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Research into plant invasions in a crossroads region: history and focus

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Abstract

The Czech Republic is a central European country whose geographical location, natural conditions, history of human settlement, and present land-use management make it relatively prone to plant invasions, hence it represents a convenient model for their study. Research in plant invasions, which date to the late 19th century, is reviewed in the present paper. A long-term floristic tradition allowed for the accumulation of a large body of floristic data on alien plants. During the 1960s–1970s, the main research focus was on their distribution. In this period, attempts were also made to predict potential invasiveness of weeds of arable land. The success rate of this prediction was about 39%. Considerable effort was put into a detailed classification of human-accompanying plants and the terminology associated with the issue. There is a high level of taxonomic research conducted in the country, and the new Flora of the Czech Republic treats the immigration status of taxa with reasonable care and detail. A complete, serious catalogue of the alien plants of the country has been published recently: there are currently 1378 alien plants (33.4% of the total flora). The core of present research in plant invasions is in ecological, biological, and biogeographical studies, focussed on (i) the history of invasion of particular species since their introduction, (ii) the role and importance of alien species in vegetation, including their participation in succession, and (iii) the major invasive species of the Czech flora and comparison of congeners. *Reynoutria* spp., *Heracleum mantegazzianum*, *Oenothera* spp., *Pinus strobus,* and *Bidens frondosa* are among the taxa most intensively studied in recent time. A complete list of 69 invasive plants in the Czech flora introduced after the year 1500 [following the definition of Richardson et al. (2000a) Diversity and Distributions 6: 93–107] is given. The available legal instruments relevant to the issue are reviewed.

Introduction

Invasions by introduced plants constitute one of the most serious threats to biodiversity, and invaders can profoundly alter ecosystem structure and function (Vitousek et al. 1987; Zavaleta 2000). The field has attracted considerable attention after becoming the topic of the SCOPE programme in the 1980s (Drake et al. 1989) and its importance has been increasing since then (Pyšek 1995a; Richardson et al. 2000a; McNeeley et al. 2001). Various efforts to generalize the information available on invasive species have been made, mostly concerned with analysing their biological and ecological properties (Williamson 1996; Crawley et al. 1996). At present, it appears that generalizations and predictions are possible at the level of particular taxonomical groups or life forms (Rejmánek and Richardson 1996). Rejmánek (1996) has achieved success with a promising theory linking together biological and ecological properties and role of dispersal vectors, and predicts that species with a low amount of DNA might have an increased invasion potential within

a given taxonomic group (see also Grotkopp et al. 2002).

Alien species exhibit specific spreading dynamics (Pyšek and Prach 1993; Kowarik 1995) for various reasons: they may escape from natural enemies, are able to occupy vacant niches and by not having a common past with native flora, they may not be regulated by the same abiotic factors (Keane and Crawley 2002). The differential success of introduced species as invaders provides a useful natural experiment for deriving empirical evidence on the factors that determine whether an introduced species will invade or not. Similarly, the differential success of particular species in different areas provides us with the potential to recognize the factors that determine why it has succeeded in invading some regions and failed elsewhere (Tucker and Richardson 1995).

At the community level, there is a consensus on the importance of the recipient vegetation for the outcome of invasions (Rejmánek 1989). Considerable attention has been devoted to the question of whether some communities are more invasible than others (Williamson 1996) and, consequently, whether some regions are more susceptible to invasions than others (Lonsdale 1999). Fluctuation in available resources was proposed as a crucial mechanism explaining invasibility of ecosystems (Davis et al. 2000; Davis and Pelsor 2001). There is now evidence that an alteration of the disturbance regime may be the most profound effect that an invading species can have on ecosystem structure and function (Mack and D'Antonio 1998). The potential effect of global warming on the dynamics of invasions is also recognized (Mooney and Hobbs 2000; Richardson et al. 2000b).

