Plant invasions and the role of riparian habitats: a comparison of four species alien to central Europe

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Abstract. We compared the rate of invasion of four plant species which are alien to central Europe and the highest-growing representatives of different life-forms: *Impatiens glandulifera* (annual), *Heracleum mantegazzianum* (monocarpic perennial), *Reynoutria japonica* and *R. sachalinensis* (polycarpic perennials). The spread of these species in the Czech Republic was reconstructed on the basis of floristic data. Cumulative numbers of localities reported from the time of introduction to the present were used for comparison. Exponential regression models were found to best fit the increase in the cumulative number of localities over time and the slope *b* was considered a convenient measure of the invasion rate. The ranking of species according to the decreasing rate of invasion was: *I. glandulifera, Reynoutria japonica, Heracleum mantegazzianum, R. sachalinensis*. The rate of invasion in riparian habitats, if these were treated separately, decreased in the following order: *I. glandulifera, R. sachalinensis, R. japonica, H. mantegazzianum*. The lag and exponential phases of spread were distinguished and the tim-

ing of the beginning of invasion was estimated at 1936 in *I. glandulifera*, 1938 in *R. japonica*, 1943 in *H. mantegazzianum* and 1952 in *R. sachalinensis*. *H. mantegazzianum* and *I. glandulifera* began to spread exponentially after having reached only a few localities in the area studied and their invasion rates during the exponential phase were higher than those of both *Reynoutria* species, whose invasion proceeded at a more even rate. Habitat preferences differed between species in both lag and exponential phases of spread. Different patterns of affinity to riparian habitats were found among the species studied. The role of river corridors in encouraging plant invasions is discussed on the regional scale with respect to the autecology of the species and frequency of suitable habitats.

Key words. Plant invasions, riparian habitats, floristic records, spreading dynamics, timing of invasion, historical reconstruction, central Europe.

INTRODUCTION

In the process of plant invasion rivers may act as dispersal agents, supporting downstream movement of diaspores by water (e.g. Staniforth & Cavers, 1976; van der Pijl, 1982; Schneider & Sharitz, 1988; Skoglund, 1989). Moreover, periodic disturbances resulting from destructive flooding generally destroy or damage a large part of riparian vegetation (Ellenberg, 1988) thus creating openings that provide suitable habitats and favourable nutrient conditions for seedling establishment and subsequent colonization (Walker, Zasada & Chapin, 1986). Consequently, riparian habitats into which an alien species was successfully introduced and naturalized may serve as foci for subsequent spread into the adjacent landscape (Pyšek, 1991, 1993).

The present paper is based on historical reconstructions of spreading dynamics of four species alien to the flora of the Czech Republic, central Europe. All these species are extremely successful invaders in the present central European landscape (Kees & Krumrey, 1983; Pyšek, 1991;

Pyšek & Prach, 1993a; Sukopp & Schick, 1993) and are the highest-growing central European representatives of the following life forms: annual (*Impatiens glandulifera* Royle), monocarpic perennial (*Heracleum mantegazzianum* Somm. et Lev.), and polycarpic perennial (*Reynoutria japonica* Houtt. and *R. sachalinensis* (F. Schmidt Petropolit.) Nakai). Basic life history characteristics of the species under study are summarized in Table 1.

Based on floristic records covering more than a hundred years, the present paper addresses the following questions. (1) What are the between-species differences in the rate and timing of invasion? (2) Did the relationship of species to riparian habitats change during their invasions? Moreover, this paper aims to demonstrate how historical floristic records may be exploited for illustrating ecological phenomena.

METHODS

Both published and unpublished floristic data including

TABLE 1. Characteristics of species investigated.

	Impatiens glandulifera	*Heracleum mantegazzianum*	*Reynoutria japonica*	*Reynoutria sachalinensis*
Area of origin	Himalayas	Caucasus	Far East	Far East
Life form	Annual	Monocarpic perennial (up to 4 years)	Polycarpic perennial	Polycarpic perennial
Maximum height	2.5 m	4–5 m	> 3 m	4 m
Dispersal*	Water, man/explosive seed capsule	Man, wind, water, animals	Man, water/ vegetative	Man, water/ vegetative
Main way of regeneration	Only by seeds	Seeds, tuberous root	Rhizomes (in Europe)	Rhizomes (in Europe)

Sources: Grime, Hodgson & Hunt, 1988; Perrins, Fitter & Williamson, 1990; Pyšek, 1991, personal obervations.
*Listed according to decreasing importance (based on authors' field experience).

