Diversity and Distributions (1998) **4**, 9–16

BIODIVERSITY RESEARCH

The role of human density and climate in the spread of *Heracleum mantegazzianum* in the Central European landscape

PETR PYŠEK[1], MIROSLAV KOPECKÝ[2], VOJTĚCH JAROŠÍK[3] and PAVLA KOTKOVÁ[2]
[1] *Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice, Czech Republic, e-mail: pysek@ibot.cas.cz;* [2] *Institute of Applied Ecology, University of Agriculture Prague, CZ-281 63 Kostelec nad Černými lesy, Czech Republic;* [3] *Department of Zoology, Faculty of Science, Charles University, Viničná 7, CZ-128 01 Praha 2, Czech Republic*

Abstract. This study, by using Caucasian *Heracleum mantegazzianum* as a model alien species, analyses the factors determining its invasion in the Czech Republic. Both the climatic factors and human influence were taken into account. The data were evaluated by analysis of covariance (ANCOVA) with Poisson errors, using general linear modelling in GLIM. January isotherm and density of human population were the factors significantly affecting the species. *Heracleum* is less represented in regions with warmer winter and low population density. The importance of low winter temperatures could explain the species distribution pattern over Europe, i.e. rare or absent in its warm southeastern parts while thriving in the northwest. In the Czech Republic, *Heracleum* is principally limited only by factors related to its establishment, i.e. dispersal possibilities and factors affecting the germination. If these are met, the species is extremely successful as an invader.

Key words. *Heracleum mantegazzianum*, alien plant, invasion history, climatic parameters, human activities, distribution pattern, dispersal, Czech Republic, Central Europe.

INTRODUCTION

Invasion dynamics of alien species (understood as those which reached the area as a consequence of the activities of neolithic or post-neolithic man or of his domestic animals, see Webb, 1985; Pyšek, 1995 for definitions) are not followed directly from the very start because invasions are identified in a post-hoc manner. Any invasion usually comes into the focus of interest long after it had started because its accelerated dynamics is the main reason for it being recognized. However, ecologists have various techniques and data sources available to reconstruct invasion histories (see e.g. Trepl, 1984; Pyšek, 1991; Pyšek & Prach, 1993, 1995). The studies based on repeated consecutive records over time are very valuable but rather rare (e.g. Lonsdale, 1993). Maps showing the changes in species distribution over time are useful (Şwieboda, 1963; Kornaş, 1990; Guillerm *et al*., 1990) and their detailed analysis can contribute to better understanding of invasion process.

At the community level, there is a consensus on the importance of recipient vegetation for the outcome of invasions (Rejmánek, 1989; Lodge, 1993; Pyšek & Pyšek, 1995). At the landscape level, however, the information about the factors affecting invasion success of an alien is rather scarce. There is an evidence of the restrictive effect of climate on the present distribution of alien species (Beerling, 1993; Wilson *et al*., 1992; Scott & Panetta, 1993). The focus on the effect of climate in such studies is due to it being known as a principle factor affecting plant distribution (Grace, 1987; Carter & Price, 1988, but see Bond & Richardson, 1990). The approach is based on the assumption that if the species' response to climatic factors is known, it should be possible to predict the area of potential distribution (Medd & Smith, 1978). However, attempts to make such correlation are often confounded by habitat differences (Wilson *et al*., 1992) and, moreover, other factors believed to promote invasion such as disturbance (Hobbs, 1991; Hobbs & Huenneke, 1992;

Daehler & Strong, 1993) are very difficult to measure in studies approaching invasions through the 'landscape grain'.

The differential success of introduced species as invaders provides a useful natural experiment for deriving empirical evidence on the factors that determine whether an introduced species will invade or not (Tucker & Richardson, 1995). Similarly, the differential success of particular species in different areas provides us with the potential to recognize the factors that determine why it has succeeded in invading some regions and failed elsewhere.