Although invasions are a global problem extending over political boundaries, their extent and impact vary considerably among different parts of the globe (Pyšek 1995a). The approach of particular countries may differ in the awareness of the problem by local authorities, in research intensity and the problems studied, and in the legislative tools available. The present paper deals with the situation in the Czech Republic.[1] It is aimed at summarizing the history of research in plant invasions in the country, reviewing the current focus and topics studied, and suggesting future research topics. Moreover, the country's geographical location, history, and intensity of present human impact on the landscape as well as tradition of botanical research makes it a convenient model on which it can be demonstrated how different approaches can be used to tackle the problem of plant invasions. In any region suffering from the impact of plant invasions, an integrated research built on the interplay of natural history, plant taxonomy, and modern ecological approaches is needed to provide a more fundamental look at invasion theory.

Geographical and historical context

The Czech Republic, a central European country with an area of 78,864 km^2 and 10.3 million inhabitants, has some specific features related to invasions by alien plants. Due to its geographical location in the very centre of the continent, the country was a crossroad between West and East, and South and North of Europe since early times, and intensive movement of people and goods have contributed to the introduction of many species. The country is considered one of the important gates for introducing species of eastern origin farther to the northwest of Europe. This route has been probably effective as early as the Neolithic period, and many archeophytes were introduced during the Bronze Age (2000–1000 B.C) (Opravil 1980). More recently, many species of Asian and east-European origin entered the central part of the continent *via* one of the largest railway stations on the east–west oriented railway system, i.e. Čierna při Čope in the Slovak part of former Czechoslovakia (Jehlík and Hejný 1974; Jehlík 1998). Besides railways and roads, river traffic on the Elbe River, the Donau River and their tributaries significantly contributed to the richness of present alien flora (Jehlík 1998).

Once introduced, an alien species has a relatively high chance of establishing for the following reasons: The country is rather diverse in terms of physiogeographical features, primarily due to diverse geology and geomorphology, resulting into a fine-scale mosaic of diverse habitats. There is a rather dense human population (131 inhabitants/km^2) and high settlement density, resulting in a rather dense network of roads (0.71 km/km^2) and railways (0.11 km/km^2), which contributes to the invasibility of the territory. The intensively used landscape is rather fragmented due to the long-term effect of human activities and large undisturbed areas of landscape are virtually missing.

The country has relatively well developed industry (from the late 18th to the middle of the 20th century it was one of the most industrialized parts of Europe) and a long-term gardening tradition going back to the 19th century, which was responsible for the introduction of many ornamental plants; some of them are

present day invaders. A similar role was played by intensive forestry, converting the original broad-leaf woodlands into conifer plantations and using some species of alien origin. The process of tree planting can serve as an important vector for spreading alien species (Prach et al. 1995).

Later on, the invasibility of the territory was increased by large-scale changes in land use imposed during the time of the communist economy (1948–1989). Many sites were abandoned, especially in settlements and industrial zones as well as in extensive border areas and military zones, resulting in relatively large proportion of ill-managed wasteland. Many formerly managed meadows and pastures were either abandoned or over-exploited. Arable land was heavily fertilized which leads to a highly eutrophicated landscape. Various building activities and the transport of materials supported the spread of invasive aliens. The present landscape is therefore relatively fragmented and prone to invasions (see Pyšek et al. 1998b for a classification of particular habitats and their relationship to invasions). Built-up areas are disproportionally prone to invasions, covering 10.4% of the country but contributing 53.6% to the number of localities of alien species; the corresponding figure for riparian habitats, another disproportionally invaded type, being 2.0% and 22.4%, respectively (Pyšek et al. 1998b).

There are 1378 alien species reported from the country; of these 332 are archaeophytes and 1046 neophytes (Pyšek et al. 2002b, 2003c). There are 891 casual and 397 naturalized species (in the sense of Richardson et al. 2000a). The total number of invasive species is 90 of which 21 are archaeophytes and 69 neophytes (Table 1). Analysis of the temporal patterns of immigration to the country showed that neophytes of European origin and exhibiting CSR strategy arrived earlier than those of other origins and strategies. Deliberately introduced neophytes appeared earlier than accidental arrivals, and those cultivated for utilitary reasons on average arrived earlier than ornamentals. Species capable of early flowering were remarkably more represented among early newcomers (Pyšek et al. 2003b)

Although nature reserves represent an effective barrier against invasion by alien species (Pyšek et al. 2003d), protected areas included within the system of nature conservation are also endangered by alien species (Pyšek et al. 2002a) because the reserves are mostly small-scale, adjacent to disturbed landscape

Table 1. Invasive plants of the Czech Republic.

