

**Explanation and risk assessment of alien woody
plants invasion in Central Europe
by historical and ecological factors**

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*Mamince
In memoriam*

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Hereby I declare that I have not submitted or presented any part of this thesis for any other degree or diploma.

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*There is nothing but questions that were given shape
and that bear the seeds of answers to them.
And there is nothing but answers that are impregnated
by the questions.*

Gustav Meyrink, *The Golem*

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Introduction

Some people call them one of the riders of the new global apocalypse, others call them the second major cause of extinction, the first and most important factor being the direct destruction of habitats (Wilcove et al. 1998): biological invasions. A number of financial studies demonstrate how serious the problem of biological invasions is. The global cost of alien species invasion amounts to 1.4 trillion USD per year (Pimentel et al. 2002). In total, 6.6 million CZK were spent on control of alien species during the period 1997–2002 in the Czech Republic under the state countryside conservation program (Křivánek 2004). Between 2000 and 2003 the control of alien tree species *Pinus strobus* and *Larix decidua* in Bohemian Switzerland National Park cost 4.5 million CZK (Hentschel & Hentschelová 2003). Just during the year 2003, the Bohemian Paradise (Český Ráj) Protected Landscape Area administration invested 450,000 CZK in the eradication of six of the locally most invasive alien species (Český Ráj PLA – Annual Report 2003, Křivánek 2006a). These few examples indicate that biological invasions are a very serious problem also in the Czech Republic.

The most important problem is to predict which species can become invasive. Are there any common, globally applicable, characteristics that determine the future invasive behaviour of a species? Although every introduction will entail unquantified risks, the only predictable aspect of introduced species is their unpredictability (Lever 2004). Only a low percentage of all alien species will become naturalized and invasive. According to Williamson's Rule of Ten, only one in ten introduced species becomes casual, one in ten casuals becomes naturalized and only one in ten naturalized species becomes a harmful pest (Williamson 1996, Williamson & Fitter 1996). Likewise, DiCasti (1989) showed that of every 100 species introduced, only about two or three will expand from cultivation. Similarly, Kowarik (1995) suggested that of all alien woody species, about 1% will invade natural vegetation. The disproportion between the number of species introduced and that escaping from cultivation or invading natural habitats can be explained as the base rate effect (Smith et al. 1999). The base rate effect amplifies the role of unpredictability due to chance during the invasion process. However, invasion biologists have tried to find the specific characteristics associated with the most invasive species. Most studies are based on biological and ecological variables. Although the history of planting, propagule pressure and lag phase are no less important, they have been the focus of only a minority of studies. The lack of data available is probably the main reason for this absence.

The group of alien woody species represents a very important section of alien vascular plants (Weber 2003). In 2001 the Invasive Species Specialists Group of the IUCN selected 100 of the worst alien invasive species worldwide. Of these, vascular plants constituted 32%, and more than one fifth (22%) of all selected species were woody species (Lowe et al. 2001). Many invasive woody species change the character, conditions and form of the habitats they invade. These species are called transformers *sensu* Richardson et al. (2000). Their impact includes the suppression of native plants (Richardson et al. 1989), reduction of habitats (Zavaleta 2000), increased sedimentation and water loss (Carmen & Brotherson 1982, Zavaleta 2000) and nutrient enrichment (Vitousek & Walker 1989, Richardson & Higgins

1998). On the other hand, the high pressure of their commercial use in timber production, ornamental gardening and landscape planning demands the continuing introduction and planting of new species. These conflicting interests – conservation and commercial production and planting – both need an effective tool for selecting the “safe” species from a group of potentially invasive ones.

Alien woody species represent a well-known group of vascular plants with many data available. A comparison of importance of historical and ecological factors during the invasion process could be made due to the availability of many historical data on time of introduction, lag phase, propagule pressure by forestry and ornamental gardening. The aim of the studies presented is to find the relationships between historical and ecological characteristics and propagule pressure imposed by man, and also to describe the importance of these factors in the invasion process. In the following chapters and included papers a) the alien woody flora of the Czech Republic and the correlation between ecological and historical variables (Chapters 1 and 3), b) the results from testing the historical and spatial importance of forestry during the process of naturalization – the propagule pressure created by human activity (Chapter 2), c) and the potentials and possibilities of predicting the woody species' invasion by use of different risk assessment schemes (Chapter 4) are presented.

