_4 & G_5 & 0 \end{pmatrix} \tag{2}$$

and n the vector describing the number of individuals in each category. The dominant eigenvector of the matrix (λ) represents the intrinsic growth rate of the population. Increase in population number results in a $\lambda > 1$, for $\lambda < 1$ the population is projected to go extinct and $\lambda = 1$ indicates a stable population size. The method by Cochran and Ellner (1992) was used to calculate the eigenvalues and to perform elasticity analyses.

Individual-based model

Some programs (e.g. Ramas/Stage; Ferson, 1994) are able to handle matrix models with discrete individuals. Still, those individuals undergo distinct stages, and size parameters are not assigned continuously. Also, the spatial aspect of dispersal is not included in those approaches. Thus, we used a custom-tailored IBM (Fig. 2).

The model was designed to investigate the consequences of local spread and of continuous variability of individual behaviour of *H. mantegazzianum*. Model rules and parameters were derived from the same data as the matrix models. Elasticity analyses of the original matrix model served as an indicator which life-cycle stages were most relevant for changes in growth rate. Following, the parameters for growth and survival were modelled in detail, including the found variation in the transition behaviour of the individual. The model was constructed rule-based; in the description the parameterizations of the model follow each introduced rule.

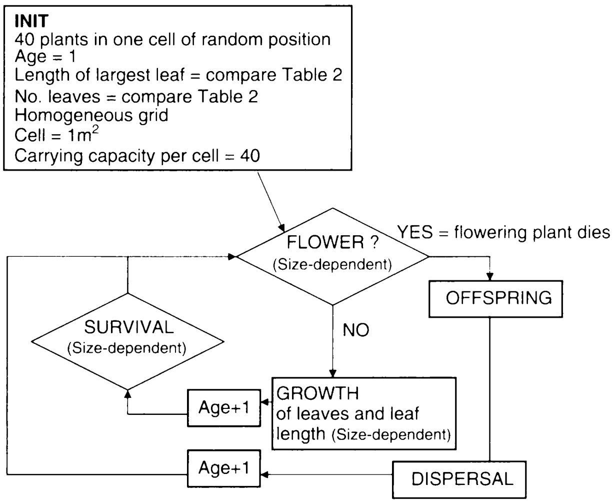


Fig. 2. Flow chart of the individual-based model. Each simulation is initialized and then carried out for 50 time-steps (years) in which the different modules of plant development are accessed for each individual on requirement.

Time

The model is discrete in time. One time step represents the year from one flowering period to the next, such as in the matrix model.

Space

The model was spatially explicit in a two dimensional grid, consisting of 2500 cells (50*50). Each grid cell represented one square meter. The entire grid represented the area of habitat one population could locally invade. Single cells were characterized by a maximum carrying capacity, representing habitat suitability. Landscape was assumed to be homogeneous. Population dynamics were regulated locally in each cell, but cells were connected via dispersal. Carrying capacity for a cell was set to 40 individuals, as was found in empirical studies. It was implemented as ceiling capacity (no density regulation before the maximum number is reached).

Plants

Plants were treated as individuals. Each individual was characterized by a set of traits: age, number of leaves and length of largest leaf. The latter was implemented as a continuous variable. The fate of a plant was recorded as soon as it got established in a cell. In a complete life-cycle a plant grew over several years, flowered, produced offspring and died.

Reproduction, offspring and dispersal

As Giant Hogweed is monocarpic, only plants older than 2 years could flower. Flowering probability was determined by a combination of the two size attributes (number of leaves and length of the largest leaf, see Table 1). After flowering an individual died. If not flowering, vegetative growth continued a further year (see below).

The number of offspring produced by a plant could not be correlated with any trait of the maternal plant, and data to estimate the probability for individual flowering plants to have a certain number of offspring were not available. Hence, in the model all plants created the same mean number of offspring. Offspring production per plant was adapted to a fat-tailed probability distribution, resembling a Poisson distribution, but with a higher probability for low offspring production and allowance for rare events of high offspring productions (Fig. 3). Thus, this distribution comprised the different average values from the populations under study. The function had the same mean value as the empirical data ($M = 2.6$; weighted mean from all populations). New plants with the age of zero were assigned a randomly chosen number of leaves between one and four. Initial size (length of the longest

Table 1. Flowering probability for plants

Number of leaves	Length of largest leaf (cm)	Flowering probability
<3		0
3	≤140	0
3	>140	0.51
4	≤180	0.33
4	>180	0.77
5		1.0

The flowering probability is determined by a combination of the number and the size of the largest leaf. Individuals need to be at least years old and have a leaf length of > 140 cm to be able to flower.