TABLE 2. Characteristics of the invasion process of the species studied.

	First appearance in Czech Republic		Duration of L	Beginning of E		Present number of localities	
	T	R		Loc. no.	Year	T	R
Impatiens glandulifera	1896	1900	40	12	1936	742	396
Heracleum mantegazzianum	1862	1900	80	4	1943	411	41
Reynoutria japonica	1892	1892	46	39	1938	515	128
R. sachalinensis	1869	1935	83	22	1952	152	36

See Methods for details of distinguishing the lag phase from the exponential one. T: in total; R: in riparian habitats; L: lag phase; E: exponential phase; Loc. no.: number of localities.

herbarium collections (Charles University Prague, National Museum Prague, and regional museums) were used in the reconstruction of invasion dynamics. For *Heracleum mantegazzianum* and *I. glandulifera*, complete referenced lists of localities have been published (Pyšek & Pyšek, 1993; Pyšek & Prach, 1993b). Information on the year of observation and habitat type was summarized. If the year of observation was not provided by the original author, the year of publication was used. As shown for *H. mantegazzianum* in a previous paper (Pyšek, 1991), the year of publication closely corresponds to the year of observation, since 81% of records are published within 5 years from the observation (the proportion of published localities significantly decreased with the interval between the observation and its publication, $Y = 1.22X^{-0.072}$, $r = -0.90$, $P < 0.0001$).

A previous paper (Pyšek, 1991) demonstrated how floristic data, systematically gathered over an area for a long time, may be used to reconstruct the pattern of invasion of a species on a large geographical scale. There are, however, some limitations to floristic data which should be emphasized. A sufficient intensity of floristic research within an area is necessary for a successful retrospective analysis of species spread. This is clearly kept because of the strong, long-term floristic tradition in the Czech Republic. If systematic recording of the flora is carried out, one can assume that the more common a species is, the more often it is recorded. The species itself should be currently (1) worthy of note, i.e. rare enough or otherwise interesting

from the point of view of ecology, spreading dynamics etc., (2) conspicuous in order not to be overlooked and (3) taxonomically unproblematic, i.e. easily recognizable by amateur botanists who are the main producers of floristic data. These points may be considered reasonably fulfilled by the species studied.

Because of the data character (point records and a priori defined geographical area) it was not possible to use the size of the area occupied by a species as a measure of invasion (Hengeveld, 1989). Exponential regression models were thus fitted to the cumulative numbers of localities plotted against time (further termed as invasion curves) and the slope *b* of the regression line was used as a measure of the invasion rate (Trewick & Wade, 1986; Pyšek 1991; Pyšek and Prach, 1993a). Differences in slopes were tested using *F*-test (Snedecor & Cochran, 1967).

The beginning of exponential phase was defined as a year in which the parameters of the invasion curve are changing. This was detected using the maximum likelihood estimation of classic regression model parameters for partitioned model (Quandt, 1958, 1960). The variance of white noise was assumed to be equal in both parts of the partitioned model.