The present study is, on a regional scale of 72,000 km^2, using *Heracleum mantegazzianum* as a model species. The previous analysis has shown that the process of this species' invasion was affected by complex climatic characteristics such as altitude and climatic regions (Pyšek, 1994). This study, by using methods of geographical information systems (GIS) aims at (a) analysing the effect of principle climatic factors and finding those particular climatic characteristics that are responsible for the invader's current distribution, and (b) assessing the relative importance of both natural and man-induced factors by taking the intensity of human influence into account.

DATA SOURCES AND METHODS

Study species

Heracleum mantegazzianum Somm. et Levier (*Apiaceae*) is a monocarpic perennial with a thick tap-root, a stout stem attaining 5.5 m height, large pinnate leaves (up to 3 m) and usually seven to ten umbels bearing oval-elliptical, broadly winged fruits 9–11 mm in size (see Tiley, Dodd & Wade, 1996 for a detailed morphological description). The species spreads exclusively by seed, and its seed production per plant may reach several tens of thousands (Pyšek *et al.*, 1995). In most of Central Europe, the species germinates in early spring (April), flowering period starts in May, fruits appear in July and are shed from September onwards.

The species is native to the western Caucasus where it occurs in the upper forest belt of the southern slopes, mainly in meadows, clearings and forest margins (Mladenova, 1950). It was introduced into Czech Republic in the 19th century. The beginning of exponential phase of spread was, on the basis of the statistical analysis of the increase in the number of localities, dated in 1943, the rapid increase in the number of localities and associated massive spread into the landscape started in the 1970s (Pyšek, 1991; Pyšek & Prach, 1993). The pattern of spread, though not analysed in such a detail elsewhere, was probably similar in other European countries (Lundström, 1984; de Waal *et al.*, 1994; Tiley *et al.*, 1996). Replacement of native vegetation and injuries to human skin caused by phototoxic substances (Drever & Hunter, 1970) are the main reasons for efforts to eradicate the species from infested areas (Williamson & Forbes, 1982; de Waal *et al.*, 1994). *Heracleum* rapidly attains dominance in invaded communities. Being the largest central European forb, part of the species' competitive superiority over other plants is ascribed to its size and its ability to shade the surrounding vegetation with its huge ground leaves. The large seed-set (Neiland, 1986; Brondegaard, 1990) with dispersal encouraged by water, wind, and human-related factors (Pyšek & Prach, 1993) also contribute to its rapid spread into various vegetation types. It was shown that disturbed habitats with good possibilities of dispersal for *Heracleum* seeds are more easily invaded (Pyšek & Pyšek, 1995).

The species was chosen as a model for the purpose of the present study for the following reasons.

(1) Its invasion has been relatively well documented, and the list of localities is available for the territory under study (Pyšek & Pyšek, 1994). This list covers all the known records from what is believed to be the first report on the species' occurrence in 1862 up to the present. Consequently, the resulting distribution map may be considered as reasonably complete to allow the analysis of factors influencing distribution pattern to be carried out.

(2) The species is one of the most noxious invaders in European flora; possible prediction of further spread, based on the factors determining its current distribution, would be of practical interest for the authorities of nature conservation and landscape management.

Data sources

The historical list of localities of *H. mantegazzianum* in the Czech Republic was compiled (Pyšek & Pyšek, 1994), using (a) reports on the species' occurrence published in botanical periodicals, (b) specimens in herbarium collections, and (c) unpublished floristic records obtained from botanists (see Pyšek, 1991). The total number of records reported from the territory was 472 (up to 1990). However, only those described with sufficient accuracy in the original source could be used for the present analysis, which was thus based on 336 records. Based on this data set, the distribution map was compiled (published in Pyšek, 1991, 1994). Because the list includes all the localities ever reported and such localities were treated as 'present' when constructing distribution map, the assumption was made that once the species has established in a locality (which was usually when it was first noted), it is supposed to persist. This assumption seems reasonable with *H. mantegazzianum*, considering the very persistent nature of its occurrence associated with its aggressiveness and competitive ability (Pyšek & Pyšek, 1995), and verified by a number of repeated records from different periods in our data set.

For the purpose of the present study, the geographical information system covering the territory of the Czech Republic was created using PC Arc/INFO.

