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

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Summary

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

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

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

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

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

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Introduction

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

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

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

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

Methods

STUDY SPECIES

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

Heracleum mantegazzianum is the largest central European forb, native to the western Caucasus (Mandenova 1950) and naturalized or invasive in a number of European countries (Tiley, Dodd & Wade 1996; Collingham *et al.* 2000), Canada (Morton 1978) and the USA (Kartesz & Meacham 1999). It was introduced to the Czech Republic as a garden ornamental in the region studied here (Slavkovský les, west Bohemia) in 1862. The species has spread from there to other parts of the country (Pyšek 1991; Pyšek *et al.* 1998) and become invasive (Pyšek, Sádlo & Mandák 2002).

STUDY AREA

The study area was located in the Slavkovský les Protected Landscape Area, west Bohemia, a region heavily invaded by *H. mantegazzianum* (Pyšek & Pyšek 1995). The total size of the protected area is 617 km^2, altitudinal range is 373–983 m a.s.l. (Kos & Maršáková 1997), minimum and maximum temperatures are for January –5·1° to –0·2 °C and for July 10·5–21·5 °C. The annual sum of precipitation is 1094 mm (Mariánské Lázně meteorological station, 50-year average). The natural vegetation of the area is mainly beech and spruce forests, peat bogs, and pine forests on serpentine (Neuhäuslová & Moravec 1997). This vegetation is now only present in remnants, and has been replaced over much of its original extent by extensive wetlands, with a high diversity of flora, pastures and spruce plantations that cover 53% of the area (Kos & Maršáková 1997).

Colonization of the region by humans started at the end of the 13th century. After World War II, German inhabitants were displaced and part of the region was a military area with restricted access until the 1960s. The lack of appropriate landscape management associated with disturbances from military activities, as well as climatic conditions matching those in the native distribution area (Pyšek 1991), are probable reasons for the rapid spread of the species in the study area over the study period.

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

The oldest herbarium specimen documenting with certainty a spontaneous occurrence in the study area, in close proximity to the introduction site, is from 1877

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

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

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

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

PHOTO-INTERPRETATION AND ANALYSIS OF AERIAL PHOTOGRAPHS

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

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

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

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

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

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

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

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

STATISTICAL ANALYSIS

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

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

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

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

Results

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

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

RATE OF SPREAD

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

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

Locality	Invaded area (m^2)	Relative invaded area (%)	Flowering intensity (%)	Beginning of invasion	Year	Contribution to the invaded area (%)			Proportion of land-use type invaded (%)		
						Forest	Treeless	Urban	Forest	Treeless	Urban
Arnoltov	47 170	7·9	57·7	1973	2000	9·3	90·5	0·2	1·9	11·7	1·5
Dvorečky	24 817	4·1	68·1	1973	1996	27·8	71·6	0·6	1·9	7·8	1·1
Krásná Lípa II	9 454	1·6	43·9	1987	1996	15·6	83·1	1·3	0·8	2·1	0·0
Lískovec	8 174	1·4	47·3	1987	1996	0·7	99·2	0·1	0·0	1·9	0·0
Litrbachy	4 711	0·8	42·2	1973	1996	17·2	82·7	0·0	0·9	0·8	0·0
Potok	39 774	6·6	52·7	1962	1996	50·7	49·0	0·3	4·6	12·4	1·6
Prameny	55 575	9·3	69·2	1973	1996	8·0	86·7	5·3	8·9	9·4	7·7
Rájov	5 198	0·9	39·3	1996	1996	0·0	100·0	0·0	0·0	1·0	0·0
Žitný I	113 236	18·9	52·5	1957	1987	10·1	86·0	3·9	5·8	24·9	32·7
Žitný II	111 351	18·6	54·2	1962	1991	12·0	84·9	3·1	5·1	28·8	32·2
Mean		7·0				15·1	83·4	1·5	3·0	10·1	7·7

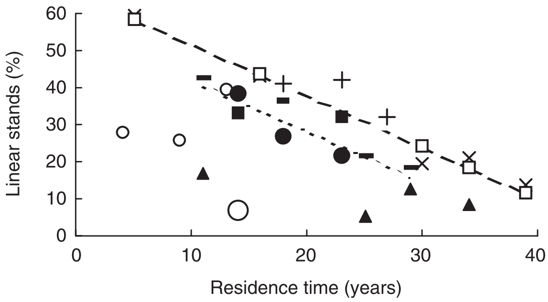

Fig. 2. Changes in the importance of linear stands (defined as the proportion of the total invaded area accounted for by stands up to 20 m from the axis of a linear habitat) for *Heracleum* invasion. Fitted lines show significant slopes for Žitný I (percentage of linear stands = 65·57–1·38 residence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

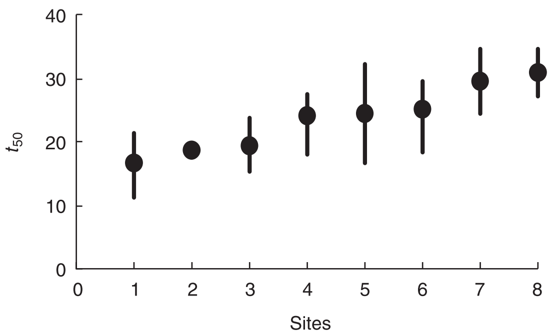

Fig. 3. Mean rates of spread (with 95% confidence intervals) expressed as t_{50}, the estimated time to 50% of the total area invaded. Means at individual sites, ranked in ascending order, whose confidence intervals do not overlap, are significantly different. 1, Prameny; 2, Lískovec; 3, Žitný II; 4,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