Species	Family	1st record	Habitat	Introduction	Origin	Life form
Acer negundo	Acerac	1835*, 1875	hn	del	America N	t
Amaranthus powellii	Amaran	1853	h	ac	America	a
Amaranthus retroflexus	Amaran	1818	h	ac	America S	a
Rhus hirta	Anacard	1835*, 1900	hn	del	America N	s
Angelica archangelica	Apiac	1517	hn	del	Europe N	pm
Heracleum mantegazzianum	Apiac	1862	hn	del	Caucasus	pm
Imperatoria ostruthium	Apiac	1809	hn	del	Europe SW	pp
Myrrhis odorata	Apiac	1819	hn	del	Europe SW	pp
Ambrosia artemisiifolia	Asterac	1883	h	ac	America N	a
Aster × *salignus*	Asterac	1872	hn	del	hybrid	pp
Aster lanceolatus	Asterac		hn	del	America N	pp
Aster novi-belgii	Asterac	1850	hn	del	America N	pp
Aster versicolor	Asterac		hn	del	hybrid	pp
Bidens frondosa	Asterac	1894	hn	ac	America N	a
Conyza canadensis	Asterac	1750	h	ac	America N	a
Echinops sphaerocephalus	Asterac	1871	h	ac	Europe S, SE	pm
Erigeron annuus subsp. *septentrionalis*	Asterac		h	ac	America N	a
Galinsoga ciliata	Asterac	1901	h	ac	America S	a
Galinsoga parviflora	Asterac	1867	h	ac	America S, C	a
Helianthus tuberosus	Asterac	1885	hn	del	America N	pp
Matricaria discoidea	Asterac	1851	h	ac	Asia	a
Rudbeckia laciniata	Asterac	1859	hn	del	America N	pp
Solidago canadensis	Asterac	1838	hn	del	America N	pp
Solidago gigantea	Asterac	1851	hn	del	America N	pp
Telekia speciosa	Asterac		hn	del	Europe E	pp