The information layer containing particular localities of *H. mantegazzianum* was built by drawing the data from Pyšek & Pyšek (1994) into the map which was then digitalized. Further, the GIS contained the information layers of particular factors which were considered as potentially affecting the species distribution pattern; these layers were built by digitalizing the relevant maps. Climatic characteristics were taken from Vesecký *et al.* (1958).

The following layers were used: (1) January isotherm (average annual temperature in January) with the following classes distinguished: <2, 2–3, 3–4, and >4°C; (2) June isotherm (average annual temperature in June): <4, 4–5, 5–6, 6–7, and >7°C; (3) annual sum of precipitation: <300, 301–400, 401–500, 501–600, 601–700, 701–800, >800 mm; (4) altitude: <300, 301–500, and >500 m a.s.l.; (5) density of human population: <60, 61–100, 101–150, 151–200, and >200 inhabitants per km^2. For each factor, the distribution of particular classes in the Czech Republic was obtained as well (Fig. 1) (further termed 'area').

Two phases of invasion were considered when analysing the data in order to reveal whether the factors affecting invasion change in time. These phases were distinguished on the basis of previous studies (Pyšek, 1991), i.e. (1) the early phase: 1862–1970, and (2) the current phase characterized by the rapid increase in the number of localities and associated massive spread into the landscape: 1971–1995.

Statistical analysis

The data were evaluated by analysis of covariance (ANCOVA) with Poisson errors, using general linear modelling in GLIM® v. 4 (Francis, Green & Payne, 1994). The distribution of *Heracleum* localities was the response variable, the phase of invasion (the early phase 1862–1970, and the current phase 1971–1995) a factor, and the human population density (<60, 61–100, 101–150, 151–200, and >200 inhabitants per km^2), altitude (<300, 301–500, >500 m a.s.l.), January isotherm (<2, 2–3, 3–4, and >4°C), June isotherm (<4, 4–5, 5–6, 6–7, >7°C), annual sum of precipitation (<300, 301–400, 401–500, 501–600, 601–700, 701–800, >800 mm), and the area corresponding to the actual distribution of altitude, population density and climatic variables at the territory studied as covariates.

The aim of the analysis was to determine the minimal adequate model. In this model, all parameters were significantly ($P<0.05$) different from zero and from one another. This was achieved by a step-wise process of model simplification, beginning with the maximal model (containing all factors, interactions and covariates that might be of interest), then proceeding by the elimination of non-significant terms (using deletion tests from the maximal model), and the retention of significant terms. After the minimal adequate model has been fitted, the data were checked for overdispersion (Crawley, 1993). To compare absolute values of the significant terms, the covariates of the minimal adequate model were standardised (zero mean, variance one).

RESULTS

Filtering out the effect of area, the minimal adequate model of ANCOVA ($\chi^2=353.5$, df 5, $P=3.1\times10^{-74}$, $R^2=14.3\%$) revealed that the distribution of *Heracleum* was significantly affected by January isotherm ($\chi^2=9.10$, df 1, $P=0.003$), and by the density of human population ($\chi^2=6.65$, df 1, $P=0.01$).

Taking into account the actual area covered by the determinants significantly affecting distribution of the species, the expected occurrence of *Heracleum* increased with increasing area corresponding to different January isotherms (ln of expected occurrence in 1862–1970 = $-3.892\pm0.227+3.831\times10^{-5}\pm5.105\times10^{-6}$ km^2, ln of expected occurrence in 1971–1995 = $-2.386\pm0.141+3.831\times10^{-5}\pm5.105\times10^{-6}$ km^2, $\chi^2=203.9$, df 2, $P=5.3\times10^{-45}$), and with increasing area having different densities of human population (ln of expected occurrence in 1862–1970 = $-5.476\pm0.334+9.212\times10^{-5}\pm9.3\times10^{-6}$ km^2, ln of expected occurrence in 1971–1995 =

