Biol Invasions (2007) 9:383–395
DOI 10.1007/s10530-006-9040-6

RESEARCH PAPER

A simulation model of plant invasion: long-distance dispersal determines the pattern of spread

**Nana Nehrbass · Eckart Winkler ·
Jana Müllerová · Jan Pergl · Petr Pyšek ·
Irena Perglová**

Received: 3 November 2005 / Accepted: 12 July 2006 / Published online: 14 November 2006

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.

Keywords Individual-based modelling · Invasion history · Local spread · Long-distance dispersal · Land-use change

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

---

N. Nehrbass (✉) · E. Winkler
Department of Ecological Modelling, Centre for
Environmental Research UFZ Leipzig,
Permoserstrasse 12, Leipzig 04318, Germany
e-mail: nana.nehrbass@ufz.de

J. Müllerová · J. Pergl · P. Pyšek · I. Perglová
Institute of Botany, Academy of Science of the Czech
Republic, Průhonice CZ-25243, Czech

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 spatio-temporal 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 *H. 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 upto 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. 2006a). 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. 2006). 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 3 years (Moravcová et al. 2006).

The 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 II, 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).

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 18 different habitat types and classified them as suitable or unsuitable for *H. mantegazzianum*, based on the empirically observed habitat preferences in the study area (Table 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 in resolution 800 dpi; (ii) rectification using orto-photographs (40–60 ground control points distributed along the rectified photograph, second order of transformation and nearest neighbour rectification method; Lillesand and Kiefer 1999); (iii) visualization 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. 2006b) 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. 2006b). 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 × 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

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

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.

As a monocarpic perennial plant *H. mantegazzianum* flowers at earliest in its second year (Tiley et al. 1996; Holub 1997; Pergl et al. 2006a), the model thus considered plants 2 years and older as capable of flowering. Flowering probability was not only age-dependent, 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 (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 non-flowering 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.

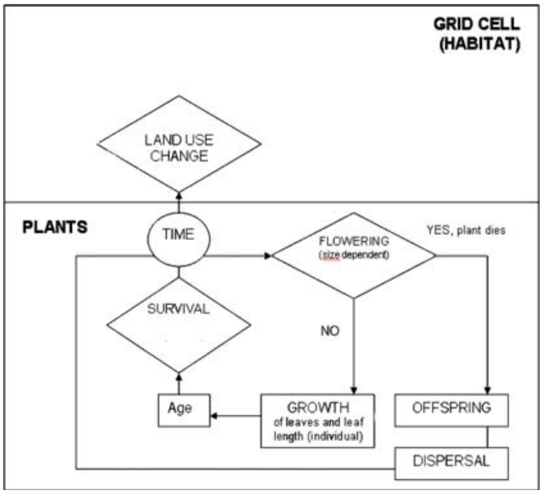

Fig. 1 Flow chart of the individual-based model of *Heracleum mantegazzianum*. Within one time-step (year) different probabilities determine the fate of an individual plant. Changes in landscape structure (i.e., if one land-use type changed into another) were incorporated in the model in the year when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

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 (long-distance) 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.

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 2 as in Fig. 2 only cells are shown in which at least two individuals occurred.

Table 2 gives average percentages of correct matching P_M 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.

Table 2 Comparison between actual occupation data and modelled spread of *Heracleum mantegazzianum* (standard scenario)

Characteristic	Year (Simulation)				
	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

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 m^2 (19,600 grid cells of 5 × 5 m^2)

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.