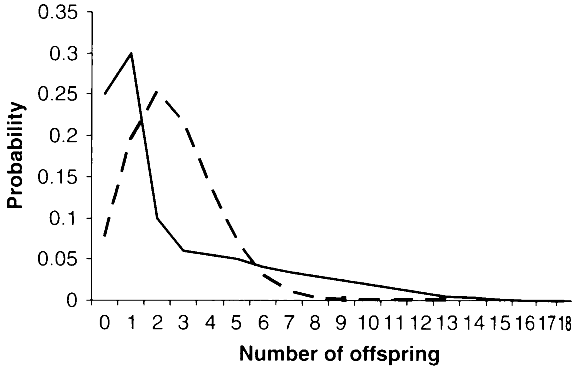


Fig. 3. Probability function for the number of offspring produced by a flowering individual (black line). The realized mean of the chosen function is the same as in the empirical data ($M = 2.6$). In comparison a Poisson distribution with $M = 2.6$ (broken line) is shown.

ble 2. Assignment for the initial size of a plant at tablishment

umber of aves	Probability	Length of longest leaf
	0.40	52.2 ± 30.6
	0.38	53.4 ± 39.1
	0.15	94.8 ± 67.7
	0.07	105.7 ± 59.5

e number of leaves is determined by chance, following empirically served probabilities. Dependent on the number of leaves the length the longest leave is calculated, again using empirical-based values.

ble 3. Dispersal probability for offspring

istance from cell of origin	Offspring (%)
(mother cell)	46
	29
	14
	4
	5
andom dispersal	2
otal	100

obability to disperse into a neighbouring cell is dependent on its stance from the cell of origin. All cells within one radius have the ame likelihood to be occupied. Additionally 2% of the offspring are ndomly dispersed across the grid.

eaf) was determined depending on this number Table 2). Plants could not die in the year that they were created; any mortality within the first year was already considered in the offspring values. New plants were placed in the cell of origin (parent plant), or in the neighbourhood. The number of offspring dispersing into neighbouring cells was decreasing with distance Table 3). All cells within one radius around the cell of origin were considered equal in the probability of new plants established there. Additionally, we incorporated long-distance dispersal of 2% of the new plants at random over the whole grid.

Establishment of new plants could only take place in cells, where carrying capacity was not reached.

Vegetative growth

Growth of an individual from year t to year $t+1$ was dependent on its previous size, defined as length of largest leaf and leave number. The new number of leaves was calculated on the basis of probabilities from a transition matrix (Table 4).

The length of the longest leaf (l) was calculated using linear relationships between leaf-length values l in years t and $t+1$ (Eqs. (3a)–(3d) and Fig. 4) where each relationship depended on the number of leaves in year $t+1$:

Table 4. Transition probabilities for the annual decrease and increase in leaf number, based on empirical findings

Leaves in year ($t+1$)	Leaves in year (t)			
	1	2	3	4
1	0.36	0.18	0.04	0
2	0.35	0.28	0.15	0.09
3	0.24	0.30	0.41	0.18
4	0.04	0.19	0.33	0.09
5	0.01	0.05	0.07	0.45
6	0	0	0	0.18

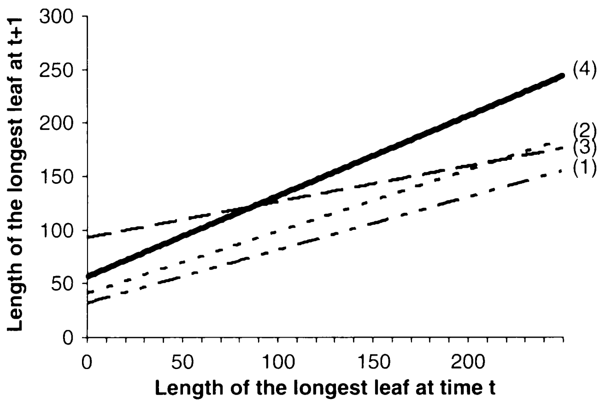


Fig. 4. Growth functions for the length of the largest leaf in dependence of the number of leaves, derived by logistic regression from empirical data. One leaf (1), two leaves (2), three leaves (3), and four leaves (4).

$$\text{One leaf}: \; l_{t+1} = 31.8 + 0.44 * l_t \qquad (3a)$$

$$\text{Two leaves}: \; l_t + 1 = 41.0 + 0.57 * l_t \qquad (3b)$$

$$\text{Three leaves}: \; l_t + 1 = 92.7 + 0.33 * l_t \qquad (3c)$$

$$\text{Four leaves}: \; l_t + 1 = 57.1 + 0.75 * l_t \qquad (3d)$$

These functions were derived through regression of empirical values. Retrogression of leaf length was possible through a reduction in leaf number (see Table 4) and hence through a change in calculation basis.