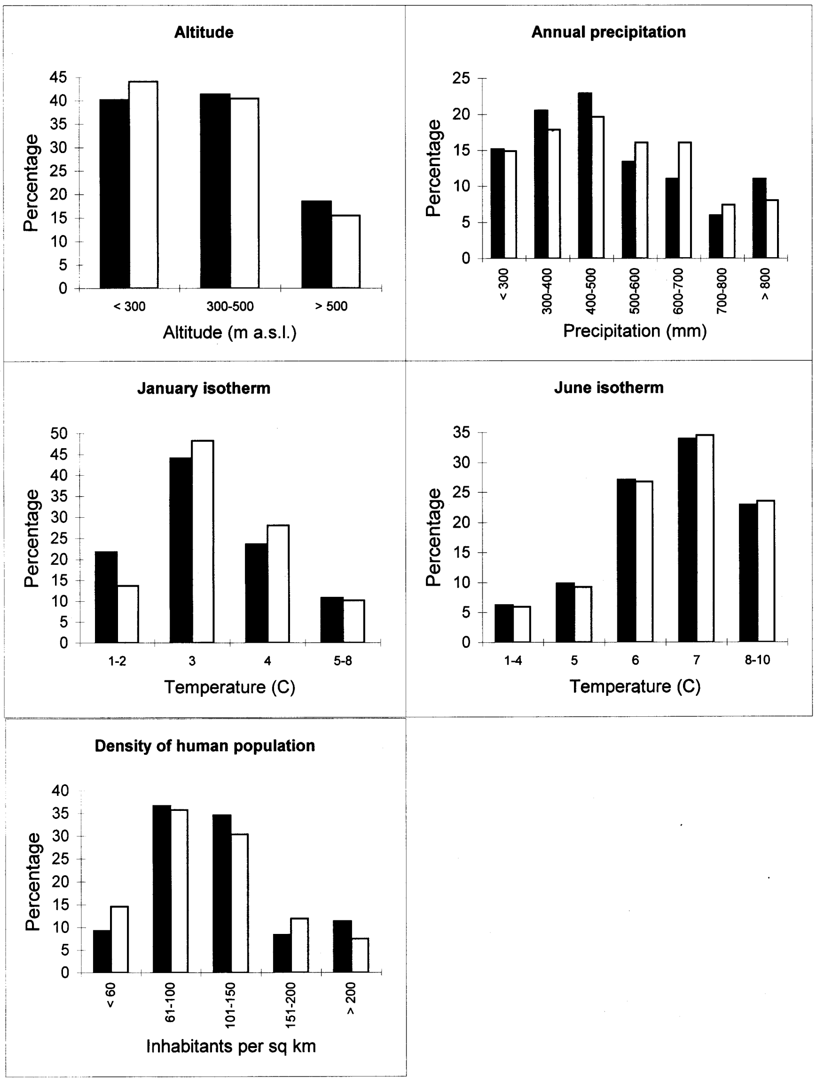

Fig. 1. Frequency distribution of localities of *Heracleum mantegazzianum* in the territory studied with respect to particular factors analysed (black bars, $n = 336$) and frequency distribution of the factors in the Czech Republic (empty bars, based on the area covered by the respective classes, $n = 72{,}000\ \text{km}^2$).

$-3.97 \pm 0.141 + 9.212 \times 10^{-5} \pm 9.3 \times 10^{-6}\ \text{km}^2$, $\chi^2 = 267.9$, df 2, $P = 6.7 \times 10^{-59}$).

Heracleum appears to be less represented in regions with warmer winter, as the expected occurrence decreased in regions with warmer January isotherm. The species was also less represented in regions with lower population density (Table 1). The determinants affecting the distribution did not change in the course of invasion, as the effect of January isotherm and population density did not differ between 1862–1970 and 1971–1995 (minimal adequate model of ANCOVA: interaction between both phases of invasion for January

Table 1. Minimal adequate model of ANCOVA describing the distribution of *Heracleum mantegazzianum* in the study area. See text for the description of the model. Parameters describing ln of expected occurrence of *Heracleum* are shown for particular phases of invasion. January isotherm in °C, population density in inhabitants per square kilometer

