INTRODUCTION

HISTORY

Among aliens successfully naturalized in central European natural and semi-natural vegetation (Kornaš, 1990), so far only a few have caused practical problems. Giant hogweed (*Heracleum mantegazzianum* Somm. et Levier), introduced in the nineteenth century from western Caucasus, is at present becoming a serious threat to the landscape in some European countries, especially Sweden (Lundström, 1984), Scotland (Bingham, 1990; Neiland et al., 1987) and the Czech Republic (Pyšek, 1991). Replacement of native vegetation (for a summary of possible consequences, see Pyšek, 1991) and injuries to human skin caused by phototoxic substances (Drever and Hunter, 1970) are the main reasons for efforts to eradicate the species from infested areas. However, once a large area is infested, eradication efforts have brought only limited success so far (Lundström, 1990; Williamson and Forbes, 1982).

Being the largest central European forb, part of the competitive superiority of *H. mantegazzianum* over other plants is ascribed to its size and its ability to shade the surrounding vegetation with huge ground leaves. High seed set (Brondegaard, 1990; Neiland, 1986) and dispersal encouraged by water, wind and human-related factors (Jehlik and Lhotská, 1971) also contribute to its rapid spread into various vegetation types.

In a previous paper (Pyšek, 1991), the historical dynamics of the spread of the species in the Czech Republic was reconstructed using floristic data. Having been introduced into the Czech Republic in the middle of the nineteenth century as a garden ornamental (Kratzmann, 1862), *H. mantegazzianum* was initially spread through cultivation in parks and gardens. Up to 1950, only nine localities had been reported, some of them serving as foci for sub-
sequent spread. The beginning of rapid invasion occurred in the late 1960s and early 1970s. Since then, the number of reported localities has increased exponentially from 67 in 1970 to 472 in 1990 (Pyšek and Pyšek, 1994). The current distribution of *H. mantegazzianum* in the Czech Republic is presented in Figure 5.1. The species abundance in the landscape decreases with the distance from the region of the earliest introduction, which was in the westernmost part of the country (Pyšek, 1991). The present paper, which is based on the same data set as the previous one (Pyšek, 1991), focuses upon ecological aspects of invasion by *H. mantegazzianum*. The following questions are addressed: (1) whether the dynamics of spread differ with respect to the type of invaded vegetation and (2) what was the role of climatic conditions in the process of the species’ invasion?

**DATA SOURCES**

Analysis included both published and unpublished floristic data. The total number of localities registered in the Czech Republic in 1990 was 472. An updated reference list was provided by Pyšek and Pyšek (1994) for those localities described with sufficient accuracy in the original source. However, only those localities for which the information on habitat type was provided by the original author were analysed in this paper. This number (n = 378) is therefore lower than the total number of localities reported in the list mentioned above (n = 410).

Distribution of *H. mantegazzianum* was expressed as the presence or absence in squares 11 × 12 km (Schönfelder and Bresinsky, 1990).

**RESULTS AND DISCUSSION**

**SPREAD IN VARIOUS VEGETATION TYPES: THE ROLE OF RECIPIENT HABITAT**

The main habitat types were arbitrarily classified according to the intensity of disturbance. Habitats that encourage the greatest movement of diaspores (referred to as transport habitats) were included in group A, consisting of (i) pond margins and wetlands; (ii) valleys and banks of rivers and brooks; (iii) road verges, ditches and adjacent habitats; and (iv) railway areas including railway tracks and open spaces of railway stations. The following habitats were included among man-made, usually heavily disturbed, habitats in group B: (i) dumps, rubbish tips and various deposits, in settlements or in the open landscape; (ii) gardens and parks; and (iii) urban areas, i.e. habitats in towns and villages other than those belonging to (i) or (ii). The group of semi-natural habitats (C) was represented by (i) scrub communities, (ii) meadows and grasslands and (iii) forests and their margins.
Figure 5.1 Historical outline of distribution of *Heracleum mantegazzianum* in the Czech Republic. Earliest records (up to 1960) are indicated by the year of the first report. Different symbols are used to show subsequent spread: localities discovered in the 1960s ●, 1970s □ and 1980s ○; bold lines show the location of warm districts, which differ in having >50 summer days, <110 days with frost, mean July temperature >18°C, mean April temperature >8°C, and >160 days with mean temperature 10°C or more (Quitt, 1975)
Table 5.1. Summary of rate of spread of *Heracleum mantegazzianum* in different habitats in the Czech Republic