Death

The probability of death before reproduction decreased with increasing size of a vegetative individual (Table 5). All plants died after reproduction.

Simulations

Each simulation started by placing 40 individuals with the age of one within one randomly chosen cell. Simulations were timed for 50 years, and 50 repetitions were calculated. Global growth rates R for the IBM

Table 5. Survival probability of vegetative plants below the maximum age

Number of leaves	Length of largest leaf (cm)	Survival probability
1		0.50
2	$\leqslant 140$	0.61
2	> 140	1.00
3		0.85
4	$\leqslant 180$	0.60
4	> 180	1.00

The probability is dependent on the number of leaves and the length of its largest leaf. Plants with no leaves will die. Individuals with more than five leaves reproduce and die in the following. Therefore, for both cases the survival probability is zero.

were calculated by:

$$R = N_{t+1}/N_t, \quad (4)$$

where N_t is the individual number from last year and N_{t+1} this year's individual number summarized over all cells.

Virtual Ecologist sampling

In the context of our study, the VEco approach was designed to address the question how sampling probabilities for $R<1$ change with time since invasion. Hence, we first had to create an invasion scenario from our original IBM. Therefore, we increased survival rates for individuals (i.e. we had death only for flowering, aged, and individuals with no leaves, but no size dependent mortality). Also, a smaller grid size (10 x 10 cells) was chosen so carrying capacity for the entire grid (area) was reached within a reasonable time span. The simulations were again initiated with ten plants in one randomly chosen cell, simulations repeated ten times. The VEco was parameterized to sample all occupied grid cells (representing permanent plots) for each time-step (year) and calculate the growth rates R_P from the individuals in the cell P. We categorized the results into growth rates $R_P \geqslant 1$ and $R_P < 1$.

Results

Matrix model

Where data were available, the intrinsic growth rate (λ) and the elasticities for each plot (population) and transition between years were calculated. From the 11 study sites only two data sets were completely covering both transitions. For four study sites, only pooled matrix across 3 years were available. In two populations there were not enough individuals in the permanent plot to fill all matrix entries; three study sites were destroyed during the study. However, for a pooled matri transition data of individuals from all eight undamage sites were used. Instead of an invasive behaviour th data indicating a decreasing trend in population individual number with only two exceptions, where slight growth was projected (Table 6). The poole matrix, using the data, of all populations had a intrinsic growth rate of $\lambda = 0.85$. From pooled set populations, the calculated average age of flowerin plants was 5.8 ± 3.2 years. The elasticity analysis of t pooled matrix revealed that the most important tran tions were survival and growth (Table 7). Changes those values would result in the largest changes growth rate (λ). This result was taken into account f the implementation and parameterization of the IBM

Table 6. Summary of growth rates based on matrices fo available plots (populations)

Transition Plot site	2002–2003	2003–2004	2002–200
1	n.a.	n.a.	0.667
2	n.a.	n.a.	1.002
3	1.077	0.634	0.864
4	0.901	0.880	0.882
5	n.a.	n.a.	0.727
6	n.a.	n.a.	0.887
Pooled λ	0.779	0.823	0.792

Where possible, values for the intrinsic growth rate (λ) of each plot s shown.