Table 1. Continued

Species	Family	1st record	Habitat	Introduction	Origin	Life form
Impatiens glandulifera	Balsamin	1896	hn	del	Asia: Himalayas	a
Impatiens parviflora	Balsamin	1870	hn	ac	Asia	a
Mahonia aquifolium	Berber	1844*	hn	del	America N	s
Bunias orientalis	Brassic	1856	h	ac	Europe E, SE	b, pm
Sisymbrium loeselii	Brassic	1819	h	ac	Europe SE, Africa N, Asia	a
Cannabis ruderalis	Cannab	1868	h	ac	Asia M, Caucasus	a
Symphoricarpos albus	Caprifol		hn	del	America N	s
Kochia scoparia subsp. *scoparia*	Chen	1819	h	ac	Europe SE, Asia	a
Cuscuta campestris	Convol	1883	h	ac	America N	a, cl
Sedum hispanicum	Crass		h	ac	Europe S, Asia	pp
Echinocystis lobata	Cucurbit	1911	hn	del	America N	a
Virga strigosa	Dipsac	1864	h	del	Asia	b
Amorpha fruticosa	Fabac	1865*, 1932	h	del	America N	s
Cytisus scoparius subsp. *scoparius*	Fabac	1819	hn	del	Europe W	s
Lupinus polyphyllus	Fabac	1895	hn	del	America N	pp
Robinia pseudacacia	Fabac	1710*, 1874	hn	del	America N	t
Quercus rubra	Fagac	1799*	n	del	America N	t
Geranium pyrenaicum	Geran	1819	h	del	Europe med, Caucasus	b, pm
Elodea canadensis	Hydroch	1879	hn	ac	America N	pp
Juncus tenuis	Juncac	1851	hn	ac	America N	pp
Galeobdolon argentatum	Lam		hn	del	hybrid	pp
Fraxinus pennsylvanica	Oleac	1834*	hn	del	America N	t
Syringa vulgaris	Oleac	1809	hn	del	Europe SE	s, t
Epilobium ciliatum	Onagr	1926	hn	ac	America N	pp
Oenothera biennis	Onagr	1831	h	ac	America N	b
Pinus strobus	Pinac	1800	n	del	America N	t
Arrhenatherum elatius	Poac		hn	ac	Europe	pp
Persicaria polystachya	Polyg		hn	del	Asia: Himalayas	pp
Reynoutria × *bohemica*	Polyg	1942	hn	del	hybrid	pp
Reynoutria japonica	Polyg	1892	hn	del	Asia E	pp
Reynoutria sachalinensis	Polyg	1869	hn	del	Asia E	pp
Rumex alpinus	Polyg	1819	hn	del	Europe S,C, Caucasus	pp
Rumex longifolius	Polyg	1961	hn	ac	Europe SW	pp
Rumex thyrsiflorus	Polyg		h	ac	Europe E	pp
Physocarpus opulifolius	Rosac	1874	hn	del	America N	s
Prunus serotina	Rosac	1811	hn	del	America N	t, s
Populus × *canadensis*	Salic		h	ac, del	America N	t
Digitalis purpurea	Scroph	1790	hn	del	Europe W, SW	b, pm
Mimulus guttatus	Scroph	1853	hn	del	America N	pp
Veronica filiformis	Scroph	1938	hn	del	Asia M, Caucasus	pp
Veronica persica	Scroph	1809	hn	ac	Asia C	a
Ailanthus altissima	Simar	1865*, 1874	hn	del	Asia: China	t
Lycium barbarum	Solan	1870	hn	del	Asia: China	s
Parthenocissus inserta	Vitac	1900	hn	del	America N	pp, cl

Species fitting the definition of Richardson et al. (2000a) are included, i.e. naturalized plants that produce reproductive offspring, often in very large numbers, at considerable distances from parent plants (approximate scales: >100 m; <50 years for taxa spreading by seeds and other propagules; >6 m/3 yrs for taxa spreading by roots, rhizomes, stolons, or creeping stems). Included also are taxa which spread previously, but do not spread currently because the total range of suitable habitats and landscapes has been occupied. Only neophytes (species supposed to be introduced after 1500) are listed. Species are also included which went through the phase of invasion in the past and then retreated (i.e. *Elodea canadensis*). The archaeophytes which also fit the definition of invasive species (e.g. *Atriplex sagitatta*, *A. oblongifolia*, *Ballota nigra* subsp. *nigra*, *Apera spica-venti*, *Cymbalaria muralis*, *Echinochloa crus-galli*, *Orobanche minor*, *Viola odorata*) were omitted (see Pyšek et al. 2002b for their list). Family names are abbreviated. Date of the first record in the wild from the country is given where known; if marked by asterisk, it refers to the date of introduction to cultivation. Habitas invaded: h = human-made, n = (semi) natural. Type of introduction: ac = accidental, del = deliberate (the species has been planted). Origin: S = south, N = north, E = east, W = west, C = central, med = mediterranean, M = minor, (?) = uncertain. Life form: a = annual, b = biennial, pm = monocarpic perennial, pp = polycarpic perennial, cl = climber, s = shrub, t = tree. Species are arranged alphabetically by families. Nomenclature follows Kubát et al. (2002).

and therefore easily reached by the diapores of alien species. At present, there are intensive efforts to use these areas commercially, which brings about disturbances, and increases the number of visitors and traffic intensity. Since there is a positive relationship between the number of visitors and reserve invasibility (Macdonald et al. 1988; Lonsdale 1999), these trends represent a serious danger to the biodiversity of the country (Pyšek et al. 2003d).