				1862–1970		1971–1995	
	χ^2	d.f.	*P*-level	Intercept ± S.E.	Slope ± S.E.	Intercept ± S.E.	Slope ± S.E.
January isotherm	9.10	1	0.003	−3.892 ± 0.227	−0.181 ± 0.060	−2.386 ± 0.141	−0.181 ± 0.060
Population density	6.65	1	0.01	5.476 ± 0.334	0.135 ± 0.062	−3.970 ± 0.141	0.135 ± 0.062

isotherm $F_{res} = 0.19$, df 1, $P = 0.7$, NS, interaction between the early and the current phase of invasion for population density $F_{res} = 1.0$, df 1, $P = 0.3$, NS).

The minimal adequate model of ANCOVA with standardized values indicated that the distribution of *Heracleum* was much affected by the increasing extent of areas with different density of human population (standardized regression slope 0.712 ± 0.072), and by the increasing extent of areas with different January isotherm (standardized regression slope 0.392 ± 0.052). The increase of occurrence with increasing population density (standardized regression slope 0.223 ± 0.090), and the decrease of occurrence with warmer January isotherm (standardized regression slope −0.203 ± 0.067) were less conspicuous.

DISCUSSION

The present study indicates that *Heracleum* is less represented in regions with warmer January and low population density. The effect of population density appears to be stronger than that of January isotherm and the factors affecting invasion did not change in time, i.e. were the same for both periods of the invasion process. The close relationship between the distribution of *Heracleum* and density of human population reflects the fact that the intensity and diversity of disturbances, which are closely related to the density of human population (e.g. Thompson, 1994) provide the species with safe sites (*sensu* Harper, 1977) for establishment, and create suitable habitats for its subsequent invasion. Though not restricted from seminatural vegetation, the species depends to a large extent on humans as long as dispersal is concerned. In their study analysing the pattern of invasion by *Heracleum* in a landscape section, Pyšek & Pyšek (1995) found that the species was able to enter a diversity of habitats, depending on site conditions and composition of recipient vegetation. However, dispersal possibilities were the only significant factor affecting the magnitude of infestation, i.e. large stands were only formed if there was a good possibility of seed spread (Pyšek & Pyšek, 1995).

As pointed out by Panetta & Mitchell (1991), more confidence can be placed in bioclimatic predictions when these are concordant with known physiological responses of a species. The under-representation of *Heracleum* in regions with warmer January isotherm could be related to the germination ecology of the species (Grime *et al*., 1981; Andersen & Calov, 1996). Many species of *Apiaceae* are spring-germinating, often have chilling requirements which imposes winter dormancy with germination delayed until more favourable conditions in spring (Grime *et al*., 1981). This pattern indicates innate dormancy, also known for the native congener *H. sphondylium* where the embryo is immature and further development is needed after seed release from mother plant. The breaking of dormancy in *H. mantegazzianum* requires chilling (Grime *et al*., 1981; Tiley *et al*., 1996) which is provided by a certain period for seeds to stay in cold, humid soil during winter. Experimentally, the frost treatment resulted in higher germination rate and velocity of *Heracleum mantegazianum* seed (Andersen & Calov, 1996). The importance of low winter temperatures could, at least in part, explain why the species is absent or very rare from southeastern parts of Europe (Hungary, Roumania, Bulgaria etc.), while growing best in more northernly and temperate areas, e.g. British Isles, Denmark, Sweden, Germany (Pyšek, 1991; Ochsmann, 1992; Tiley *et al*., 1996).

The method of creating a bioclimatic profile (BIOCLIM, i.e. an estimate, for a number of climatic parameters, of the range of conditions within which a species will grow) in a species' natural range and determining climatically suitable areas by identifying homoclines in its adventive distribution area has been used to predict weedy status or further potential for spread of alien species (Panetta & Dodd, 1987; Panetta & Mitchell, 1991; Honig, Cowling & Richardson, 1992).