<table>
<thead>
<tr>
<th>Habitat Type</th>
<th>1st Record Year</th>
<th>Number (n)</th>
<th>Slope b</th>
<th>( \text{SE (10}^{-3} )</th>
<th>Intercept a</th>
<th>( \text{SE} )</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Transport habitats</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ponds, wetlands</td>
<td>1963</td>
<td>16</td>
<td>0.0803</td>
<td>3.323</td>
<td>-4.412</td>
<td>0.234</td>
</tr>
<tr>
<td>River banks</td>
<td>1901</td>
<td>41</td>
<td>0.0851</td>
<td>2.037</td>
<td>-2.914</td>
<td>0.143</td>
</tr>
<tr>
<td>Roads</td>
<td>1963</td>
<td>76</td>
<td>0.1188</td>
<td>4.424</td>
<td>-6.452</td>
<td>0.312</td>
</tr>
<tr>
<td>Railway areas</td>
<td>1953</td>
<td>29</td>
<td>0.0834</td>
<td>4.534</td>
<td>-4.492</td>
<td>0.320</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td>162</td>
<td>0.1037</td>
<td>2.401</td>
<td>-4.255</td>
<td>0.169</td>
</tr>
<tr>
<td><strong>Man-made habitats</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dumps, deposits</td>
<td>1966</td>
<td>20</td>
<td>0.0894</td>
<td>4.212</td>
<td>-4.940</td>
<td>0.297</td>
</tr>
<tr>
<td>Urban areas</td>
<td>1947</td>
<td>118</td>
<td>0.1003</td>
<td>2.679</td>
<td>-4.387</td>
<td>0.189</td>
</tr>
<tr>
<td>Parks, gardens</td>
<td>1862</td>
<td>19</td>
<td>0.0524</td>
<td>1.791</td>
<td>-1.797</td>
<td>0.126</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td>157</td>
<td>0.0972</td>
<td>2.373</td>
<td>-3.704</td>
<td>0.167</td>
</tr>
<tr>
<td><strong>Semi-natural habitats</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Scrub</td>
<td>1950</td>
<td>7</td>
<td>0.0395</td>
<td>2.181</td>
<td>-1.531</td>
<td>0.154</td>
</tr>
<tr>
<td>Meadow</td>
<td>1960</td>
<td>22</td>
<td>0.0848</td>
<td>3.708</td>
<td>-4.639</td>
<td>0.261</td>
</tr>
<tr>
<td>Forest</td>
<td>1947</td>
<td>30</td>
<td>0.0619</td>
<td>1.449</td>
<td>-2.289</td>
<td>0.102</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td>59</td>
<td>0.0822</td>
<td>1.908</td>
<td>-3.351</td>
<td>0.134</td>
</tr>
<tr>
<td><strong>Grand Total</strong></td>
<td></td>
<td>378</td>
<td>0.1031</td>
<td>1.932</td>
<td>-3.313</td>
<td>0.136</td>
</tr>
</tbody>
</table>

Slopes and intercepts of the regression equation \( \text{LOG (CUMULATIVE NUMBER OF LOCALITIES + 1)} = a + b \times \text{YEAR} \) are given. Only records after 1945 were included in the calculation. Total number of localities known for a given habitat type in 1990 is given (n).

A study of the habitat groups indicates that the species occurs most frequently in man-made (41.5%) and transport habitats (42.8%); 15.8% of the localities were recorded in semi-natural habitats. At present, the highest number of records is reported from urban areas and road verges (Table 5.1). The total number of localities has increased exponentially between 1947 and 1990 in each habitat type considered (Table 5.1, Figure 5.2). The rate of expansion was compared among habitats using a semi-log scale of the cumulative number of localities over time. The year 1947 was used as the starting point for regression equations, since, prior to this year only five records had been reported (see Figure 5.1) and thereafter the records started to occur more frequently. The slopes of regression lines reflect the rate of expansion (Table 5.1). The highest values of b were found in roads and settlements, whereas the lowest values were in scrub, parks and gardens. This indicates a tendency for a lower expansion rate of populations in semi-natural, less disturbed vegetation types. However, the pairwise comparisons did not reveal any significant differences between the slopes of regression lines (F-test, according to Snedecor and Cochran, 1965). Similarly, if pooled data for each
group of habitats (A–C) were analysed, no significant differences between slopes were found.

A conclusion may thus be drawn that the expansion rate in the last four decades was similar in each of the habitat types invaded. This suggests that the recipient habitat plays a less important role (Pyšek and Prach, 1994) than may be expected for a strongly competitive species (Newsome and Noble, 1986; Roy, 1990). Once *H. mantegazzianum* had entered a certain habitat type, it spread exponentially, regardless of the characteristics of the invaded vegetation.

Data on the first year of appearance (Table 5.1) show that, with the exception of (i) parks and gardens in which it had been originally cultivated and (ii) river habitats, the species was introduced in most of the habitat types during the 1950s or early 1960s. There was no difference between the man-made and semi-natural habitats.

The expansion was initially encouraged by the courses of main rivers. Mapping squares that contain main rivers (i.e. those indicated on the map in Figure 5.1) accounted for 66.7% of the total number of squares occupied by *H. mantegazzianum* in 1950. This proportion gradually decreased to 36.4% in 1990 (Figure 5.3a). Similarly, the percentage of occupied squares was higher among “river squares” than among squares without rivers (Figure 5.3b). The magnitude of this difference was greatest between 1965 and 1975, i.e. at the beginning of rapid exponential spread. If the data on
Figure 5.3 Spread of *Heracleum mantegazzianum* along the courses of main rivers in the Czech Republic: (a) river squares (i.e. those through which a main river flows, see Figure 5.1) occupied by the species as a proportion of the total number of squares occupied in the respective year; the value of Kendall non-parametric correlation coefficient was 0.64, significance level \( \alpha < 0.01, n = 10 \); and (b) probability of occurrence of *H. mantegazzianum* in river squares ■ and terrestrial squares □.