Research history

Floristic tradition

The alien status of some plants present in the Czech flora was recognized and commented on in the first complete catalogue (Čelakovský 1867–1881). More detailed interest in this group of plants dates to the early 20th century when botanists started to recognize human-made and disturbed habitats as source of additions to the native flora (Laus 1908, 1936; Domin 1917–1919; Rohlena 1922–1931 cited by Hejný et al. 1973). Alien plants started to be systematically recorded during 1940s and 1950s in many countries of central and western Europe (Wittig 1991). In the Czech Republic, the field was put on a more solid footing by the founding a specialized research section devoted to alien plants in the Institute of Botany, Průhonice, in the 1960s. Systematic research has been focussed on specific habitats (ports, railways, oilseed or wool processing factories, grain silos, mills, rubbish tips, arable land, etc.). Interest in the taxonomy and distribution of alien plants, as well as their ecology and impact, was triggered during this period and remains quite remarkable since then (see Hejný et al. 1973; Pyšek 1995c; Jehlík 1986, 1998 for references). In addition to this research, valuable floristic information about species immigration status can be derived by a careful analysis of old floral works, some of which date to 1600 (Hendrych 2001).

Classification and terminology associated with alien plants

More than a century of effort by European botanists to classify human-accompanying plants has yielded a number of classification systems (De Candolle 1855; Ascherson 1883; Thellung 1922; Schroeder 1969) mostly based on the time of immigration of a species into the region, the means of its introduction by humans (intentionally or unintentionally), and the degree of its naturalization. The Czech contribution to this field is represented by a classification system proposed by Holub and Jirásek (1967), one of the most carefully elaborated. Some of these systems are rather complicated and have led to the creation of an extensive jargon (Binggeli 1994; Richardson et al. 2000a). Their complexity, as well as the fact that they attempt to reflect circumstances specific to central Europe, is probably the main reason they became restricted to this region (Pyšek 1995b). Complicated classification schemes repeatedly produced by central-European botanists may be the consequence of a strong 'classificatory' tradition in this part of the world (Mayr 1982; Jahn 1998; see discussion in Richardson et al. 2000a). This concerns not only plant immigration status; complicated classification systems were used also for the purpose of describing the means of dispersal, each variant being given a special term (e.g. Hejný et al. 1973).

Vegetation and autecological studies

An interest in vegetation of human-made habitats, backed up by a strong phytosociological tradition, led to the publication of numerous studies in large cities, villages, and other disturbed habitats (see Pyšek 1995c for a review). The large number of phytosociological relevés accumulated make it possible to synthesize overviews of the ruderal vegetation of the Czech Republic (Hejný et al. 1979; Kopecký and Hejný 1992). In these studies, special attention was paid to communities dominated by alien plants. Using the so-called 'deductive method' of phytosociological classification (Kopecký and Hejný 1978) it was possible to classify most of the stands found in the field, including those built by newcoming alien species whose dynamics makes phytosociological treatment of their stands rather complicated (Pyšek 1991b).

At present, because of the shift from vegetation classification to ecological studies and experimental research of invasive plants, vegetation studies dealing with alien plants are less frequent (e.g. Kolbek et al. 1994). A significant proportion of the vegetation relevés containing alien taxa, both published and unpublished, has been loaded into the TURBOVEG database program (Hennekens 1995; Chytrý and Rafajová 2003).

Ecological studies from previous period were focussed mostly on dispersal (Slavík and Lhotská 1967; Lhotská 1968; Lhotská and Hejný 1979). Autecological work was largely descriptive but the

large body of accumulated information allowed for some generalization, e.g. the classification of several migration routes of alien plants into the country (Jehlík and Hejný 1974) or one of the earliest attempts to predict future potential invasiveness (Hejný et al. 1973). Interestingly enough, another paper published recently by the same research team (Jehlík 1998) using the same methodology made it possible to assess the success of these predictions after a quarter of a century. The predictions were successful for 39.3% of species included (Pyšek 2001).