RESULTS

History of invasions

According to our current knowledge, all the species investigated were introduced to the Czech Republic at
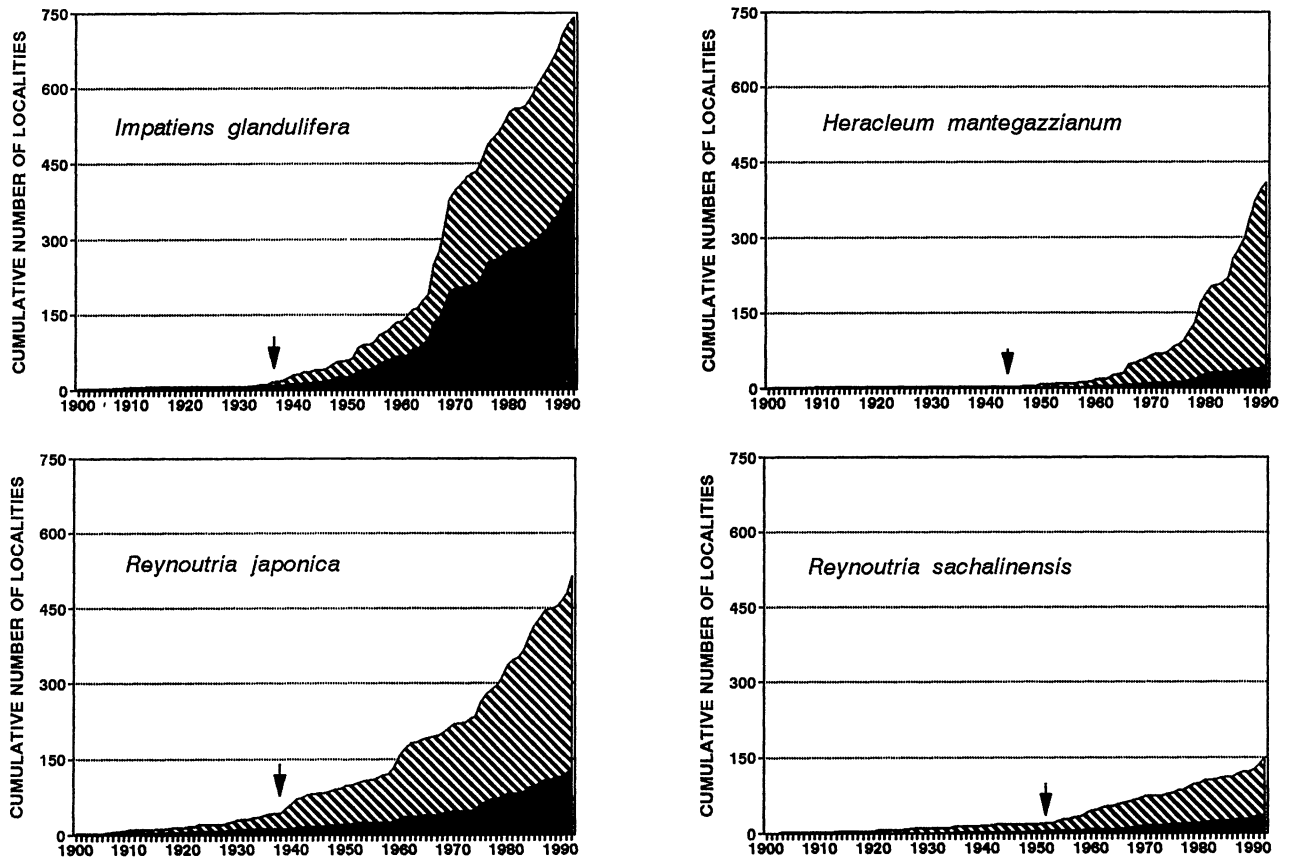
FIG. 1. Invasion curves of the species studied in the Czech Republic. Only the 20th century is shown. Total cumulative number of localities is given on the y-axis and the part formed by riparian habitats is indicated by the solid area. The beginning of the exponential phase (see Methods for details on estimation) is indicated by an arrow. See Table 2 for summary of the number of localities. ■, Riparian; ▨, others.

approximately the same time (Table 2), i.e. in the second half of the 19th century, having originally been planted as garden ornamental plants (see Pyšek, 1991 and Pyšek and Prach, 1993a for details on the history of introduction in *H. mantegazzianum* and *I. glandulifera*, respectively).

Considering the whole invasion process (i.e. since the time of introduction), the spreading rate was highest in *I. glandulifera*, followed by *R. japonica*. The spread of *H. mantegazzianum* and *R. sachalinensis* was slower and the slopes *b* were not significantly different (Fig. 1, Table 3).

There was a lag phase of more than 80 years in *H. mantegazzianum* and *R. sachalinensis*. In two other species, the lag phase took about half of this period. The number of localities at the end of the lag phase was very low in *I. glandulifera* and *H. mantegazzianum*, indicating that the exponential phase began immediately after the species has established several foci in the area. On the other hand, both *Reynoutria* species did not begin to spread exponentially until having more than twenty localities in the region. The time at which the exponential phase of invasion began was similar in all species (1936 in *I. glandulifera*, 1938 in *R. japonica*, 1943 in *H. mantegazzianum*) except *R. sachalinensis* in which it was delayed until 1952 (Table 2). *H. mantegazzianum* showed the

highest rate of invasion during the exponential phase, followed by *I. glandulifera*. Both *Reynoutria* species were spreading at slower rates, the difference between both being not significant (Table 3).

Total numbers of localities reported up to 1992 are given in Table 2 for each species.