Outline of the thesis

Chapter 1 ~ Database DAWIS

Křivánek, M., Pyšek, P. 2007: Forestry and horticulture as pathways of plant invasions: a database of alien woody plants in the Czech Republic. In: B. Tokarska, J.H. Brock, G. Brundu, L.E. Child, C.C. Daehler, P. Pyšek (eds.): Plant Invasions: human perception, ecological impacts and management. Backhuys Publishers, Leiden, Netherlands, pp.: 19-36.

Database of alien woody species with special regard to alien invasive woody species in the Czech Republic

There currently exist many checklists, overviews and databases of native and/or alien plant species in European floras. However, neither a database with special attention to woody species, nor a database combining data on species escaping from cultivation and non-escaping alien species has been developed. The goal of the study presented in this chapter was to develop a special database of alien woody species present in cultivation, as well as species currently present in the wild in Central Europe, with special regard to the Czech Republic. The second goal was to describe in general the basic characteristics of (not only) Czech alien woody flora.

The total number of woody plant species introduced to the Czech Republic is not known exactly. Thus, species selection was based on data about planting (historical and recent seed catalogues of garden centres and botanical gardens, national floras and atlases) and occurrence in the wild (UHUL 2000, Pyšek et al. 2002, FLDOK). In total, 1,691 alien tree, shrub and woody vine species from 90 families were included in the database. The characteristics in taxonomy, geography, invasion, history of planting, biology and ecology, horticulture and use were collected for each species. In total, 126 characteristics were described, but not all characteristics were available for each species because of lack of data. Although a lot of information was obtained from the area of the Czech Republic, most of it is applicable to the whole of Central Europe and potentially also to other regions with a temperate climate.

Of the total number of alien woody species that data were collected on, 128 species had previously escaped from cultivation (Pyšek et al. 2002). This ratio reflects the base rate effect

described for invasions by Smith et al. (1999; see also *Chapter 4*). Of 1,564 non-escaped species, 333 species are planted only in specialized collections – especially because of low climatic compatibility. Based on the database statistics, the most typical alien woody species in the Czech Republic (Central Europe) belongs to the *Malaceae* family with origin in Asia. It has not escaped from cultivation yet, despite being widely planted in parks and gardens. If it had escaped from cultivation, it would occur rarely in the wild as a casual with 1 – 50 known localities, especially in human-made habitats. The species was introduced into the Czech Republic between 1850 and 1900 primarily for ornamental purposes. If it were invasive or at least naturalized, it would have to have been introduced earlier than species not escaping from cultivation (see also *Chapter 4*). The mean lag between introduction and escape from cultivation would be approximately 112 years. The species' life form is a deciduous shrub that reproduces generatively. It is a colourful, hermaphroditic species pollinated by insects. In cultivation, and also in the wild, it persists successfully in areas with annual mean temperature of at least 5°C and annual mean precipitation of 400 mm. The species has been included in seed catalogues of garden centres and botanical gardens, where one or two ornamental cultivars are also offered.

The DAWIS database was developed in MS Access software. It is freely available on the web pages of the Institute of Botany, Department of Invasion Ecology (<http://www.ibot.cas.cz/invasions/projects.htm>) and also as the appendix of the Ph.D. thesis.

Chapter 2 ~ Forestry and its role in naturalization

Křivánek, M., Pyšek, P., Jarošík, V. 2006: Planting history and propagule pressure as predictors of invasion by woody species in a temperate region. Conservation Biology 20 (5): 1487-1498.