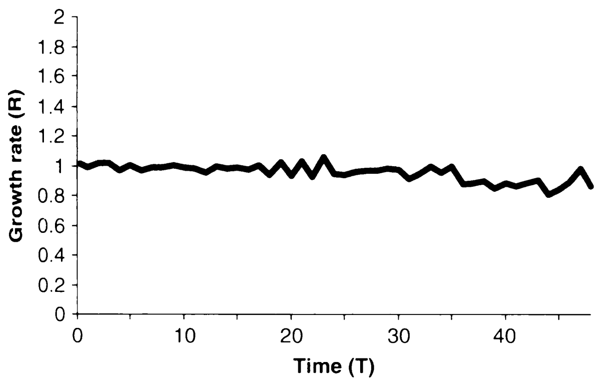
Table 7. Elasticity matrix for a matrix pooled across plots and years

	Seedling	Juvenile	Rosette	Flowering
Seedling	0.0664	0.0368	0	0.0968
Juvenile	0.1016	0.1344	0.0378	0.0752
Rosette	0.0320	0.1300	0.1169	0
Flowering	0	0.0478	0.1242	0

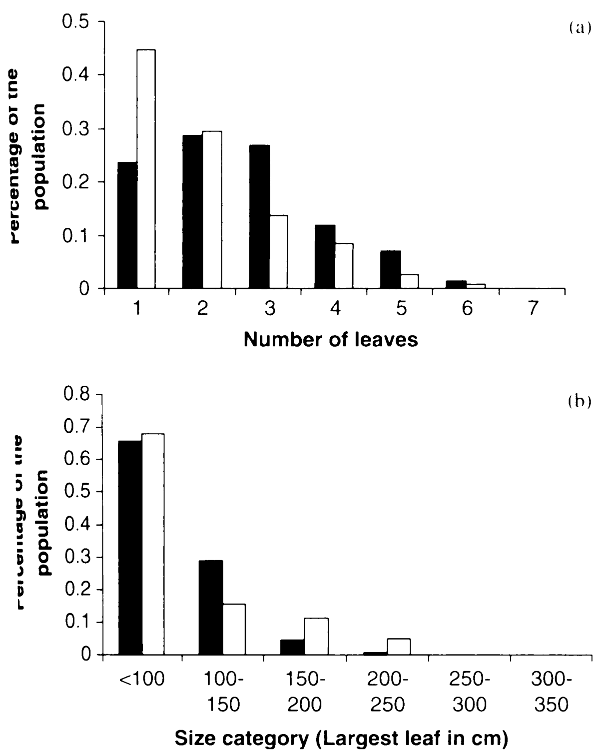
Survival of the juvenile stage was the most decisive transition in th observed populations and years.

Individual-based model

The simulated populations, which were started wi 100 individuals, showed a sustaining behaviour but lit or no invasion with an average growth rate $R = 1.003 \pm 0.33$ (Fig. 5). By comparing the long-ter size structure calculated in the IBM with the empirica recorded values, we were able to make a stateme about the ability of the model to reflect Giant Hogwe demography. Both measures for size of the plan length of the longest leaf and number of leaves, we well approximated in the model (Fig. 6a and b). Me



g. 5. Annual development of the mean growth rate in the nulated populations. Overall mean was $R = 1.003 \pm 0.33$ SD = 5000, 100 simulation runs each for 50 years). But 54.7% ' the annual growth rates were $R < 1$. The mean annual owth rate decreased with time since invasion.



;. 6. Comparison of population structures from the model ack bars, $n = 65.535$) and from empirical observations hite bars, $n = 460$ and 777; a, number of leaves; b, length of : largest leaf).

e of flowering plant however was lower than in the atrix models ($M = 3.2 \pm 1.2$). But both model results not significantly differ and the parameter cannot be lidated by empirical data. Mean number of offspring oduced was $M = 2.6 \pm 1.4$, thus with a slightly lower ındard deviation than in the empirical data. The erall population growth rate, averaged over all simulation runs and simulation years, was slightly above one ($R = 1.003$; $n = 5000$). However, in a majority of years (54.7%) we found a growth rate below one. If growth rates in subsequent years are statistically independent the probability for an observer to witness 2 years with an annual growth rate below one is $p = 0.3$. This result of IBM-modelling may explain the discrepancy between the well-established long-term dynamics of *H. mantegazzianum* on the one hand and the observed short-term population decrease together with the matrix-model analysis on the other hand.

This consideration was reason to assess sampling probabilities for $R < 1$ with the VEco approach.

Virtual Ecologist sampling

In an ideal course of a local invasion the population develops from one introduced plant to a stand that has reached local carrying capacity, where population growth rate is approximating $R = 1$ and further invasion can only take place as long distance-dispersal events into other habitat. In the study case the observed growth rate of the population was $R \leqslant 1$ and thus we assume that the local carrying capacity had been reached. After calculating the probability to sample to independent years of growth rate $R < 1$ under current population dynamics, we further wanted to evaluate the probability to sample a growth rate R in the course of an invasion. By means of the VEco approach we explored the probability to sample growth rates in a plot (represented by one grid cell) with $R_P < 1$ in a growing population and the dependence of this probability on the time since the start of invasion. This model used as a basis for the evaluation had a mean growth rate $R = 1.12 \pm 0.18$. The number of offspring remained similar to the original simulations ($M = 2.3 \pm 1.09$), the slight decrease being caused by enhanced effects of carrying capacity and border losses, due to the smaller grid size.