Role of riparian habitats

Treating riparian habitats separately, the highest rate of spread was found for *I. glandulifera*, followed by both *Reynoutria* species and *H. mantegazzianum* (Table 3). During the exponential phase, *I. glandulifera* ($F_{1,112} = 5.59$, $P < 0.05$) and *R. sachalinensis* ($F_{1,80} = 5.54$, $P < 0.05$) were spreading faster in riparian habitats than in the others. Conversely, the spread of *H. mantegazzianum* in other habitats was faster than in riparian ones ($F_{1,96} = 11.71$, $P < 0.01$) and no differences were found in *R. japonica* ($F_{1,108} = 3.70$, NS).

Assuming that different habitat types may play different parts in various periods of the invasion process, the lag and exponential phases of spread were analysed separately for assessing habitat preferences in the species studied (Fig. 2). During the lag phase, the species differed significantly with respect to their habitat preferences (chi-square, $P < 0.0001$,

TABLE 3. Summary of invasion rates of the species studied.

	Whole period of invasion		Exponential phase		
	T	R	T	R	O
Impatiens glandulifera	$0.070 \pm 0.0024a$	$0.064 \pm 0.0027a$	$0.070 \pm 0.0037a$	$0.074 \pm 0.0040a$	$0.066 \pm 0.0037a$
Heracleum mantegazzianum	$0.045 \pm 0.0035b*$	$0.042 \pm 0.0056bc$	$0.107 \pm 0.0032b$	$0.096 \pm 0.0062b$	$0.110 \pm 0.0038b$
Reynoutria japonica	$0.059 \pm 0.0026c*$	$0.050 \pm 0.0015c$	$0.040 \pm 0.0016c$	$0.043 \pm 0.0013c$	$0.040 \pm 0.0017c$
R. sachalinensis	$0.047 \pm 0.0014b$	$0.058 \pm 0.0028ab$	$0.043 \pm 0.0034c$	$0.053 \pm 0.0033d$	$0.043 \pm 0.0024c$

Invasion rate was expressed as a value of slope b from the regression equation CUMULATIVE NUMBER OF LOCALITIES = exp $(a + b \times \text{YEAR})$. Slopes with their confidence intervals are given separately for all habitats (T), riparian (R) and other than riparian (O). Slopes that were not significantly different in F-test (according to Snedecor & Cochran, 1967) are bearing the same letter columnwise. See Methods for estimation of the beginning of the exponential phase.
$*P < 0.025$, otherwise $P < 0.01$.

Table 4). The closest relationship to riparian habitats was found for *I. glandulifera*; this species was also successful in settlement sites. Similarly, *R. japonica* also preferred these two habitat types. Both species appeared in riparian sites immediately following their introduction to the Czech Republic (Table 2). In *H. mantegazzianum*, the number of localities reported for the lag phase (Table 2) was too low to draw conclusions; however, of the first four records, two were from parks. *R. sachalinensis* established successfully in semi-natural vegetation (forests, meadows) and parks in which it has originally been planted. There was a long period between the first recorded appearance of *R. sachalinensis* in the Czech Republic and its first appearance in riparian habitats (Table 2).

The between-species differences in habitat preferences during the exponential phase of spread were also significant (chi-square, $P < 0.0001$, Table 4). The habitat preferences were similar in both *Reynoutria* species (Fig. 2). In this period, the proportion of riparian localities (Fig. 3) increased significantly in *I. glandulifera*, *R. sachalinensis* and *R. japonica* and decreased in *H. mantegazzianum* (Table 5).

When the habitat preferences between lag and exponential phases were compared for particular species, significant differences (chi-square, $P < 0.01$) were found in all but *R. japonica* (Table 4).

DISCUSSION

Although our results show that spreading along water courses played an important role in all the species investigated, at least in some period of their invasion, the behaviour of particular species with respect to riparian habitats is far from uniform (Table 5). *I. glandulifera* is an annual species producing large numbers of seeds which are effectively dispersed by stream and thus the water is, apart from man, the main dispersal factor. The seeds float for only a short period; however, they are transported along the bottom by stream and washed out and deposited on river banks during heavy floods (Lhotská & Kopecký, 1966). Moreover *I. glandulifera* is, among those species studied, the one confined ecologically most closely to wet habitats (Trewick & Wade; 1986, Grime, Hodgson & Hunt, 1988; Perrins, Fitter & Williamson, 1990). Consequently, it is less frequently leaving riverbanks, brook shores or ponds

and its spread into the landscape from these habitats was observed to be somewhat rare and/or temporary in the Czech Republic (Table 5). Generally, *I. glandulifera* is an example of the invasive species whose invasion abilities are, however, strongly limited to a certain habitat type (Pyšek and Prach, 1993a).

