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Historical Dynamics of *Heracleum mantegazzianum* Invasion at Regional and Local Scales

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> *Fashionable country gentlemen had some cultivated wild gardens in which they innocently planted the Giant Hogweed throughout the land*
> (Genesis, 1971)

Introduction

For several reasons, historical data on the occurrence of *Heracleum mantegazzianum* Sommier & Levier are fairly detailed, especially in countries with a strong floristic tradition. Such data allow a retrospective analysis of this species' spread. This species is attractive enough to be recorded by botanists, because of its alien origin and tendency to spread, and above all its conspicuousness (Fig. 3.1). In parts of the continent, such as Central Europe, it is also taxonomically unproblematic, hence easily recognizable by amateur botanists who are the main collectors of floristic data (Pyšek, 1991). The taxonomic problems referred to earlier (see Jahodová *et al.*, Chapter 1, this volume) are of little significance in the Czech Republic as the vast majority of the observations concern this species (Holub, 1997).

Probably the most systematically gathered data on the occurrence of *H. mantegazzianum* in Europe are those for the Czech Republic (Pyšek, 1991, 1994; Pyšek *et al.*, 1998a) and the UK (Collingham *et al.*, 2000), countries with a strong floristic tradition (Preston *et al.*, 2002; Pyšek *et al.*, 2002). Such data allow the invasion dynamics of *H. mantegazzianum* over the last 150 years to be reconstructed. These two data sets are complementary because they: (i) come from climatically different geographical areas of Europe (continental and oceanic climate); and (ii) were collected using different methods, i.e. collation of localities from the literature in the Czech Republic, and repeated

*Ecology and Management of Giant Hogweed (*Heracleum mantegazzianum*).* (eds P. Pyšek, M.J.W. Cock, W. Nentwig and H.P. Ravn)

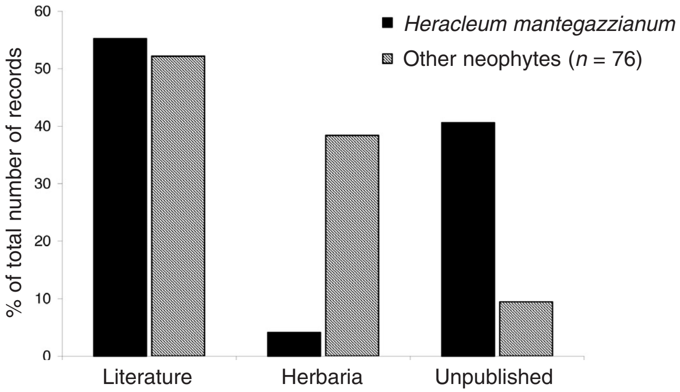

Fig. 3.1. Sources of floristic data for *H. mantegazzianum* differ from those for other neophytes, based on a sample of 76 neophytes recorded in the Czech Republic (based on 28,330 floristic records). The percentage of literature sources is very similar (55.6% and 52.2% of all records of *H. mantegazzianum* and all neophytes, respectively). However, *H. mantegazzianum* is avoided by herbarium collectors because of its large stature, which accounts for why only 4.1% of the records (25 of the 603 in total) are from herbaria, compared to 38.4% for an average neophyte. Interestingly, 245 unpublished records (40.6% of the total) were supplied by botanists, which greatly exceeds the average number for other neophytes (35.2 records).

mapping in different periods in the UK. That these different approaches yield similar results, as shown below, is an indication that conclusions drawn about the history of invasion at regional/geographical scale are robust.

Furthermore, floristic data not only make it possible to reconstruct the invasion, and describe the pattern of species abundance in the landscape and its development over time, but also provide information on species ecology and the temporal changes in the spectrum of habitats occupied during the course of the invasion (Pyšek, 1991). The present chapter reviews information on the historical dynamics of *H. mantegazzianum* and aims to: (i) describe the dynamics of the invasions of the Czech Republic and UK; (ii) compare the pattern of spread at local and regional/geographical scales; and (iii) place the invasion potential of *H. mantegazzianum* into a wider context of plant invasions by comparing its rate of spread recorded in these two countries with that recorded for important invasive species elsewhere.