"river" and "terrestrial" squares are compared in the last decade, i.e. 1980s, the percentages of squares in which *H. mantegazzianum* was present were becoming similar, which indicates the species’ spread from river squares to terrestrial ones.

Neiland (1986) has suggested that the increased occurrence on river banks in Scotland was not only because of the efficiency of seed dispersal by water but also because the river bank habitats are suitable for seedling establishment, being relatively free from competition by other species (see also Thébaud and Debussche, 1991).

**TO WHAT EXTENT WAS THE SPECIES INVASION AFFECTED BY THE CLIMATE?**

Comparison of altitude of localities with *H. mantegazzianum* over two decades showed an obvious shift towards lower elevation (Figure 5.4). At the beginning of the exponential phase of spread (approximately 1970, Pyšek, 1991), 28.5% of localities were >600 m above sea level; at present (1990), the respective value is only 14.7%. The mean altitude in 1970 was significantly higher than in 1990 (\( t = 2.32, P = 0.02 \)). These results indicate that, at the beginning of spread, *H. mantegazzianum* occurred mainly at higher altitudes, which is no longer true. The frequency distribution of *H. mantegazzianum* according to altitude in 1990 corresponds closely to the overall
Figure 5.4 Frequency distribution of altitudes at which *Heracleum mantegazzianum* was found in the Czech Republic. Percentage of localities is shown for each altitudinal range. Data from the beginning of exponential phase of spread (1970, $n = 56$) are compared with the current state (1990, $n = 375$). Frequency distribution of altitudes in the Czech Republic (according to Novotný, 1971) is given in the third column. Number of localities in 1990 is lower than the total number known up to this year because in some cases it was not possible to obtain data on altitude owing to a vague location given in the original source.

Distribution of altitude in the Czech Republic (Novotný, 1971) (Figure 5.4).

Assessment of the effect of climate produced similar results. There are two large continuous warm climate districts in the Czech Republic: (i) the Elbe, Vltava and Ohře Lowlands, in the North of the country and (ii) the lowlands in south Moravia (Quitt, 1975; Figure 5.1). Up to 1970, only two localities were reported from the former district and one was known from south Moravia (i.e. only three out of 67 known at that time). During the next decade, the spread into both warm districts was represented only by four localities that appeared in the Elbe lowland. In the 1980s, *H. mantegazzianum* invaded partly into the Elbe lowland (remaining relatively unsuccessful along the Ohře river), but it is still almost absent in south Moravia. However, this evidence must be treated with caution since there is a large region adjacent to the south Moravian lowlands, which has a moderate climate, and *H. mantegazzianum* is absent in this region as well. Nevertheless, from the beginning of massive spread up to recent time, the probability of a square being occupied was notably lower in those located in warm regions (Figure 5.5). Thus, it may be concluded that there was a strong tendency for *H. mantegazzianum* to avoid the warmest climatic regions. This trend is, to a certain extent, still obvious.

The preference for cooler, more humid areas corresponds to the fact that
H. mantegazzianum is native to the upper forest belts of western Caucasus (Mladenova, 1950), i.e. it is originally a montane species. Similarly, on a continental scale, its more frequent occurrence in northern Europe may reflect a more favourable climate for the species (Pyšek, 1991).

CONCLUSIONS

From the historical point of view, the performance of Heracleum mantegazzianum in the Czech Republic may be divided into three periods:

Period 1 (approximately 80 years): It appears that from the first introduction (1862) up to the 1940s the spread of H. mantegazzianum had been exclusively due to its cultivation as a garden ornamental. The localities where it occurred in this period served as independent foci for the subsequent spread.

Period 2 (approximately 30 years): From the 1940s, the spread of H. mantegazzianum started along main rivers. In this period, the species invaded more successfully in the regions of higher altitudes and avoided the warmest districts.

Period 3 (Approximately 20 years): The 1960s and 1970s may be considered as the starting point of an exponential phase of the species' spread (Pyšek, 1991). Since then, H. mantegazzianum has invaded the landscape regardless of altitude, and the effect of warm climate was less restrictive. The rate of expansion was similar in the heavily disturbed, man-made
habitats and in the semi-natural vegetation (meadow, scrub, forest). At the end of this period, the preference for river valleys was no longer evident, since *H. mantegazzianum* was spreading into the wider landscape.

The lack of quantitative data on spread dynamics from other European countries prevents direct comparisons. Although the duration of particular periods, as described in the previous paragraphs, may be expected to differ in different parts of Europe, the pattern of spread, at least in some of them, was similar (Pyšek, 1991) and the scheme presented appears to be generally valid.

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