Water flow is also an important dispersal agent for vegetative fragments of both *Reynoutria* species (Conolly, 1977; Grime *et al.*, 1988; Wade, 1992) but the spread by man (at present mostly unintentional, see Sukopp & Sukopp, 1988) still prevails in the studied region. Both *Reynoutria* species probably only rarely set viable seeds (Jehlík & Lhotská, 1970; Bailey, 1988) and therefore spreading by rhizomes plays a decisive part in species invasion. In the Czech Republic, floodplains areas are often used for allotments and both *Reynoutria* species are still being used as garden ornamental plants. Consequently, their rhizomes are often deposited with other garden waste close to rivers. Various building activities associated with the transport of soil containing rhizomes (Grime *et al.*, 1988) serve as another important vector transporting vegetative fragments in the study region (personal observation). Whereas *R. japonica* appears to be an extremely successful invader, the invasion of *R. sachalinensis* might recently have begun (note the magnitude of occurrence compared to the other species, Fig. 1) and the species seems to be in the period of 'river affinity'.

The lower proportion of riparian localities in *H. mantegazzianum* is due to its ability to expand massively to other habitat types (Table 5), namely settlements, road verges and forests. This fact may be explained by its competitive success over native flora in the wide range of habitats (Pyšek, 1993). Furthermore, the factors responsible for its dispersal are more variable than in other species studied. As well as water and man, animals and wind play an important role in dispersion (Jehlík & Lhotská, 1970; Williamson & Forbes, 1982; Lundström, 1984; Wyse Jackson, 1989; Pyšek 1991). However, even this species was found to spread first down the courses of great rivers during its invasion (Neiland *et al.*, 1972; Pyšek, 1991) and there was a period during which the riparian habitats were supporting its spread considerably (Pyšek, 1993). In general, however, the relatively low preferences of *H. mantegazzianum* for riparian habitats and, in spite of
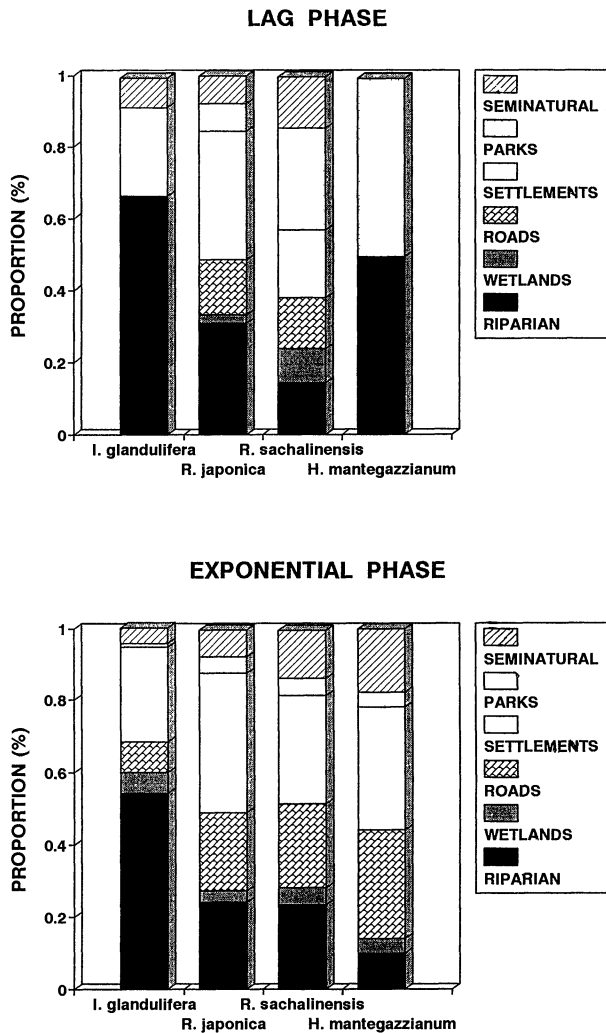
LAG PHASE