Good correlations with some climatic parameters have been repeatedly found and, though limited by its inability to predict the potential distribution of an alien plant which has not yet reached climatic limits for its successful growth and reproduction (Sindel & Michael, 1992) the approach was successfully used for identifying those plants which are not climatically pre-adapted to invade New Zealand (Panetta & Mitchell, 1991). However, there is usually some discrepancy between distribution and the best-fitting climatic factor, possible reasons being inaccuracy of published climate maps, and possibility that the distribution reflects dispersal limitation (Wilson *et al*., 1992). In some studies, no single environmental variable was an effective predictor of sites vulnerable to invasion, indicating that the regulating factors are complex (Chicoine, Fay & Nielsen, 1985). Further, in alien species it is probable, that the present limits of their distribution rather represent an active invasions with the species absent from some areas because seed of the species has not yet arrived (Wilson *et al*., 1992) than stable and climatically-determined distribution pattern. Our results suggest that both types of distribution-driving factors hold for *Heracleum* in the Czech Republic. In higher altitudes, dispersal limitations probably act (due to lower population density), whereas higher winter temperature and its possible effect on germination could limit the species success in warm regions which are otherwise densely populated and with good dispersal possibilities.

Since in the Czech Republic, as in the whole Central Europe, majority of aliens come from warmer regions (North America, Asia etc.) and have greater demands for temperature (Pyšek, Prach & Šmilauer, 1995; Sukopp & Werner, 1983), their distribution and spread are usually limited by low temperatures (Beerling, 1993). *Heracleum* is rather an exception in this respect; similarly, in their study of exotics invading along roads in New Zealand, Wilson *et al*. (1992) found out of twenty-four species which could be correlated to some degree with climatic factors, only four species occurred in colder/wetter areas (resembling thus the case with *Heracleum*).

CONCLUSIONS

In the Czech Republic, *Heracleum* is principally limited only by the factors related to its establishment, i.e. dispersal possibilities and factors affecting the germination. If these, i.e. cold conditions during winter, are met, there is very little that can prevent the species from further spread because, as shown by the previous study (Pyšek & Pyšek, 1995) the recipient vegetation has rather little 'resisting' effect.

ACKNOWLEDGMENTS

Our thanks are to an anonymous referee for helpful comments. The study was supported by the Grant Agency of the Czech Republic, grant no. 206/93/2440.

REFERENCES

Andersen, U.V. & Calov, B. (1996) Long-term effects of sheep grazing on Giant Hogweed (*Heracleum mantegazzianum*). *Hydrobiologia*, **340**, 227–284.

Beerling, D.J. (1993) The impact of temperature on the northern distribution limits of the introduced species *Fallopia japonica* and *Impatiens glandulifera* in north-west Europe. *J. Biogeogr.* **20**, 45–54.

Bond, W.J. & Richardson, D.M. (1990) What can we learn from extinctions and invasions about the effects of climate change? *S. Afr. J. Sci.* **86**, 429–433.

Brondegaard, V.J. (1990) Massenausbreitung des Bärenklaus. *Naturwiss. Rundsch.* **43**, 438–439.

Carter, R.N. & Prince, S.D. (1988) Distribution limits from a demographical viewpoint. *Plant population ecology* (ed. by A.J. Davy, M.J. Hutchings and A.R. Watkinson), pp. 165–184, Blackwell Scientific Publications, Oxford.

Chicoine, T.K., Fay, P.K. & Nielsen, G.A. (1985) Predicting weed migration from soil and climate maps. *Weed Sci.* **34**, 57–61.

Crawley, M.J. (1993) *GLIM for Ecologist*. Blackwell, Oxford.

Daehler, C.C. & Strong, D.R. (1993) Prediction and biological invasions. *Trends Ecol. Evol.* **8**, 380.

Drever, J.C. & Hunter, J.A. (1970) Giant hogweed dermatitis. *Scot. Med. J.* **15**, 315–319.

Francis, B., Green, M. & Payne, C. (eds) (1994) *The GLIM System. Release 4 Manual*. 821 pp. Clarendon, Oxford.

Grace, J. (1987) Climatic tolerance and the distribution of plants. *New Phytol.* **106**, (suppl.) 113–130.