The overall probability to sample a plot with growth rate of $R_P < 1$ was 11.4% and thus markedly lower than in the simulations using actual empirical findings for survival. But, when analysing the development over time, it becomes apparent that the probability increases with time since invasion (Fig. 7).

Discussion

Heracleum mantegazzianum is known to be invasive in Europe and its spread has been observed for the last 50 years in the Czech Republic (Pyšek, 1991; Pyšek and Prach, 1993; Tiley et al., 1996; Müllerová et al., 2005). This study was concerned with populations of the plant, situated in the vicinity of what is thought to be the

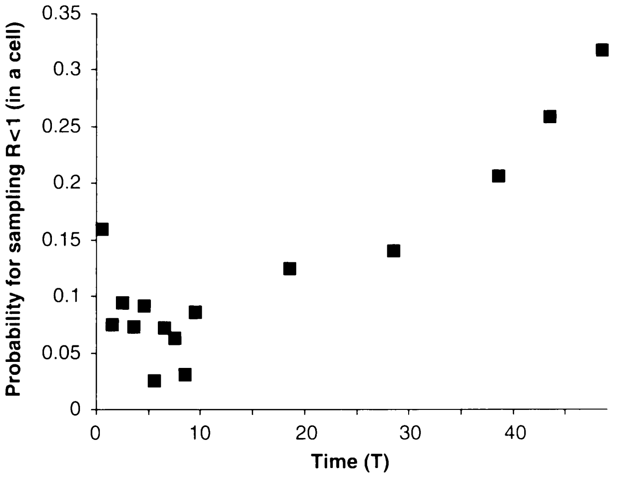


Fig. 7. Probability to sample a plot (represented by one grid cell) with a growth rate $R<1$ depending on the time elapsed since the start of population development. Evaluated in a simulation (10 repetitions) with the Virtual Ecologist approach. In the beginning of the invasion this probability strongly fluctuates due to low individual numbers. With progressing invasion of the populations the probability to sample plots which have reached local carrying capacity and thus have a growth rate fluctuating around $R = 1$ exponentially increases. At $t = 50$ the probability to sample a plot with $R<1$ is $p = 0.32$ ($n = 912$).

nascent focus of the invasion in the Czech Republic. Empirical observations during three consecutive years led to the unexpected result of decreasing individual numbers in a majority of the observed populations. Data was analysed with deterministic matrix models. Such models are often used in population ecology due to their relatively easy applicability. They provide insights into the importance of different life cycle stages or transitions between them (Heppell et al., 2000a). Yet, in their simple form they have some structural deficiencies when it comes to the incorporation of characteristics essential for invasions, such as dispersal events leading to spatial extension. Moreover, some important mechanisms, like density-dependent development and stochasticity are often neglected as they require some effort to be successfully incorporated (Fieberg and Ellner, 2001; Claessen, 2005; Ehrlen et al., 2005). The analysis of our data with deterministic matrix models showed that the intrinsic growth rate λ of the entire region (pooled data) was smaller than one and hence projected further decrease. Thus, the development of a management scenario seemed no longer required. Even more, the elasticity analyses on which such a management suggestion would be based was derived from a matrix model of decreasing populations. Thus it might be misleading, as for expanding populations the relative influences of transitions on growth rate might change. Some authors even argue that in any case realistic predictions of future development cannot be deriv from λ, but that it allows to develop ideas about t current state of a population and the importance individual transitions on the population dynami (Silvertown et al., 1996; Caswell, 2000; Heppell et a 2000b). As there was no repeated sampling with populations, statements about differences betwe populations could not be made. Empirical resu suggest that populations within the region show simil dynamics and that for an evaluation of the populati dynamics it is possible to pool the data from censuses. Additionally the pooling of matrices is common technique to account for missing data (e. Sinclair et al., 2005).