EXPONENTIAL PHASE

FIG. 2. Distribution of localities with respect to habitat types. Localities recorded during the lag phase are compared with the distribution of those recorded during the exponential phase (see Methods for details on estimation). Semi-natural habitats (excluding riparian and wetlands) include meadows, forest margins, and forests. Roads and railways were grouped together.
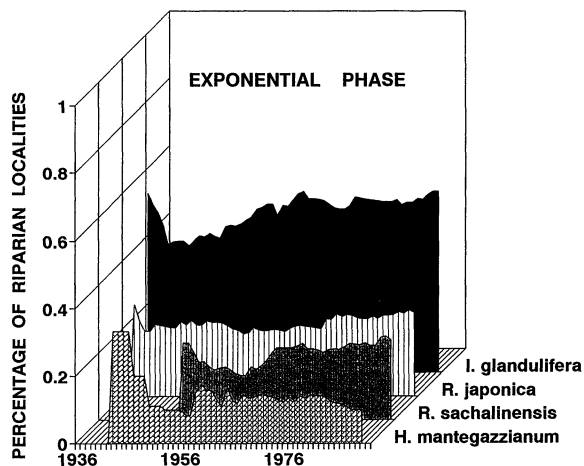

FIG. 3. Changes in the proportion of riparian localities during the exponential phase of spread (see Methods for details on estimation). See Table 5 for testing the trends over time.

that, its high rate of spread indicates that other suitable 'transport habitats' (roads, railways, see Fig. 2) may serve as alternative routes for species spread.

In all species spreading in riparian habitats, the downstream movement of diaspores is assumed as demonstrated previously for *I. glandulifera* (Pyšek & Prach, 1993a) and *H. mantegazzianum* (Pyšek, 1993). However, the upstream movement cannot be excluded because of other dispersal vectors acting in river corridors not as unidirectionally as the water flow (Schneider & Sharitz, 1988).

Association with riparian habitats during the process of plant invasion seems also to be related to the character of the landscape in a given region. For all the species covered by our study, closer relationships to riparian habitats have been reported for the United Kingdom than is the case in the Czech Republic (e.g. Wyse Jackson, 1989; Wade, 1992). This may be explained by the fact that in the Czech landscape there are a number of various abandoned, disturbed and ill-managed sites outside rivers. These sites can be more easily colonized by invasive aliens. In the United Kingdom such suitable sites are more confined to river corridors, as the rest of the country is intensively managed.

Kornas (1990) reported thirty-three alien species established in Poland in semi-natural vegetation, of which seventeen are confined to disturbed riverside habitats. This author distinguished four stages of the naturalization process and suggested that the invasion of an alien into less disturbed sites should have been preceded by its establishment in heavily disturbed, so-called ruderal sites. Considering our results, this statement seems to be overgeneralized; at least *H. mantegazzianum* and *R. sachalinensis* were invading, although at a lower frequency than in man-made sites, into semi-natural forests and meadows immediately after introduction. Both these species were planted in parks and competed successfully with grass sward and herbs present in these sites as well as in adjacent semi-natural vegetation. On the other hand, *I. glandulifera* was planted as an ornamental plant in flower beds, i.e. kept from competition from spontaneous vegetation. This is reflected in the relatively high proportion of localities in settlement habitats where this species was present during the early period of invasion (40.3% in 1945) due to frequent escapes from cultivation; many of the earliest records refer to its occurrence as a garden weed. Correspondingly, during its invasion *I. glandulifera* was more confined to disturbed habitats, including river banks, and this is still true.

Considering the relationship between the life form of an invader and its invasion success, the present study indicates that the shorter the life span, the higher the rate of invasion. Both non-perennials included in the study, *I. glandulifera* and *H. mantegazzianum*, began to spread exponentially after having reached only a few localities in the area (although in the case of the latter species it was preceded by the long-lasting lag phase) subsequently, their invasion continued at a higher rate than in the case of both perennials. Taking into account the characteristics generally suggested to encourage any species invasion (Baker, 1965; Newsome & Noble, 1986; Roy, 1990; Prach & Wade, 1992), some kind of trade-off between these traits may be

TABLE 4. Differences in habitat preferences between species and for each species between both phases of the invasion process (see Methods for distinguishing lag and exponential phases).

	Chi-square value	d.f.	*P*
Lag phase	205.78	15	< 0.0001
Exponential phase	68.75	15	< 0.0001
Lag *v.* exponential phase			
Impatiens glandulifera	17.80	5	0.0031
Heracleum mantegazzianum	151.82	5	< 0.0001
Reynoutria japonica	3.03	5	0.6950
R. sachalinensis	25.48	5	< 0.0001

Chi-square values are given.