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

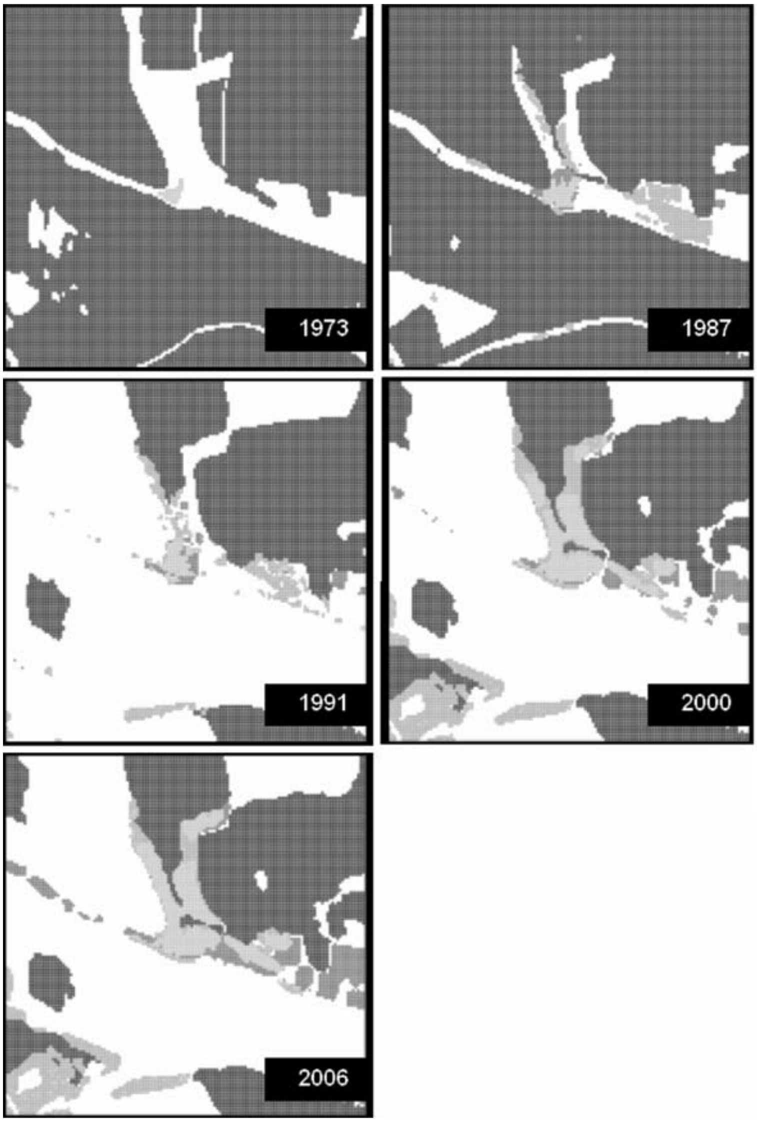

Fig. 2 Exemplary model simulation of the population development of *Heracleum mantegazzianum* in the study site Arnoltov (710 × 710 m, pixel size 25 m^2). White area represents suitable habitat, dark-grey area is the matrix of unsuitable landscape (see Table 1). Population spread as derived from aerial 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

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.

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. Figure 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.

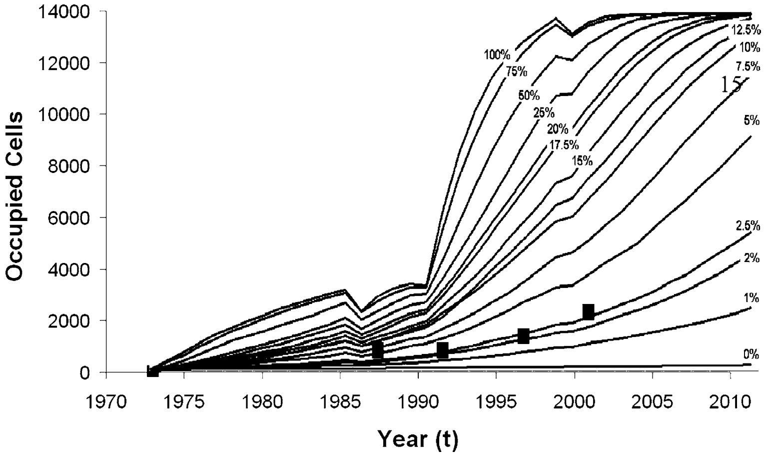

Fig. 3 Effect of long-distance dispersal on invasion in exemplary simulation runs in the standard landscape scenario. The categories of long-distance dispersal are based on the percentage of the total number of offspring involved in long-distance dispersal events. The changes in land-use structure at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

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 al. 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.