Reconstruction of the Invasion of the Czech Republic

Previous work (e.g. Pyšek, 1991; Pyšek and Prach, 1995; Delisle *et al.*, 2003) shows how floristic data, systematically gathered over an area for a long time, may be used to reconstruct the pattern of a species invasion on a regional geographical scale. The history of the invasion by *H. mantegazzianum* is well described for the Czech Republic, in terms of the overall dynamics of spread (Pyšek, 1991) and changes in species ecology during the course of the invasion (Pyšek, 1994; Pyšek and Prach, 1993; Pyšek *et al*., 1998a). This species was first introduced in the Slavkovský les region, in the western part of the country, as a garden ornamental, reportedly in 1862. In 1877 it was first collected in the wild, as an escape from cultivation, and documented by a herbarium specimen (Holub, 1997). It soon became popular among gardeners, which is assumed to have contributed to its spread. Up to 1950, only a few localities were known for the entire country, and their spatial distribution (Pyšek, 1991: Fig. 1a) indicates that at least some localities in the east must have resulted from humans translocating the species.

The same pattern is apparent in the UK. In general, the distribution of an invasive species spreading across a landscape is expected to show autocorrelation because the probability that an area will be colonized is a function of its distance from neighbouring populations. However, Collingham *et al*. (2000) found no evidence of a significant spatial autocorrelation using distribution data for *H. mantegazzianum* in the UK, although this species is believed to spread its fruits by both wind and water (see Moravcová *et al*., Chapter 5, this volume). Although local aggregations of this species are obvious regionally and nationally, the majority of records in the UK are isolated. Collingham *et al*. (2000) conclude that this pattern reflects the importance of long-distance anthropogenic dispersal in the intial phase of the invasion in the UK. This suggests that in this country, as in the Czech Republic, *H. mantegazzianum* might have been spread as a garden ornamental over long distances in the early stages of invasion. This results in the existence of new sites, which subsequently act as foci for further spread (Pyšek, 1991).

Nevertheless, the current distribution in the Czech Republic (232 grid squares occupied in 1996; Williamson *et al*., 2005) still indicates that the species has spread from the original place of introduction in the western part of the country, because its abundance decreases from west to east. The effect of distance from the source is highly significant and the form of the relationship is the same as it was at the end of the 1980s, i.e. some 20 years after the beginning of the period of rapid spread, but the effect of time, significant then, is no longer so when recent data are analysed (Fig. 3.2).

Based on the plot of the cumulative number of localities over time, the start of the exponential phase of invasion was 1943 (for details, see Pyšek and Prach, 1993). Williamson *et al*. (2005) used a more recent data set of the cumulative number of grid squares occupied, instead of the number of localities. This study also revealed a distinct lag phase, defined as the period before the log plot of the cumulative number of squares occupied against time becomes straight. Such a lag phase was only found in 19 species of neophytes of the 63 examined in the Czech Republic. This paper gives the beginning of the exponential phase as 1936, which is similar to the previous estimate of Pyšek and Prach (1993). Both estimates are close enough to conclude that the lag phase, from the first record outside cultivation to the beginning of exponential spread, lasted 60–70 years in the Czech Republic. Nevertheless, a comparison of these papers indicates that the exact date of the transition from the lag to the exponential phase depends on the method used to analyse the data (Pyšek and Prach, 1993; Williamson *et al*., 2005).