Grime, J.P., Mason, G., Curtis, A.V., Rodman, J., Band, S.R. & Mowforth, M.A. (1981) A comparative study of germination characteristics in a local flora. *J. Ecol.* **69**, 1017–1059.

Guillerm, J.L., Le Floch, E., Maillet, J. & Boulet, C. (1990) The invading weeds within the Western Mediterranean Basin. *Biological invasions in Europe and the Mediterranean Basin* (ed. by F. di Castri, A.J. Hansen and M. Debussche), pp. 61–84, Kluwer Academis Publishers, Dordrecht.

Harper, J.L. (1977) *Population biology of plants*. Academic Press, New York.

Hobbs, R.J. & Huenneke, L.F. (1992) Disturbance, diversity, and invasion: implications for conservation. *Conserv. Biol.* **6**, 324–337.

Hobbs, R.J. (1991) Disturbance a precursor to weed invasion in native vegetation. *Plant Prot. Quart.* **6**, 99–104.

Honig, M.A., Cowling, R.M. & Richardson, D.M. (1992) The invasive potential of Australian banksias in South African fynbos: a comparison of the reproductive potential of *Banksia ericifolia* and *Leucadendron laureolum*. *Austr. J. Ecol.* **17**, 305–314.

Kornaş, J. (1990) Plant invasions in Central Europe: historical and ecological aspects. *Biological invasions in Europe and the Mediterranean Basin* (ed. by F. di Castri, A.J. Hansen and M. Debussche), pp. 19–36, Kluwer Academis Publishers, Dordrecht.

Lodge, D.M. (1993) Biological invasions: lessons for ecology. *Trends Ecol. Evol.* **8**, 133–137.

Lonsdale, W.M. (1993) The rate of spread of an invading species—*Mimosa pigra* in northern Australia. *J. Ecol.* **81**, 513–521.

Lundström, H. (1984) Giant hogweed, *Heracleum mantegazzianum*, a threat to the Swedish countryside. *Weeds and weed control*. 25th Swedish Weed Conference, Uppsala, Vol. **1**, p. 191–200.

Medd, R.W. & Smith, R.C.G. (1978) Prediction of the potential distribution of *Carduus nutans* (nodding thistle) in Australia. *J. Appl. Ecol.* **15**, 603–612.

Mladenova, I.P. (1950) *Caucasian species of the genus Heracleum*. Systematics & Plant Geography Monographs, ser. A, Tbilisi. [in Russian].

Neiland, M.R.M. (1986) *The distribution and ecology of Giant hogweed (Heracleum mantegazzianum) on the River Allan, and its control in Scotland*. Thesis Univ. Stirling.

Ochsmann, J. (1992) *Riesen-Bärenklaus (Heracleum spec.) in Deutschland: morphologie, Ökologie, Verbreitung und systematische Einordnung*. Thesis Univ. Göttingen.

Panetta, F.D. & Dodd, J. (1987) Bioclimatic prediction of the potential distribution of skeleton weed *Chondrilla juncea* L. in Western Australia. *J. Austr. Inst. Agr. Sci.* **53**, 11–16.

Panetta, F.D., Mitchell, N.D. (1991) Bioclimatic prediction of the potential distribution of some weed species prohibited entry to New Zealand. *N. Z. J. Agr. Res.* **34**, 341–350.

Pyšek, P. (1991) *Heracleum mantegazzianum* in the Czech Republic: the dynamics of spreading from the historical perspective. *Folia Geobot. Phytotax.* **26**, 439–454.

Pyšek, P. (1994) Ecological aspects of invasion by *Heracleum mantegazzianum* in the Czech Republic. *Ecology and management of invasive riverside plants* (ed. by L.C. de Waal, E.L. Child, P.M. Wade and J.H. Brock), pp. 45–54, John Wiley & Sons, Chichester.

Pyšek, P. (1995) On the terminology used in plant invasion studies. *Plant invasions—general aspects and special problems* (ed. by P. Pyšek, K. Prach, M. Rejmánek and M. Wade), pp. 71–81, SPB Academic Publishing, Amsterdam.