Current research

Taxonomic knowledge

A previous flora of the Czech Republic (Dostál 1948–1950) consistently distinguished native species from aliens and listed the information on the immigration status, albeit with numerous imprecisions and errors. The recently published new flora, which is still in progress (Hejný and Slavík 1988–1992; Slavík 1995–2000), considers species origin as an important part of species accounts, although in some taxa, the origin is not explicitely given and, depending on the author of the account, the level of detail varies. The work for the flora yielded some modern comprehensive taxonomic elaboration of genera with a large amount of alien species, e.g. *Amaranthus* (Jehlík 1990), *Chenopodium* (Dostálek et al. 1990), *Oenothera* (Jehlík 1997), *Solanum* (Štěpánek and Tomšovic 2000), *Mentha* (Štěpánek 2000).

Despite the long-term floristic research and large body of taxonomic knowledge and distribution data accumulated, a complete list of alien species of the Czech flora has been published only recently. The first catalogue of alien species covers all alien taxa recorded at the territory level of the country, with information on their immigration status (using the scheme proposed by Richardson et al. 2000a), habitats occupied, abundance and character of the occurrence as well as numerous biological and ecological attributes (Pyšek et al. 2002b).

Ecological studies

Recent ecological research, conducted since the beginning of the 1990s, reflects both species- and habitat-centred approaches to plant invasions.

General aspects of plant invasions

These studies, focussed on both regional and global levels, were carried out in order to (i) describe various aspects of general patterns of plant invasions, (ii) identify invasive species and genera relevant to the territory of the Czech Republic, evaluate the role they play in the process of plant invasions and choose appropriate objects for further population-biological and comparative studies, and (iii) formulate hypotheses to be tested by other approaches.

General aspects of plant invasions were studied by analysing the alien flora of the Czech Republic. Various characteristics of invading species were compared to reveal which of them favour successful invasion. It was found that the sets of biological and ecological properties contributing to successful invasion into human-made habitats differed from those supporting invasion into relatively undisturbed vegetation (Pyšek et al. 1995b). The dynamics of alien species spread has been studied, based on more than 32,000 floristic records covering more than two centuries (Pyšek et al. 1998b). Representatives of different life forms were compared with respect to the rate of invasion. The lag and exponential phases of spread were distinguished and the timing of the beginning of invasion was estimated for some species. Habitat preferences differed between species in both the lag and exponential phases of spread and a different pattern of invasion dynamics with respect to the life form was indicated (Pyšek and Prach 1993, 1995). The Czech alien flora was used as one of the data sources in global studies examining the role of taxonomic position (Pyšek 1998c) and clonality (Pyšek 1997) in the invasion process.

Extent of invasions in particular habitats

The pattern of occurrence of alien species in urban habitats was analysed in 54 European cities, including 4 Czech cities (Pyšek 1998a) and 42 Czech villages (Pyšek 1998b). City size and temperature were the best predictors of representation of alien species while in the villages, the size and distance from the nearest middle sized town played the most important role (Pyšek 1998b). The role alien species play in extreme habitats represented by 96 rubbish dumps is driven by the interaction of dump age with toxicity of substrata and density of human population as a surrogate of propagule pressure (Pyšek et al. 2003a). The occurrence of aliens in relatively undisturbed vegetation was

studied by using floristic lists of 302 nature reserves in the Czech Republic (Pyšek et al. 2002a). In total, there were 153 species of archaeophytes (introduced before the year 1500) and 169 species of neophytes (introduced after that date), representing 7.1% and 7.8% of the total number of vascular species of the reserves, respectively. The proportion of aliens dramatically decreased with increasing altitude. Other factors showing significant effects on the infestation of a reserve by aliens were mean January temperature, climatic district, and vegetation type prevailing in the reserve (Pyšek et al. 2002a). The role alien species play in various successional seres of a different age in human-made habitats was assessed (Bastl et al. 1997), concluding that 10 years old successional stages were more sensitive to invasions than those exposed to succession immediately after the disturbance. Mihulka (1998) described the occurrence of alien species in a landscape section running from a medium sized city to a forested landscape at higher altitude. The frequency of aliens decreased with the distance from the city.