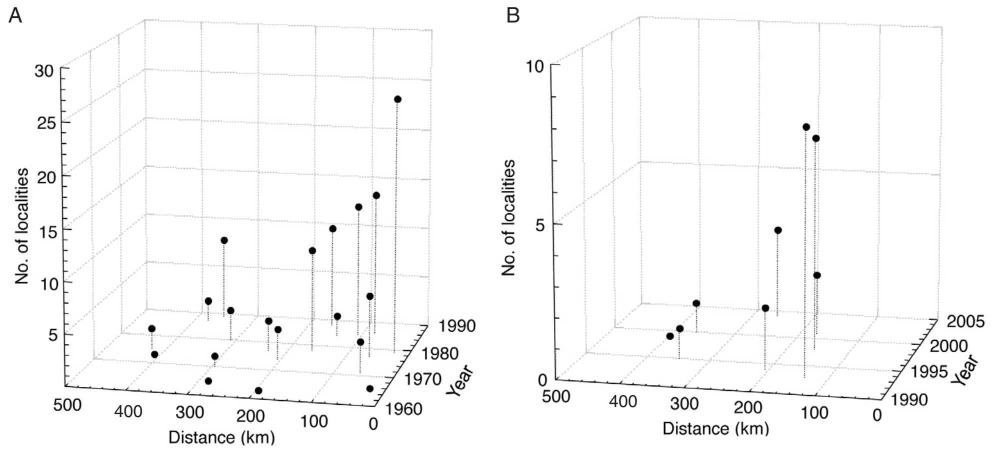

Fig. 3.2. (A) Effects of the distance from the locality of the original introduction in 1862 and of time on the frequency of occurrence of *H. mantegazzianum* in the Czech Republic, at the end of the 1980s, approximately 20 years after the onset of rapid spread in this country (Pyšek, 1991; Pyšek and Prach, 1993). Data are the number of localities recorded by annual floristic summer schools organized by the Czech Botanical Society, during which a region is systematically sampled and standardized data are obtained. Both year ($F = 27.13$; $df = 1, 17$; $P < 0.001$) and distance ($F = 5.59$; $df = 1, 17$; $P < 0.05$) were significant predictors in the multiple regression derived in 1989: LN (NUMBER + 1) = –194.2 + 0.099 YEAR + 33.06 (1/DISTANCE); $F = 14.72$; $df = 2, 16$; $R^2 = 0.65$. See Pyšek (1991) for details; additional localities are: 15 – Svitavy 1965; 16 – Lanškroun 1970 (Kovář *et al.*, 1996); 17 – Humpolec 1974 (Skalický and Štech, 2000); 18 – Blovice 1986 (Nesvadbová and Sofron, 1996); 19 – Tábor 1988 (Štech, 2005). Note that the regression coefficients differ from the original data in Pyšek (1991), as five more data points are included. (B) Fifteen years later, the relationship is only significant for distance; deletion test on the effect of year, using ANCOVA with the two time periods (1963–1989; 1990–2004) as a factor, and year and distance as covariates: $F = 0.04$; $df = 1, 22$; NS. The average abundance in the 1990–2004 period is significantly higher ($F = 23.85$; $df = 1, 24$; $P < 0.001$) than at the end of the 1980s. The effect of distance remains highly significant ($F = 18.91$; $df = 1, 24$; $P < 0.001$) and the same as in 1989 (deletion test in ANCOVA on a different slope of distance in each time period: $F = 0.28$; $df = 1, 23$; NS). Data for the latter period: 1 = Mělník 1993 (Hrouda *et al.*, 1996); 2 = Světlá nad Sázavou 1994 (Čech, 2003); 3 = Břeclav 1995 (Danihelka and Grulich, 1996); 4 = Česká Lípa 1998 (Kubát *et al.*, 1998); 5 = Nový Jičín 1999 (Grulich, 2003a); 6 = Kroměříž 2000 (Grulich, 2003b); 7 = České Budějovice 2001 (Lepší *et al.*, 2005); 8 = Kostelec nad Orlicí 2004 (Kaplan, 2005).

Heracleum mantegazzianum started to spread exponentially in the Czech Republic after colonizing very few localities (Pyšek and Prach, 1993). This implies that the lag phase, the time necessary for adaptation to a new region, is not too important in this species; it started to spread in the second half of the 20th century and as for most invasive aliens, changes in the landscape were the main trigger (Williamson *et al.*, 2005). This seems to accord with the small genetic difference between populations from Europe and the Caucasus Mountains (see Jahodová *et al.*, Chapter 1, this volume).

