3 How Important are Rivers for Supporting Plant Invasions?

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INTRODUCTION

Invasion success of a plant species introduced to the region in which it did not previously occur depends on its dispersal. Habitats in central European landscapes differ in encouraging the movement of diaspores. Linear habitats usually contribute to easier spread of species through the landscape. With respect to the main dispersal agent, they may be divided into (a) terrestrial "transport habitats", including road verges and ditches as well as railway embankments and stations; and (b) water "transport habitats", including river and stream banks. Human activity is the main dispersal factor in the former group. In the latter, water acts as the main dispersal agent supporting downstream movement of diaspores (Skoglund, 1989; Thébaud and Debussche, 1991). In addition, seedling establishment and survival are made easier in these sites by periodic disturbances from flooding, which creates openings in vegetation cover (Ellenberg, 1988; Walker *et al.*, 1986). The present paper analyses historical dynamics of four species alien to central Europe during their invasions in the Czech Republic. Special attention was paid to their performance in riparian habitats and to the role of this habitat type in supporting their invasion.

SPECIES SELECTION AND CHARACTERISTICS

The species selected for this study are those included in the *Control and Management of Invasive Riparian Weeds* project, launched by the International Centre of Landscape Ecology, Loughborough University, UK: *Impatiens glandulifera, Heracleum mantegazzianum* and *Reynoutria japonica.* In

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addition, another knotweed species, *Reynoutria sachalinensis*, showing similar biological attributes to *R. japonica*, but not so expansive so far in the study area, was added for comparison. All of them are troublesome weeds in riparian habitats. In central Europe, as well as in Great Britain, each species is the highest representative of its life form: *I. glandulifera* among annuals (maximum height 2.5 m), *H. mantegazzianum* among monocarpic perennials (4–5 m), and both *Reynoutria* species among polycarpic perennials (>2 m).

Impatiens glandulifera Royle is native to the Himalayas. It reproduces only by seeds and possesses an explosive seed capsule (Grime *et al.*, 1988; Perrins *et al.*, 1990).

Heracleum mantegazzianum, native to the western Caucasus, reproduces by seeds and regenerates from tuberous roots. Among the species studied, it is the one that may cause the most serious problems. Not only replacement of native vegetation but also injuries to human skin caused by phototoxic substances are the main reasons for efforts to eradicate the species from infested areas (Lundström, 1984; Pyšek, 1991).

Reynoutria japonica and *R. sachalinensis* have areas of origin in the Far East. The species are capable of effective vegetative regeneration, spreading by rhizomes, which is probably the only method of regeneration in the study region (however, see Bailey, 1994).

All species studied were introduced into the Czech Republic in the nineteenth century; the first reports are 1862 for *H. mantegazzianum* (but see Pyšek, 1991), 1869 for *R. sachalinensis*, 1892 for *R. japonica* and 1896 for *I. glandulifera*. They were originally planted as ornamentals in gardens and parks. They are capable of forming large monospecific stands spontaneously and hence, besides other serious problems, replace native vegetation and reduce species diversity.

METHODS

Historical reconstructions of the dynamics of spread were based on (i) published floristic records, (ii) unpublished floristic data obtained by personal communication and (iii) herbarium specimens (Charles University Prague, National Museum Prague). Information on the year of observation and habitat type, if available, was summarized for each record. If the year of observation was not provided by the original author, the year of publication was used instead, as both dates are closely related (Pyšek, 1991). The method of retrospective evaluation of plant species spread adopted in this paper has been discussed in detail by Pyšek (1991).

RESULTS AND DISCUSSION

TYPE OF INVASION AND THE ROLE OF RIPARIAN HABITATS

An increase in the cumulative number of localities (i.e. in the number of localities reported up to the respective year) follows an exponential curve in each species studied (Figure 3.1a). The increase was very fast in *I. glandulifera* and *H. mantegazzianum* and more gradual in *R. japonica*. In *R. sachalinensis* the number of localities increased only slightly during the twentieth century. Total numbers of localities currently known are given in Table 3.1.

If riparian habitats are considered separately (Figure 3.1b), the number of localities in 1991 was highest for *I. glandulifera* (340), followed by *R. japonica* (104), *H. mantegazzianum* (41) and *R. sachalinensis* (30). The contribution of riparian localities to the total number of localities was 51.1% in *I. glandulifera*, 27.5% in *R. sachalinensis* and 27.2% in *R. japonica*. *H. mantegazzianum* was the species with the lowest affinity to riparian habitats (only 10%). However, the detailed analysis of the invasion process revealed that even in this species there was a period when the species spread was considerably supported by rivers (Pyšek, 1994). Table 3.1 provides complete information on habitat preferences.