An IBM was parameterized with special consideratio of the observed growth variations between individua The individual number did not increase markedly a mean growth rate R approximated one. So, in contra to the deterministic matrix models the IBM simulatio showed that under consideration of the observe individual variation the populations of *H. mantegazzi num* are rather stable but not decreasing, although the growth rate becomes negative at times. This is dynamic behaviour, which can be observed for popul tions which have reached the carrying capacity of the habitat and encounter a ceiling capacity around whic their individual numbers fluctuate. For practice th between-years variation in growth rate implies a hig probability for the observation of a population to fa within such an unfavourable year. With the VEc approach it was demonstrated that this probabilit steadily increases with time since invasion and thus wit the approximation of the local carrying capacity Additional factors like global environmental stochast city (e.g. climatic conditions), which might contribute t the fact that a negative growth is encountered in a observed populations simultaneously were not quanti fied by empirical studies and thus not included in th models. Nevertheless, we can hypothesize two likel causes for the populations not being locally invasive:

(1) Local carrying capacity: For this aspect we ar aware that habitat heterogeneity might be a relevan factor, which has been neglected in the IBM. But this factor is accounted for further studies (Müllerová et al., 2005; N. Nehrbass et al., unpubl. data) The populations studied are situated in a sparsel populated and extensively managed protected landscape area. *Heracleum mantegazzianum* is presen there for more than 140 years but the invasion in the localities investigated only started approximately 40 years ago (Müllerová et al., 2005). Thus, we have to assume that growth rates of the observed populations have been $R > 1$ in past years, throughout the local invasion process and that within this time span the carrying capacity of the habitat was reached

, there is no indication that the species has lost its isive potential. Hence, although for single ulations the limits might be reached the invasion cess is likely to proceed on different scales, anced by long distance dispersal events.

ther studies annual variation in climatic condi- s have been named as a potential cause for ative growth rates (Hüls, 2005). Hot and dry son of 2003 might have influenced the perfor- nce of populations in this year. Nevertheless, as ulations did not perform any better in 2004, this or seems to have only an additional influence.

mpirical studies of plant invasions, a detailed dge of variation of individual plants between and for a number of populations is rarely le. Our analysis of the data obtained for *H. azzianum* suggests that local saturation is re- ble for observing growth rates $R \leq 1$. This is d with time since the beginning of invasion ová et al., 2005).

us assume that *H. mantegazzianum* would be a , being introduced to a new region and no ation on its invasive nature was available from ere. When using data from short-term observa- n already existing populations only decreasing and nt population growth rates were observed and d from models. Knowledge about the invasion of an existing population might thus be an ant factor, when considering invasive ability of a . Else the false conclusion could be reached that ecies does not pose the threat of invasion in the ea. The VEco approach could illustrate how the ility of such 'flawed' sampling increases with time nvasion at the original site.

owledgements

thank our referees for their detailed suggestions. lso thank the Giant Alien Project of the 5th ean Union Framework Programme (EVK2-CT-00128) for financially supporting this work. Addi- support was provided by institutional long-term ch plans no. AV0Z60050516 from the Academy of ces of the Czech Republic (to JP, IP, PP), and no. 20828 from MŠMT ČR (to PP).

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Conclusions

The set of presented studies on the population ecology of *Heracleum mantegazzianum* show that there is no simple characteristics responsible for this species' invasion success – rather this success is determined by its behaviour in various stages of the life-cycle that enabled *H. mantegazzianum* to make use of the advantage of having been introduced into a milder climate and largely human-made, or at least heavily disturbed landscape. The invasion is supported by reproductive characteristics such as possible selfing, production of thousands of easily germinable seeds and high regeneration ability. Furthermore, the species is highly plastic as far as the timing of flowering is concerned; under less favourable conditions plants are able to "wait" for reproduction up to 12 years, but under suitable conditions they are able to flower in the second year. *Heracleum mantegazzianum* has superior colonization ability with relatively high role of randomly dispersed seeds at the landscape scale, although the establishment rate of seedlings is quite low.

In spite of the fact that no transition or stage in the life cycle was found to be a weak link in the life cycle of the species studied, there are some hints that should be mentioned in context of planning control methods, i.e. a low survival rate of seedlings on undisturbed ground, high mortality during the first year and strictly monocarpic life history of *H. mantegazzianum*. Control and management efforts can be therefore targeted so as to prevent the dispersal of produced seed, which shall lead to the gradual retreat from invaded sites. Cutting or other mechanical control methods applied on vegetative plants can only prolong time needed for flowering and thus the time needed for control.