Pyšek (1991) estimated the rate of spread of *H. mantegazzianum* on a geographical scale in the Czech Republic, based on the slope of a semi-log plot of the cumulative number of grid squares occupied by the species up to a certain date. The value of 0.0835 is very similar to that obtained by Williamson *et al.* (2005) for *H. mantegazzianum* in the Czech Republic, using more recent cumulative grid square data. These authors used $\log_{10}$ base and arrived at the value of 0.0327, which is very close to 0.0363, obtained if the $\log_e$ based value given by Pyšek (1991) is transformed to $\log_{10}$ base.

Environmental Factors and Habitat Preferences During the Invasion

In the course of the invasion of the Czech Republic, this species shifted to lower altitudes; at the beginning of the 1970s, 28.5% of the localities were above 600 m a.s.l., but only 14.7% in 1990 (Pyšek, 1994). This suggests that the inherent preferences for a cooler climate that *H. mantegazzianum* acquired at higher altitudes in the Caucasus Mountains affected its ability to invade warmer areas at the beginning, but this constraint was overcome and is no longer present. Moreover, the above frequency distribution of altitudes in the Czech Republic is similar to a recent distribution of altitudes at which the localities of *H. mantegazzianum* are recorded, indicating that its occurrence is no longer affected by altitude (Pyšek, 1994).

Changes in the representation of habitats occupied in the course of the invasion of the Czech Republic are rather profound, indicating that the habitat preferences of *H. mantegazzianum* changed as the invasion progressed (Fig. 3.3). Because of its popularity as a garden ornamental, this species was more or less confined initially to parks and gardens and their immediate surroundings. Later on the importance of these habitats decreased. That 'semi-natural' habitats (Fig. 3.3) were occupied to the same degree from the very start of the invasion indicates that *H. mantegazzianum* was able to invade such less disturbed habitats and some grasslands, wetlands and scrub. The beginning of the exponential spread in the 1930s–1940s (Pyšek and Prach, 1993; Williamson *et al.*, 2005) is associated with an increase in the proportion of riparian corridors and other linear habitats (roads, railways), suitable for efficient seed dispersal (see Moravcová *et al.*, Chapter 5, this volume). Major changes in habitat spectra are detectable in the 1970s, when profound landscape changes are thought to have encouraged the spread of neophytes in the country in general (Pyšek *et al.*, 1998b; Williamson *et al.*, 2005). In this period, *H. mantegazzianum* started to spread into urban habitats and linear dispersal along corridors, such as roads and railways, became relatively more important than along rivers and water courses (Fig. 3.3). That is, large rivers in particular acted as efficient dispersal vectors in the early stages of the invasion, but later on the species started to spread to more distant areas not associated with rivers (Pyšek, 1994). Although rivers are in general a good dispersal vector for invasive plants (Pyšek and Prach, 1994), the major invasive species in the Czech flora differ significantly in their affinity to riparian habitats and

H. mantegazzianum is less confined to riparian habitats than, for example, *Impatiens glandulifera* and two *Fallopia* species (Pyšek and Prach, 1993). In general, *H. mantegazzianum* is able to invade a rather large spectrum of habitats, and the rate of invasion and dates of first records do not differ substantially among these habitats (Pyšek and Prach, 1993). This suggests that the nature of recipient habitats is less important than may be the case for most neophytes, and indicates that once *H. mantegazzianum* enters a habitat, it spreads exponentially regardless of the characteristics of the recipient vegetation (Pyšek, 1994). This is strongly supported by ecological studies on its seed bank (see Moravcová *et al.*, Chapter 5, this volume; Krinke *et al.*, 2005), reproductive biology (Moravcová *et al.*, 2005 and Chapter 5, this volume) and habitat occupation on both local (Müllerová *et al.*, 2005) and national (Pyšek, 1994) scales; these studies indicate that this species is only slightly limited by the character of the invaded vegetation or specific site conditions – once there are suitable habitats in the landscape it spreads at a constant and rather high rate.