Forestry has a long tradition in the Czech Republic. Forests have been planted in the area since the mid-18th century (Blaščák 2003). Since the 1850s alien species have also been used (Beran & Šindelář 1996). The total forest area currently covers 2,551,873 ha (i.e. 32% of the country). In total, 28 alien woody species are planted on 45,203 ha (i.e. 1.8% of the total forest area; UHUL 2000). Another 24 alien species have been tested for forestry purposes (Bažant & Škoda 2004, Beran & Šindelář 1996, Černá & Hamerník 2004). Most of these species were reported to have been first introduced after 1812, although two Mediterranean species, now casual in the Czech Republic, were introduced in the late 16th century (Svoboda 1976, 1981). Forestry authorities believe in the high production potential of these species, even though 14 of the planted species have already escaped from cultivation and 10 of those are now naturalized (Pyšek et al. 2002). In total, 7 alien species planted in forests on 23,956 ha (0.9% of total forest area) are reported as invasive. Current trends in forestry exhibit a preference for biodiversity conservation and multiple function forestry instead of timber production only. Despite this, alien and invasive alien species are still planted and preferred in many areas. What is the role of forestry in escape and naturalization of alien species? Is forestry an important player in propagule pressure leading to naturalization? If so, what is the relative importance of spatial and temporal factors in determining the probability of naturalization? Do these factors affect the probability of escape from cultivation and of subsequent naturalization in the same way?

To answer these questions, the history and the range of planting of all 28 commercially used alien tree species in forestry were examined. The species were divided into 3 categories reflecting their invasive status (*sensu* Richardson et al. 2000, Pyšek et al. 2004): have not escaped from cultivation, have escaped from cultivation but only occur as casuals, and those that are naturalized. Three variables indicating the spatial factors were included: 1) the total area the species has been planted in forests (UHUL 2000), 2) presence / absence of the species in each of the 41 forestry administrative units, so-called natural forest areas (UHUL 2000) and 3) for escaped species, the number of localities in the countryside based on the data in the national database of published floristic records (FLDOK, Institute of Botany). The

temporal factor was represented by the year of first known introduction into the Czech Republic (Svoboda 1976, 1981).

The total area planted with alien species in forests affects neither their escape nor their naturalization. On the other hand, the positive invasion process is significantly influenced by earlier introduction and the number of areas the species is planted in. Escape from cultivation has been easier for species planted for a long time in many geographically, geomorphologically and climatically different areas (Plíva & Žlábek 1986). The correlation between the probability of naturalization and planting is not so obvious, although it was also determined by the residential time and number of planting areas. The result of this weaker dependence is probably due to two possible ways of propagule pressure: once the species escapes, propagule pressure from wild populations adds to that from planted areas. The intensity of planting was also found to influence the number of localities in the wild. A significant correlation was found between total planted area and the number of localities with presence of the species in natural and semi-natural vegetation. In other words, the number of localities of the species in the wild increased with the total forest area the species is planted in. However, neither the time of introduction, nor the number of planting areas appeared significant.

Even though current forestry practices seek to incorporate biodiversity-friendly management, they have inevitably continued to facilitate the escape and naturalization of alien species. Forest management is still conservative, preferring the use of alien species in many areas where native species would be a better alternative (UHUL 1994, Beran & Šindelář 1996).

Chapter 3 ~ Propagule pressure vs. biological traits; Aliens vs. natives

Pyšek, P., Křivánek, M., Jarošík, V. Propagule pressure, residence time, climatic match, species traits and similarity to native species discriminate naturalized woody aliens from those that fail. (Submitted)

As was shown in previous chapters and studies presented here, it is possible, with some proportion of misclassification, to predict the invasive behaviour of introduced alien woody species. It was also demonstrated that human activity, here represented by forestry, facilitates the escape of alien species from cultivation and also their naturalization. The presented results, however, raise one important question: when, at which stage of the invasion process, and how much do human activity and species traits influence the success of invasion? Further, in considering species traits, which traits correspond with success? The overall accuracy of the most successful risk assessment scheme tested was “only” 85.5% (see *Chapter 4* for details). How reliable could the prediction be if the anthropogenic propagule pressure were included? It has been suggested that the species traits are only one part of successful invasion. Other factors, such as propagule pressure, residence time and/or climatic compatibility (Crawley et al. 1996, Rejmánek 2000, Brown & Peet 2003, Rouget & Richardson 2003, Foxcroft et al. 2004, Kühn et al. 2004, Pyšek & Jarošík 2005, Thuiller et al. 2005, Daehler 2006), though difficult to quantify, and the immeasurable role of chance, are also very important. Although the latter factor is impossible to analyse, analysis of the former is possible. In addition, it has been suggested that the roles of the above-mentioned factors is different during the invasion process (Kolar & Lodge 2001, Pyšek et al. 2003). The socio-economic factors, represented by time of introduction, intensity of planting and residence time, are more important at the beginning of invasion, while the species traits, such as biological, ecological and evolutionary variables are more important at later stages of naturalization and invasion (Williamson 2006). However, these hypotheses have not been tested so far with real data.