Invasion success of a species is determined by (i) its biological attributes related to the dispersal capabilities and ability to compete with the native flora; physiological attributes of successful invaders may be related to high biomass production, as this increases competitive ability as well as the number of offspring; and (ii) the characteristics of recipient habitats (Newsome and Noble, 1986).

In our data set, an increase in the number of localities (Figure 3.1a) may be considered as a measure of the former attributes, i.e. the ability to expand. Concentration of occurrence into one or more habitat types is, on the other hand, assumed to reflect ecological specialization of the species. Such a species may be expected to be restricted in its invasion by habitat types available. Correspondingly, a species occurring frequently in a wide range of habitat types is considered as less limited, if at all, in its invasion by the characteristics of the recipient habitat. The species included in this study may be classified with respect to the above mentioned criteria (Table 3.2).

Example 1: Strong invader restricted by the recipient habitat (*Impatiens glandulifera*)

This species rapidly invaded riparian habitats in the study region, which was made possible by the large number of seeds produced and easy dispersal by water, which is the main dispersal factor (Table 3.2; Lhotská and Kopecký, 1966). *I. glandulifera* is closely confined to wet and moist habitats. Its occur-

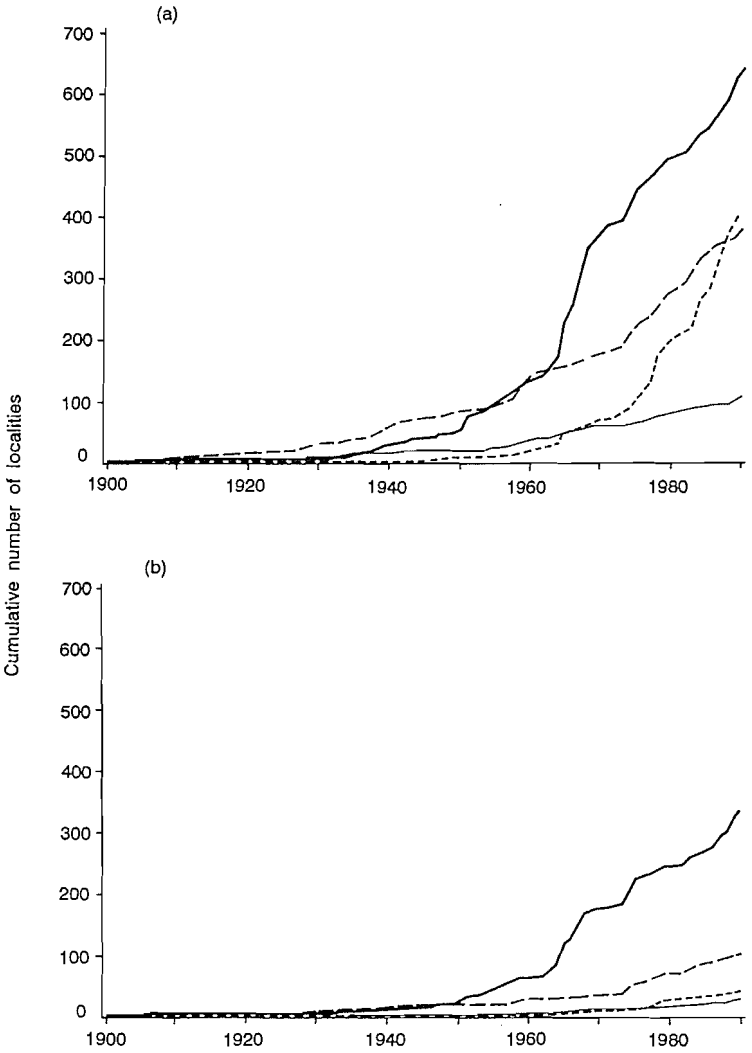

Figure 3.1 Increase in the (a) total cumulative number of localities and (b) cumulative number of localities reported from riparian habitats in the Czech Republic during the twentieth century, for *Impatiens glandulifera* (——), *Heracleum mantegazzianum* (- - -), *Reynoutria sachalinensis* (——) and *R. japonica* (– – –)

rence out of riverine habitats is rather rare in the Czech Republic. A high proportion of settlement localities, especially in the early years of invasion, is partly due to its escape from cultivation and occurrence as a garden weed. Moreover, in settlements and along roads it also prefers moist and wet sites.