In the mid 1990s, urban sites (including dumps and deposits in open landscapes) and linear habitats (such as roads, paths and railways) were frequently reported as habitats for *H. mantegazzianum*, accounting for 29.2% and 29.3% of the total records (*n* = 679 year/habitat records from 603 localities, with some localities assigned to more than one habitat type). The species was also fairly frequently recorded in various less disturbed 'semi-natural' habitats (15.6%) and riparian habitats (14.4%). Over the entire invasion history, 7.5% of the records came from parks and gardens. These numbers are cumulative,

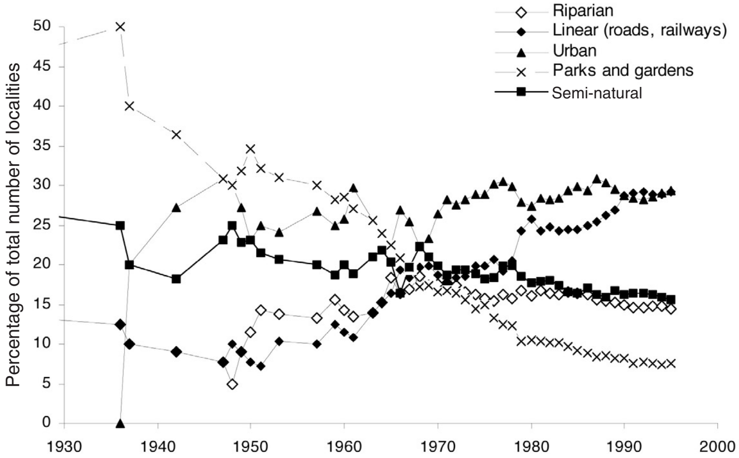

Fig. 3.3. Changes in habitat preferences of *H. mantegazzianum* during the course of its invasion in the Czech Republic. Habitat preference is expressed as the percentage of the total number of localities reported up to the given year, which are for a particular habitat. 'Semi-natural' habitats include less disturbed sites such as scrub, grassland, wetlands, forest and their margins (for details of the classification of habitats based on floristic records, see Pyšek *et al.*, 1998b). Based on data from Pyšek (1994) and updated.

therefore slightly biased if inferring current habitat spectra, but correspond reasonably well to where the species is currently found. Taking only records from the last decade (1986–1995, $n = 344$) yields very similar percentages of 28.8% (urban sites), 33.7% (linear habitats), 14.8% ('semi-natural' habitats), 12.5% (riparian habitats) and 5.8% (parks and gardens).

These figures correspond reasonably well with those of a detailed investigation of habitat preferences at a local scale in the Slavkovský les region (Pyšek and Pyšek, 1995). Taking the percentage of a habitat invaded by *H. mantegazzianum* as a measure, 40.4% of path margins, 38.2% of road ditches and 38.0% of the area adjacent to water courses are occupied by more or less dense populations of this species. In addition, 30.7% of willow scrub and 7.9% of forest margins are also invaded, but only 2.3% of dry grassland and 2.2% of wetlands (Pyšek and Pyšek, 1995).

Invasion Dynamics at a Local Scale, Analysed Using Aerial Photographs

At the local scale, regression models that establish a relationship between the area invaded from an invasion focus and time have been useful in quantifying invasion patterns (Higgins and Richardson, 1996). Data from an analysis of historical aerial photographs showing the invasion of the Slavkovský les region, Czech Republic, by *H. mantegazzianum* (Müllerová *et al*., 2005) provide an insight into the invasion history of a noxious alien species on a local scale. This species is easily detectable on aerial photographs taken at flowering and early fruiting, from June to August (Fig. 3.4). These data document the invasion from the beginning, which is rarely possible for other alien plants, and therefore allow an analysis of the rate of spread and a study of the species' population dynamics.