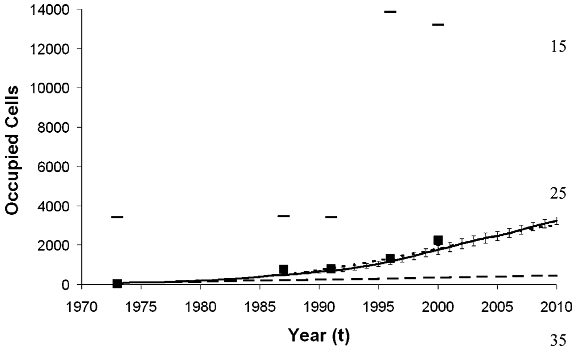

Fig. 4 Number of all occupied grid cells (5 × 5 m) in the simulation model of *Heracleum mantegazzianum* (line with SD). Land-use changes occurred in the years $t =$ 1987, 1991, 1996, and 2000. Horizontal lines indicate the maximum number of grid cells that can be occupied at those times (except for 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 2

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.

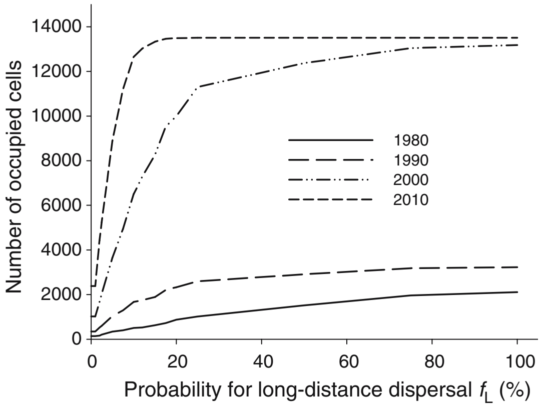

Fig. 5 Number of occupied cells for 1980, 1990, 2000, and 2010 in relation to the implemented probability for long-distance dispersal (f_L). Lower probabilities have over-proportionally higher effect on cell occupation than high probabilities

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 *H. 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-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.

References

Akcakaya HR, Burgman MA, Ginzburg LR (1999) Applied population ecology. Sinauer Associates Inc., Sunderland, MA

Buckley YM, Briese DT, Rees M (2003a) Demography and management of the invasive plant species *Hypericum perforatum*. II. Construction and use of an individual-based model to predict population dynamics and the effects of management strategies. J Appl Ecol 40:494–507

Buckley DS, Crow TR, Nauertz TR, Schulz KE (2003b) Influence of skid trails and haul roads on understory plant richness and composition in managed forest landscapes in managed forest landscapes in Upper Michigan, USA. For Ecol Manage 175:509–520

Bullock JM, Moy IL, Pywell RF, Coulson SJ, Nolan AM, Caswell H (2002) Plant dispersal and colonization processes at local and landscape scales. In: Bullock JM, Kenwart RE, Hails RE (eds) Dispersal Ecology, Blackwell Publishers, UK, pp 279–302

Chips Development Team (1998) Chips 4.3, the Copenhagen Image Processing System. University of Copenhagen, Copenhagen

Chytrý M, Pyšek P, Tichý L et al (2005) Invasions by alien plants in the Czech Republic: a quantitative assessment across habitats. Preslia 77:339–354

Clark Labs (1998) CartaLinx 1.04, the spatial data builder. Clark University, Worcester

Clark JS, Lewis M, McLachlan JS, HilleRisLambers J (2003) Estimating population spread: what can we forecast and how well? Ecology 84:1979–1988

Collingham YC, Wadsworth RA, Huntley B, Hulme PE (2000) Predicting the spatial distribution of non-indigenous riparian weeds: issues of spatial scale and extent. J Appl Ecol 37:13–27

Czárán T (1998) Spatiotemporal models of population and community dynamics. Chapman & Hall, London.