Biogeographical and comparative ecological case studies

These studies of major invading species (or genera with a high representation of invaders) of the Czech flora[2] include the history of invasion of major alien species (*Heracleum mantegazzianum* – Pyšek 1991a, 1994; Pyšek et al. 1998a; *Impatiens glandulifera* – Pyšek and Prach 1995; *Reynoutria* spp. – Pyšek and Prach 1993; *Rudbeckia laciniata* – Francírková 2001; *Oenothera* spp. – Mihulka and Pyšek 2001; *Atriplex sagittata* – Mandák and Pyšek 1998) in the Czech Republic. The course of invasion was reconstructed from floristic data, the rate of invasion was quantified and compared with neighbouring countries for some species (Pyšek and Prach 1995). Environmental factors affecting invasion of *H. mantegazzianum* were studied by using GIS methods (Pyšek et al. 1998a). Field studies were focussed on the habitat preferences of this species in heavily invaded areas (Pyšek and Pyšek 1995) and on its regeneration abilities (Pyšek et al. 1995a).

Studies on the biology and ecology of alien congeners are represented by a Polygonaceae genus *Reynoutria* (native to Asia) comprising two species (*R. japonica* and *R. sachalinensis*) and their hybrid (*Reynoutria* × *bohemica*). The resulting hybrid has been spreading rapidly in the Czech Republic, and there are observations indicating that its invasion dynamics are accelerating. This constitutes a unique and most interesting ecological situation, i.e. a pair of alien congeners and their hybrid spreading almost exclusively by clonal means in the area of their secondary distribution. The persistence of clones known from historical records was assessed in the landscape (Pyšek et al. 2001a). Experiments were carried out comparing regeneration potential (both from rhizome and stem segments) of the three congeners (Bímová et al. 2003), their response to control measures (Bímová et al. 2001) and their competitive ability. Preliminary results suggest that hybrid progeny originates in the adventive region and that the vigour of the hybrid is greater than that of both parents (B. Mandák and P. Pyšek, unpublished data). The establishment and survival of the three taxa was studied in meadow communities; the study has shown that they can be effectively controlled by mowing (Brabec and Pyšek 2000).

The North American *Pinus strobus* invades both natural *P. sylvestris* forests and its plantations in sandstone areas of the Czech Republic. Comparison of this alien tree with its native congener indicates that the former produces higher amount of more slowly decomposing litter. Under such conditions it regenerates better than the native congener, and this attribute is likely to contribute to its enormous success as an invader (Hadincová et al. 1997; Hanzélyová 1998; Härtel and Hadincová 1999).

A North American composite, *Bidens frondosa*, exhibits higher seed production, germinates better under lower temperatures, and its seeds are more easily dispersed compared with its native congeners *B. tripartita*, *B. radiata*, and *B. cernua* (Gruberová et al. 2001).

The success of *A. sagittata* (Chenopodiaceae) in the present central European landscape may be associated not only with a high biomass production, dense canopy, high fecundity, and salt tolerance, but also with its heterocarpy (Mandák and Pyšek 1999a, b). The species produces three types of fruits differing in the presence of bracteoles and level of dormancy which play different roles in the life cycle of the plant (Mandák and Pyšek 2001a, b).

Legal status and nature conservation

The Czech Republic is among the contracting parties of the Convention on Biological Diversity (Nairobi 1992), which represents the potentially most powerful legal

instrument for the control, containment, and eradication of invasive species (Shine et al. 2000). Other documents which can be effectively used for this purpose are the Bern Convention on the Conservation of European Wildlife and Natural Habitats (1979), the International Convention on Plant Protection (Rome 1951), and Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora (1992) which is relevant to the efforts of the country to become a member of the European Union. Contracting parties are supposed to fulfil the commitments resulting from international conventions by their internal legislation.