Table 3.1. Contribution (%) of particular habitat types to the total number of localities known for the studied species in the Czech Republic in 1991

	Impatiens glandulifera	*Heracleum mantegazzianum*	*Reynoutria japonica*	*R. sachalinensis*
Rivers	51.1	10.0	27.2	27.5
Pond shores	5.5	4.2	3.2	2.8
Roads and railways	8.7	27.7	16.9	28.4
Settlements	27.3	36.5	40.8	28.4
Parks	0.7	5.0	5.9	11.0
Forests and meadows	5.8	15.6	5.9	11.0
Total no. of localities	665	411	382	109

Table 3.2. Species life-form and dispersal strategy of four plant species in relation to invasion status

Species	Life form	Spread	Dispersal agents* Human or animal	Water	Wind	Invasion status	Habitat limited
Impatiens glandulifera	Annual	Seeds	1	2	0	Strong	Yes
Heracleum mantegazzianum	Perennial	Seeds	2	1	1	Strong	No
Reynoutria japonica	Perennial	Vegetative	2	1	0	Weak	No
R. sachalinensis	Perennial	Vegetative	2	1	0	Weak	No

* Assessed according to 0 no importance, 1 important and 2 principal. The classification is based on authors' personal experience and holds for central Europe.

I. glandulifera is an invasive specis whose characteristics allow it to establish only under a narrow range of habitat conditions. It corresponds to type 2 of an invader according to Newsome and Noble (1986).

Examples of invaders limited only to a certain habitat have been reported from central Europe. The majority of permanently established aliens are limited to ruderal sites (Kornaś, 1990; Świeboda, 1963; van Soest, 1941). However, time plays an important role in our view of the species' habitat preferences: *Impatiens parviflora*, an early nineteenth century newcomer from the East, was limited to ruderal sites for many years and after several decades it massively invaded forests (Trepl, 1984).

Example 2: Strong invader less limited by recipient habitat (*Heracleum mantegazzianum, Reynoutria japonica*)

H. mantegazzianum invaded various habitat types at a similar rate (Pyšek, 1994). Some preference for settlements was found and, moreover, of all species studied this was the most successful in semi-natural vegetation, i.e. forests and meadows (Table 3.1). Water as a dispersal agent seems to be less important for its spread than wind and, especially, the direct transport of diaspores by man (Table 3.2); the plant is still popular as a garden ornamental and for dried flower arrangements (Lundström, 1984). *H. mantegazzianum* is an example of a species that invaded semi-natural habitats soon after its introduction without being preceded by the stage of establishment in disturbed sites, usually considered as a necessary stage in the naturalization process (Kornas, 1990).

In case of *R. japonica*, water is an important means of dispersal of the vegetative fragments, but the spread by man still prevails in the study region. Both dispersal agents often act simultaneously.

Both *H. mantegazzianum* and *R. japonica* are invading species having distinct competetive superiority over ecologically similar native species, which has allowed them to become a permanent part of the local flora (type 1 of an invader according to Newsome and Noble, 1986).

Example 3: Weak invader (*Reynoutria sachalinensis*)

Despite life history characteristics and time of introduction being similar to *R. japonica*, this species remains less successful as an invader. Vegetative fragments are spread by water and the affinity of the species to riparian habitats has increased in the last several decades. So far it has entered various habitats (including semi-natural ones, i.e. forests and meadows), and may, therefore, be considered as less habitat restricted. It might be that its invasion has just started. However, there are some indications that, in the past, *R. sachalinensis* was planted less frequently than *R. japonica*, which might have contributed to the differences in their present abundance in the Czech landscape.

EFFECT OF LANDSCAPE CHARACTER ON HABITAT PREFERENCES

If our results are compared with reports on the same species from Great Britain (Gunn, 1986; Neiland *et al.*, 1987; Trewick and Wade, 1986), *R. japonica* and *H. mantegazzianum* are obviously more closely related to riparian habitats in Britain. Availability of recipient habitats is presumably partly responsible for this difference: in the Czech Republic, numerous dis-

turbed and ill-managed sites provide openings in the spontaneous vegetatio cover and these may be used by invaders for penetrating into communities c native species. Hence the proportion of localities situated in the open lanc scape is higher. In Great Britain, on the other hand, the landscape is mor intensively managed and sites suitable for establishment of the species ar rather rare. Suitable sites are therefore more confined to riparian areas.

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