Davis MA (2003) Biotic globalization: does competition from introduced species threaten biodiversity? BioScience 53:481–489

Delisle F, Lavoie C, Jean M, Lachance D (2003) Reconstructing the spread of invasive plants: taking into account biases associated with herbarium specimes. J Biogeogr 30:1033–1042

Everitt BJ (1998) Chronology of the spread of tamarisk in the Central Rio Grand. Wetlands 18:658–668

Everitt JH, Anderson GL, Escobar DE et al (1995) Use of remote sensing for detection and mapping of leafy spurge (*Euphorbia esula*). Weed Technol 9:599–609

Fuller RM, Boorman LA (1977) The spread and development of *Rhododendron ponticum* L. on dunes at Winterton, Norfolk, in comparison with invasion by *Hippophae rhamnoides* L. at Saltfleetby, Lincolnshire. Biol Conserv 12:83–94

Grimm V, Frank K, Jeltsch F et al (1996) Pattern-oriented modelling in population ecology. Sci Total Environ 183:151–166

Hansen MJ, Clevenger AP (2005) The influence of disturbance and habitat on the presence of non-native plant species along transport corridors. Biol Conserv 125:249–259

Heger T (2004) Zur Vorhersagbarkeit biologischer Invasionen. Entwicklung und Anwendung eines Modells zur Analyse der Invasion gebietsfremder Pflanzen. Dissertation. Neobiota 4, pp 202 [in German]

Higgins SI, Richardson DM (1996) A review of models of alien plant spread. Ecol Modell 87:249–265

Higgins SI, Richardson DM (1999) Predicting plant migration rates in a changing world: the role of long-distance dispersal. Am Nat 153:464–475

Higgins SI, Richardson DM, Cowling RM (2000) Using a dynamic landscape model for planning the management of alien plant invasions. Ecol Appl 10:1833–1848

Higgins SI, Richardson DM, Cowling RM (2001) Validation of a spatial simulation model of a spreading alien plant population. J Appl Ecol 38:571–584

Holub J (1997) *Heracleum*—bolševník. In: Slavík B, Chrtek jun J, Tomšovic P (eds) Květena České republiky 5. Academia, Praha, pp 386–395

Jensen JR (1996) Introductory digital image processing. Prentice-Hall Int., London

Kos J, Maršáková M (1997) Chráněná území České republiky. Agentura ochrany přírody a krajiny, Praha, Czech Republic

Krinke L, Moravcová L, Pyšek P et al (2005) Seed bank in an invasive alien *Heracleum mantegazzianum* and its seasonal dynamics. Seed Sci Res 15:239–248

Levin SA, Muller-Landau HC, Nathan R, Chave J (2003) The ecology and evolution of seed dispersal: a theoretical perspective. Annu Rev Ecol Evol Syst 34:575–604

Lillesand TM, Kiefer RW (1999) Remote sensing and image interpretation, 3rd edn. John Wiley & Sons, New York

Lonsdale WM (1993) Rates of spread of an invading species: *Mimosa pigra* in northern Australia. J Ecol 81:513–521

Mandák B, Pyšek P, Bímová K (2004) History of the invasion and distribution of *Reynoutria* taxa in the Czech Republic: a hybrid spreading faster than its parents. Preslia 76:15–64

Mooney HA, Hofgaard A (1999) Biological invasions and global change. In: Sandlund OT, Schei PJ, Viken A (eds) Invasive species and biodiversity management. Kluwer Academic Publishers, pp 139–148

Moravcová L, Perglová I, Pyšek P et al (2005) Effects of fruit position on fruit mass and seed germination in the alien species *Heracleum mantegazzianum* (Apiaceae) and the implications for its invasion. Acta Oecologica 28:1–10