Pyšek, P., Kučera, T., Puntieri, J. & Mandák, B. (1995) Regeneration in *Heracleum mantegazzianum*—response to removal of vegetative and generative parts. *Preslia*, **67**, 161–171.

Pyšek, P. & Prach, K. (1993) Plant invasions and the role of riparian habitats—a comparison of four species alien to central Europe. *J. Biogeogr.* **20**, 413–420.

Pyšek, P. & Prach, K. (1995) Invasion dynamics of *Impatiens glandulifera*—a century of spreading reconstructed. *Biol. Conserv.* **74**, 41–48.

Pyšek, P., Prach, K. & Šmilauer, P. (1995) Invasion success related to plant traits: an analysis of Czech alien flora. *Plant invasions—general aspects and special problems* (ed. by P. Pyšek, K. Prach, M. Rejmánek and M. Wade), pp. 39–60, SPB Academic Publishing, Amsterdam.

Pyšek, P. & Pyšek, A. (1994) Present occurrence of *Heracleum mantegazzianum* in the Czech Republic and overview of its localities. *Zpr. Čs. Bot. Společ., Praha*, **27** (1992), 17–30. [in Czech].

Pyšek, P. & Pyšek, A. (1995) Invasion by *Heracleum mantegazzianum* in different habitats in the Czech Republic. *J. Veget. Sci.* **6**, 711–718.

Rejmánek, M. (1989) Invasibility of plant communities. *Biological invasions: a global perspective* (ed. by J. Drake *et al.*), pp. 369–388, John Wiley & Sons, Chichester.

Scott, J.K. & Panetta, F.D. (1993) Predicting the Australian weed status of southern African plants. *J. Biogeogr.* **20**, 87–93.

Sindel, B.M. & Michael, P.W. (1992) Spread and potential distribution of *Senecio madagascariensis* Poir. (fireweed) in Australia. *Austr. J. Ecol.* **17**, 21–26.

Sukopp, H. & Werner, P. (1983) Urban environment and vegetation. *Man's impact on vegetation* (ed. by W. Holzner *et al.*), pp. 247–260, Dr W. Junk Publishers, The Hague.

Şwieboda, M. (1963) Distribution of *Elsholtzia patrini* (Lep.) Garcke in Poland. *Fragm. Florist. Geobot.* **9**, 239–243.

Thompson, K. (1994) Predicting the fate of temperate species in response to human disturbance and global change. *Biodiversity, temperate ecosystems and global change* (ed. by T.J.B. Boyle and C.E.B. Boyle), pp. 61–76, Springer Verlag, New York.

Tiley, G.E.D., Dodd, F.S. & Wade, P.M. (1996) Biological flora of the British Isles. 190. *Heracleum mantegazzianum* Sommier et Levier. *J. Ecol.* **84**, 297–319.

Trepl, L. (1984) Über *Impatiens parviflora* DC. als Agriophyt in Mitteleuropa. *Diss. Bot.* **73**, 1–400.

Tucker, K.C. & Richardson, D.M. (1995) An expert system for screening potentially invasive alien plants in South African fynbos. *J. Environ. Manage.* **44**, 309–338.

Vesecký, A., Petrovič, Š., Briedoò, V. & Karský, V. (1958) *Climatic atlas of Czechoslovakia*. Praha [in Czech].

Waal, L.C. de, Child, E.L., Wade, P.M. & Brock, J.H. (eds.) (1994) *Ecology and management of invasive riverside plants*. John Wiley & Sons, Chichester.

Webb, D.A. (1985) What are the criteria for presuming native status? *Watsonia*, **15**, 231–136.

Williamson, J.A. & Forbes, J.C. (1982) Giant hogweed (*Heracleum mantegazzianum*): its spread and control with glyphosate in amenity areas. *Weeds. Proc. 1982 British Crop Protection Conference*, pp. 967–972.

Wilson, J.B., Rapson, G.L., Sykes, M.T. & Watkins, A.J. (1992) Distribution and climatic correlations of some exotic species along roadsides in South Island, New Zealand. *J. Biogeogr.* **19**, 183–194.