Legal instruments available for this purpose in the Czech Republic are associated with the laws and regulations on nature protection. These are mostly focussed on the general protection of plant species; all organisms are protected by law against damage and eradication. The law does not distinguish between alien species already naturalized and well established in the landscape and native species so that protection measures are applied to the former in the same way as to every species occurring 'in the wild'. Exceptions are therefore being made to treat widely distributed and spreading invasive species (Máca 2001).

Act No. 114/1992 on nature and landscape protection determines that species of alien origin can be introduced and spread purposedly only with permission from the nature conservancy authorities. Such permission is explicitly forbidden to be given in national parks, protected landscape areas, and nature reserves.

Act No. 147/1996 on plant protection service can be also applied to invasive species. It is aimed at the protection of the state territory from the introduction and spread of noxious (so-called 'quarantine') organisms, including weeds of arable lands which are harmful to other plants, do not occur as yet in the territory of the state (or their distribution is limited), are difficult to eradicate and which can cause considerable harm and losses.

From the legal viewpoint, the Czech national legislation suffers from the following shortcoming: There are no legal measures dealing explicitly with eradication. No regulations laying down the process for allowing exceptions to the rules have been produced. No sanctions are explicitly laid down for introductions due to carelessness. Finally, the public is not sufficiently informed about the relevant legislation (Máca 2001).

Future research topics

Future research on plant invasions in the Czech Republic should be related to the 'hot topics' of contemporary invasion biology which have emerged recently or are being recognized. There is still a lack of generalization regarding invasion impacts, and the information needed to prioritize management efforts. Little formal attention has been given to defining what is meant by impact or connecting ecological theory with particular measures of impact (Parker et al. 1999). Hybridization, both between aliens and between invading aliens and native plants, can also have a profound effect on the outcome of invasion (Daehler and Strong 1996; Vilà et al. 2000) and has been receiving increasing attention. Knowledge of the genetic make up of invading populations is becoming a powerful tool for explaining invasion success (Ellstrand and Schierenbeck 2000; Lee 2002). Long-term absence of natural control agents may lead to genetic changes in the growth and biomass allocation patterns in the non-native populations. It has been predicted that they should evolve into more competitive genotypes, compared to populations of the same species growing in their native range (Blossey and Nötzold 1995).

To meet these challenges, the Czech national research programme on invasive species should focus upon (i) completing the collation of existing data on the abundance and distribution of alien species and their presence in vegetation. Analysis of such databases will provide the information on the history of invasion at the landscape scale, quantitative pattern of their distribution in various plant communities/habitats, and assessment of their impact. (ii) Ecological studies, both field and experimental, devoted to the major invading species of the Czech flora, with emphasis on their life histories, population dynamics, modes of reproduction, and genetics, represent a powerful approach, especially when conducted as comparative studies of congeners and/or within taxonomic or functional groups. (iii) Davis et al. (2001) concluded that the development of invasion ecology has been hampered for decades due to an unfortunate dissociation from other fields of ecology, particularly succession ecology, and that each seldom refers to the other. Czech invasion ecologists represent one of the exceptions to this rule and efforts have been made to relate these two issues closely, either by analysing existing data (e.g. Rejmánek 1989; Prach and Pyšek 1999) or using experimental approaches (Bastl et al. 1997). More carefully designed studies

are needed to obtain closer insight into this challenging issue. And last, (iv) close relationship between comparative ecological research and taxonomy of the groups studied is a necessary condition for meaningful studies, with both fields mutually profiting from each other.

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Notes

[1]The terms used to describe immigration status of alien species follow those suggested by Richardson et al. (2000a) throughout.

[2]At present, the following taxa are the subject of ecological studies conducted at the University of South Bohemia, České Budějovice and the Institute of Botany Průhonice: *Aster* spp., *Atriplex* spp., *Bidens frondosa*, *Conyza canadensis*, *Galinsoga* spp., *Helianthus tuberosus*, *Heracleum mantegazzianum*, *Impatiens glandulifera*, *Oenothera* spp., *Reynoutria* spp., *Rudbeckia laciniata*, *Solidago canadensis.*

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