Moravcová L, Pyšek P, Krinke L et al (2006) Seed germination, dispersal and seed bank in *Heracleum mantegazzianum*. In: Pyšek P, Cock MJW, Nentwig W, Ravn HP (eds) Ecology and management of giant hogweed (*Heracleum mantegazzianum*), CAB International, Wallingford (in press)

Müllerová J, Pyšek P, Jarošík V, Pergl J (2005) Aerial photographs as a tool for assessing the regional dynamics of the invasive plant species *Heracleum mantegazzianum*. J Appl Ecol 42:1042–1053

Nehrbass N, Winkler E, Pergl J et al (2006) Predicting plant invasions: comparing results of a matrix model and an individual-based model. Prog Plant Ecol Evol Syst 7:253–262

Nielsen C, Ravn HP, Cock M, Nentwig W (eds) (2005) The giant hogweed best practice manual. Guidelines for the management and control of an invasive alien weed in Europe. Forest and Landscape Denmark, Hoersholm

Pergl J, Perglová I, Pyšek P, Dietz H (2006a) Population age structure and reproduction behaviour of the monocarpic perennial *Heracleum mantegazzianum* (Apiaceae) in its native and invaded distribution range. Am J Bot (in press)

Pergl J, Hüls J, Perglová I et al (2006b) Population dynamics of *Heracleum mantegazzianum*. In: Pyšek P, Cock MJW, Nentwig W, Ravn HP (eds) Ecology and management of giant hogweed (*Heracleum mantegazzianum*), CAB International, Wallingfod, (in press)

Perglová I, Pergl J, Pyšek P (2006) Reproductive ecology of *Heracleum mantegazzianum*. In: Pyšek P, Cock MJW, Nentwig W, Ravn HP (eds) Ecology and management of giant hogweed (*Heracleum mantegazzianum*), CAB International, Wallingford, (in press)

Perrins J, Fitter A, Williamson M (1993) Population biology and rates of invasion of three introduced Impatiens species in the British Isles. J Biogeogr 20:33–44

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

Pyšek P, Hulme P (2005) Spatio-temporal dynamics of plant invasions: linking patterns to process. Ecoscience 12:302–315

Pyšek P, Jarošík V, Kuěera T (2002) Patterns of invasion in temperate nature reserves. Biol Conserv 104:13–24

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

Pyšek P, Richardson DM, Rejmánek M et al (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. Taxon 53:131–143

Richardson DM, Brown PJ (1986) Invasion of mesic mountain fynbos by *Pinus radiata*. S Afr J Bot 52:529–536

Richardson DM, Pyšek P, Rejmánek M et al (2000) Naturalization and invasion of alien plants: concepts and definitions. Divers Distrib 6:93–107

Robinson TW (1965) Introduction, spread and areal extent of saltcedar (*Tamarix*) in the western states. Studies of evapotranspiration. Geological Survey Professional Paper 491(A):1–12

Rouget M, Richardson DM, Cowling RM et al (2003) Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. Biol Conserv 112:63–85

Stow D, Hope A, Richardson DM et al (2000) Potential of colour-infrared digital camera imagery for inventory and mapping of alien plant invasions in South African shrublands. Int J Remote Sens 21:2965–2970

Tiley GED, Dodd FS, Wade PM (1996) *Heracleum mantegazzianum* Sommier and Levier. J Ecol 84:297–319

Weber E (1998) The dynamics of plant invasions: a case study of three exotic goldenrod species (*Solidago* L.) in Europe. J Biogeogr 25:147–154

Weber E (2003) Invasive plant species of the World. A reference guide to environmental weeds. CABI International Publishing, Wallingford

Williamson M, Pyšek P, Jarošík V, Prach K (2005) On the rates and patterns of spread of alien plants in the Czech Republic and Britain. Ecoscience 12:424–433