Mean rate of areal spread over 50 years, calculated for nine sites (Müllerová *et al*., 2005), was 1261 m^2/year, and of linear spread 10.8 m/year. Absence of a correlation between linear and areal rates of spread indicates that *H. mantegazzianum* did not spread as an advancing front but that long-distance dispersal (Higgins and Richardson, 1999; Hulme, 2003) played an important role in the invasion. The direct effect of the rate of invasion on invaded area was larger than that of residence time (defined as the time for which a species has been present at a locality, see Rejmánek, 2000; Pyšek and Jarošík, 2005), but the total, direct and indirect, effect of residence time was only slightly less than that of the rate of invasion (Fig. 3.5). As the invasion proceeded, the populations spread from linear habitats into the surroundings, i.e. a pattern similar to that observed at the geographical/national scale. Flowering intensity did not exhibit any significant trend over time (Müllerová *et al*., 2005).

Fig. 3.4. Series of aerial photographs showing *H. mantegazzianum* invading one of the localities in the Slavkovský les region, where the species was first introduced as a garden ornamental in 1862 and escaped from cultivation in 1877. Locality Žitný, showing increase in the area occupied by *H. mantegazzianum* from (A) 1962 to (B) 1973 and (C) 1991. Photographs were taken at flowering and plants of *H. mantegazzianum* appear as white dots (for details, see Müllerová *et al*., 2005).

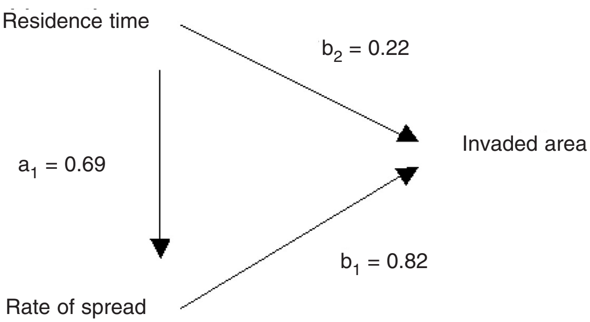

Fig. 3.5. Path model and path coefficients of the invaded area as a function of residence time and rate of spread. Based on aerial photographs of nine sites in the Slavkovský les region, Czech Republic, invaded by *H. mantegazzianum*, taken on 11 sampling dates between 1947 (before the invasion started) and 2002. The area covered by the plant in a 60 ha section of landscape was measured digitally, and used to obtain information 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. Residence time directly affects the rate of spread and both the residence time and the rate of spread directly affect the invaded area. The direct effect of the rate of invasion on invaded area (0.82) was larger 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). Based on data from Müllerová *et al.* (2005).

Rate of *Heracleum mantegazzianum* Spread Compared to that of Other Important Invasive Species

Since spread is the stage of invasion that is most easily modelled and most accessible to quantitative analysis (Williamson, 1996), there are many studies of the rate of spread of one or a few species of alien plants (reviewed in Pyšek and Hulme, 2005). Although some obvious limitations need to be kept in mind, such as multiple origins (the spread may start from several places, not just one), effect of boundaries (Williamson *et al.*, 2005) and effect of scale (Pyšek and Hulme, 2005), it is possible to make a rough comparison of the rate of spread of *H. mantegazzianum* with that of other species.

Measured by the regression slope of the increase in the cumulative number of localities over time, the rate of spread of *H. mantegazzianum* is similar to that of other important invasive species in the Czech Republic, if the whole period of invasion is considered. However, considering only the exponential phase of the invasion, the rate during this phase (slope: 1.107, $\log_e$ base) was 152% of that of *Impatiens glandulifera* (0.070), 248% of *Fallopia sachalinensis* (0.043) and 263% of *F. japonica* (0.040) (Pyšek and Prach, 1993; calculation based on their Table 3). Nevertheless, Williamson *et al.* (2005) provide estimates of spread for 31 species that can be compared. During 1971–1995, the period over which the section of the $\log_{10}$ base plot of the cumulative number of occupied mapping quadrats against time is straight, the number of squares occupied by *H. mantegazzianum* doubled every 9.21 years. This value indicates an average (geometric mean: 8.75 years; range 2.04–39.02) rate of spread (Williamson *et al.*, 2005).