TABLE 5. Behaviour of the invasive species studied assessed with respect to riparian habitats.

	Affinity to riparian habitats during the phase		Expansion out of riparian habitats	%
	Lag	Exponential		
I. glandulifera	High	High, increasing (0.68***)	Occasional	0.47
H. mantegazzianum	Moderate	Low, decreasing (− 0.30***)	Massive	0.90
R. japonica	Moderate	Moderate, increasing (0.53*)	Frequent	0.75
R. sachalinensis	Low	Moderate, increasing (0.65***)	Frequent	0.71

Changes in the percentage contribution of riparian localities to the total number of localities during the exponential phase were tested using Kendall correlation coefficient (values and significance levels are given in the parentheses, *P < 0.05, ***P < 0.001). Expansion from riparian habitats was assessed on the basis of the percentage of non-riparian localities reported up to the present, which is given in the last column.

suggested. Annual species profit from a large seed set and a rapid life cycle which is advantageous from the viewpoint of adaptations to changing environments (Grime, 1979 and others). On the other hand, long-lived species, especially the clonal ones as is the case with both *Reynoutria* species, profit from their ability to keep space once occupied, and spread consistently within the close vicinity (Callaghan *et al.*, 1992; Prach & Pyšek, 1993). The clonal life form is associated with high regeneration ability which may be considered another factor supporting species spread and dominance in a site. Regardless of the life form, the invasion success appears to be associated with high competitive ability (Noble, 1989; Roy, 1990) which is suggested to increase with plant height (Grime, 1979; Keddy, 1990). However, further research covering larger sets of species is required to test the relationship between a species' morphological and life-history traits and its invasion success. In addition, various specific species traits may be involved in determining the species' ability to spread. Different magnitudes of invasion found in *Reynoutria* species, whose life form, growth ability mode of dispersal and habitat preferences are very similar, may be explained by different density of rhizome systems in the soil (Sukopp & Schick, 1993). Another explanation for such difference may be that in the past, *R. japonica* was planted in Czech territory with a higher frequency than *R. sachalinensis* (V. Jehlík, personal communication).

Three methodological approaches may be distinguished in studies on plant invasions: (a) studies at the population level focused upon plant attributes determining invasion success, including manipulative experiments (Noble, 1989; Roy, 1990); (b) descriptive small-scale systematic studies of the invasion process (Williams, Hobbs & Hamburg, 1987; Thébaud & Debussche, 1991); and (c) landscape-viewed studies of invasions at large-scale level, up to continents, based upon decades-lasting continuous records or upon historical reconstruction from floristic or palaeological records (Woods & Davis, 1989; Trepl, 1984; Kornas, 1990; Pyšek, 1991); the former are unfortunately less frequent so far (Perring & Walters, 1962; Clegg & Grace, 1974; Williamson & Forbes, 1992; Haeupler & Schönfelder, 1988; Schönfelder & Bresinsky, 1992; Hartl *et al.*, 1992). Unfortunately, the studies at the landscape scale providing an insight into the history of species invasion on the time scale of centuries must be necessarily descriptive; an experimental approach is simply not applicable to such studies. When interpreting the results based on data sets such as those in the present study, one must be aware of the fact that some of them have only exploratory value and, consequently, some of the conclusions are necessarily speculative. However, the approach applied in the present paper may be considered useful for stating hypotheses on the species' ecological behaviour to be tested experimentally.

CONCLUSIONS

The following conclusions may be drawn to answer the questions put in the introduction.

(1) The rate of invasion differed in the species studied;

it was highest in *I. glandulifera*, followed by *R. japonica*, *H. mantegazzianum*, and *R. sachalinensis*. The exponential phase began between the 1930s and 1950s in all species studied having been preceded by a lag phase of different duration. *H. mantegazzianum* and *I. glandulifera* began to increase exponentially after having reached only a small number of localities; subsequently their spread was faster than that of both *Reynoutria* species, which proceeded at a more even rate.

(2) Habitat preferences differed between the species investigated in both phases of the invasion process. The spread in riparian habitats was fastest in *I. glandulifera*, followed by *R. sachalinensis*, *R. japonica* and *H. mantegazzianum*. Riparian habitats played an important role in the invasion process of all species studied, at least in a certain period. The species dispersibility and frequency of habitats suitable for species establishment must be taken into account when evaluating such a role. Frequency of habitats available is closely related to land-use practices.

ACKNOWLEDGMENTS

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