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

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

RELATIONSHIP BETWEEN INVADED AREA, RATE OF SPREAD AND RESIDENCE TIME

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

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

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

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

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

CHANGES IN POPULATION CHARACTERISTICS DURING INVASION

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

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

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

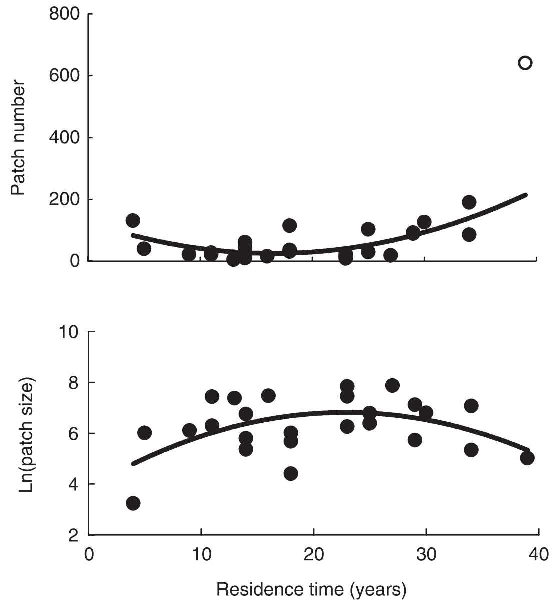

Fig. 4. Trends in the number and size of *Heracleum* patches (defined as an isolated area of minimum size 3 m^2 covered by *Heracleum* plants) in the course of invasion. Patch number = 127 – 12·34 residence time + 0·37 (residence time)^2. $F_{2,21}$ = 9·77, P < 0·01, R^2 = 48·2%; the enlarged white point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

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

Discussion

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

By selecting the study sites *post hoc* using knowledge of present-day infestation, we could select areas where it could be assumed populations had not spread outside the study plots. The majority of study sites were located in isolated open areas within otherwise mostly forested landscape, and invading populations were located in the central parts of these areas. It can therefore be assumed that the invaded area recorded at a site resulted from the foci identified on the earliest photographs. The penetration of invading plants from outside analysed plots cannot be completely excluded, but the data indicate that if this occurred it was of minor importance. Such occurrence would make the estimated values of spread more conservative. On the other hand, the maximum values found at the Žitný I and II sites (Table 1) represent a good estimate of invasion potential because they are located in a large open area of former pastures and meadows, surrounding an abandoned village, with low representation of forest and scrub patches that could represent physical constraints to the invasion. In these two sites, *Heracleum* invaded 18·6% and 18·9% of the available areas over 40 years (Table 3 and Fig. 1). Field research has confirmed and previous study (Pyšek & Pyšek 1995) has demonstrated that forests indeed represent barriers to invasion by *Heracleum*. *Heracleum* invades forest margins but only very rarely are solitary plants found in forest interior.

An absence of correlation between linear and areal measures of spread (Table 3; $F_{1,7}$ = 0·57, P = 0·47) indicates that *Heracleum* populations do not spread as an advancing front but that long-distance dispersal (within the scale involved in the study) plays an important role in the invasion process (Higgins & Richardson 1999; Hulme 2003).

The analyses presented make several assumptions. (i) Photographs were taken when *Heracleum* was flowering or fruiting and plants are easy to distinguish, so that the invaded area could have been identified and measured. The largest invaded area recorded in a site over the study period was used, rather than the most recent value recorded, because in two sites (Table 1) the total invaded area decreased slightly between the most recent dates. This was probably the result of occasional unsuccessful small-scale control efforts and/or photograph quality varying between samples. (ii) Samples were regularly distributed over the 40 years of invasion, allowing us to measure the rate of invasion. (iii) Monitoring had started before the onset of invasion, so it was possible to determine the start with reasonable precision given the intervals between monitoring dates.

These data allowed us to explore the relative role of the two determinants of invaded area. Both the residence time and rate of spread significantly contributed to the invaded, area with the direct effect of the latter being much larger than that of the former. However, as the residence time also had a significant effect on the rate of spread (the invasion proceeded faster in sites where *Heracleum* was introduced earlier), the total effects of the residence time and rate of spread were of comparable importance. If the invaded area was determined only by the year a site was invaded, the rate of invasion would be the same in each locality and the species would have spread regardless of specific site conditions. As the year of invasion was determined mainly by dispersal opportunities, the current pattern of *Heracleum* occurrence in the study area would be primarily determined by the fact that the species' propagules reached the sites at different times. However, the significant differences in the rate of invasion among sites indicate that, despite *Heracleum* being an extremely successful invader (Moravcová *et al*. 2005) and the study region being climatically suitable (Pyšek 1991; Pyšek *et al*. 1998), there are constraints to invasion that vary among sites. That the sites are not equally suited for colonization by *Heracleum* is determined by variation in environmental conditions such as soil nutrients and moisture, character of resident vegetation and site history (Rouget & Richardson 2003; Rickey & Anderson 2004; Barney, DiTommaso & Weston 2005). These features affect the species' population biology and ecology and act in concert with landscape determinants of invasion. The importance of environmental heterogeneity in influencing invasions has been highlighted (Davis, Grime & Thompson 2000). As environments differ in their spatial and temporal patterns of resource supply, the opportunities they provide for recruitment and spread differ (Higgins & Richardson 1996).

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

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

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

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

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

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

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

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

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

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