Rates of areal spread are difficult to compare as they crucially depend on the scale of the study (Pyšek and Hulme, 2005). Some indication can be obtained by using a relative value, i.e. the multiplication of invaded area over time as recorded in the local-scale study of Müllerová *et al.* (2005). *Heracleum* increased its area from the first time it was recorded at a site to the date of the largest invaded area recorded 26.7 ± 37.9 times (mean ± SD, *n* = 9); the average mean residence time in a site was 33.7 ± 5.5 years. During the invasion of New Mexico by species of *Tamarix*, part of the invasion of the south-western USA by these species, which is one of the most spectacular invasions reported in the literature (Zavaleta, 2000), the invaded area increased 20.5 times from 1915 to 1925, and 4.6 times from 1925 to 1960 (Robinson, 1965). Thus the *Heracleum* invasion in the study area proceeded at a rate similar to that of most aggressive invasive species in other parts of the world.

What can be Inferred from the Comparison of Invasion at Local and National Scales?

Since detailed information on the course of the invasion of the Czech Republic by *H. mantegazzianum* is available (Pyšek, 1991), it is possible to compare the rate of spread at local and national scales. Plotting the cumulative number of this species' records against time over the whole period of the invasion yields a doubling time of 13.2 years for localities (analysed in Pyšek, 1991) and 14.3 for mapping squares (analysed in Williamson *et al.*, 2005), and these values do not differ significantly from the doubling time at the local scale of 13.9 (Müllerová *et al.*, 2005). This indicates that *Heracleum* spread nationally at the same rate as locally in the region of its introduction to the country, and that the constraints to its spread imposed by landscape features and availability of suitable habitats were similar at both scales (see Pyšek and Hulme, 2005, also for statistical details of the comparison of spreading rates).

Invasive species of plants do not always have the same rate of spread at local and geographical scales. Data that can be compared are extremely rare. *Heracleum mantegazzianum*, however, can be compared with the *Mimosa pigra* invasion in Australia. Lonsdale (1993) compared the rate of increase of this species at local and geographical scales. At the former scale, measured by invaded area, the average doubling time over a 6-year period was 1.2 years (which indicates that this invasion was an order of magnitude faster than that of *H. mantegazzianum* in the Slavkovský les). Across the region as a whole, the doubling time for numbers of infestation was much slower, 6.7 years, probably because of the separation of suitable habitats by eucalypt savannas that are less readily colonized.

Conclusions

Studies of the dynamics of the *H. mantegazzianum* invasion allow some conclusions to be drawn that may apply to a wider geographical area of Europe.

1. This species exhibited a distinct lag phase of between 60 and 70 years, depending on the method of estimation, in the Czech Republic. Exponential phase of spread was associated with distinct changes in habitat preferences. Water courses and other riparian habitats were initially the major dispersal routes, but once the species started to spread beyond the river corridors, other linear habitats such as roads and railways became important. In the course of the invasion, the species became less confined to high altitudes and invaded warmer areas.
2. During its invasions, *H. mantegazzianum* spread at rates comparable to that of some of the most important and spectacular invaders in other parts of the world. A rigorous comparison of rates of spread is, however, limited by the variety of measures used to express and ways used to calculate this characteristic, as well as by the effect of scale at which the data were recorded.
3. The rate of spread was similar in at least two European countries (Czech Republic and the UK), which differ markedly in climate, indicating that environmental constraints imposed by the landscapes of the countries invaded may be of little importance. In addition, the fact that this species spread at a similar rate in different habitats in the Czech Republic also supports this conclusion.

Acknowledgements

We thank Mark Williamson and Claude Lavoie for helpful comments on the manuscript, Tony Dixon for improving our English, and Jan Pergl for technical assistance. 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. PP and VJ were supported by institutional long-term research plans no. AV0Z60050516, from the Academy of Sciences of the Czech Republic, no. 0021620828, from Ministry of Education of the Czech Republic and by the Biodiversity Research Centre no. LC 06073.

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