The species traits corresponding with successful invasion have been listed by a number of authors (e.g. Baker 1974, Richardson & Bond 1991, Rejmánek 1995, Rejmánek & Richardson 1996, Kolar & Lodge 2001, Pyšek 2001, Pyšek & Richardson 2007). Species traits can be analysed in two ways: firstly, by analysis of pure traits to determine which trait presence/absence most strongly influences the invasion process, and secondly, by analysis of floras and their similarities to determine which alien species are more successful – those more closely related to native species or those different from natives. The last question reflects the still open debate on the validity of Darwin's naturalization hypothesis.

The aim of the study was especially to find answers to these questions: (i) Which species traits correspond with successful invasion? How significant is the role of human factors (such as propagule pressure and residential time)? Is the significance of these traits and factors the same at all stages of the invasion process? (ii) Does the similarity of aliens to native species facilitate the invasion process or not?

To answer the above questions, the authors analysed the extensive pool of data on alien and native woody species planted and growing in the Czech Republic, Central Europe. The alien species were divided, for comparison, into (i) those escaped from cultivation and occurring as casuals in the flora of the Czech Republic, (ii) those naturalized in the flora of the country and (iii) those that have never escaped so far. The escaped and non-escaped species were compared with their native congeners. In total, 109 escaped–non-escaped pairs, 44 naturalized–non-naturalized pairs and 53 triads of escaped–non-escaped–native species were tested. The tested variables were divided into those describing the human influence and geographical factors (propagule pressure represented as intensity of planting and type of use, residence time expressed as time of introduction to Europe and the Czech Republic, and region of origin of the species – data available only for alien species), and those defining the species' biological and ecological traits (in total, 17 traits were available for alien and native taxa). Paired comparison of congeners and binary classification tree analysis were applied for statistical analysis.

The analysis of alien species indicated a high significance of introduction factors such as propagule pressure and residence time. It was impossible to eliminate the bias of these variables in determining clear influence of species traits. The relative significance of each of the factors was found to vary at different stages of the invasion process. Although the naturalization of a species depends on a combination of biological and historical factors, the probability of escape from cultivation was strictly influenced only by introduction factors. Regardless of the species' biological and ecological traits, the probability of escape sharply increased with increasing propagule pressure (intensity of planting, wide range of distribution) and long residential time. The success of the species in terms of residential time was scale dependent. The local scale and history of planting (residential time in the Czech Republic) played an important role in the species' escape. However, more important for naturalization was the residential time on a pan-European scale. Although propagule pressure and residential time contributed strongly to successful naturalization, eco-geographical traits, especially area of origin and fruit size were also important.

The results of analysis of alien-native species triads did not enable a validation of Darwin's naturalization hypothesis. The most important traits emerged as duration of flowering period, fruit size and minimum mean annual temperature necessary for good growth when the congeners in triads were compared. The alien species escaping from cultivation were significantly more closely related to native species than those that had failed during the first stages of the invasion process. At later stages, the behaviour of successful aliens did not differ greatly to that of native species, colonizing free niches or margins of niches occupied by native species, but those similar to natives tended to compete with natives in their niches. For an alien species, the key to successful invasion is not to be different.

Chapter 4 ~ Risk assessment

Křivánek, M., Pyšek, P. 2006: *Predicting invasions by woody species in a temperate zone: a test of three risk assessment schemes in the Czech Republic (Central Europe)*. *Diversity & Distributions* 12: 319-327.

Since the foundation of invasion biology was laid (Elton 1958), invasion and conservation biologists have been trying to find the characteristics associated with successful invasions in new geographical areas. Although many different methods have been used, none have proved to be completely successful. The best results have been obtained in development of risk assessment schemes. The aim of these schemes is to find potentially invasive species before their actual invasion or to predict the future invasion dynamics of species already invasive in the area, respectively. The first group of models could be called pre-introduction schemes and the second group post-introduction schemes. The pre-introduction schemes utilise a wide range of biological, ecological and historical data on the species to predict its probability of invasion. Using binary question trees is one possibility, another is rating systems with scores allocated to each answer in a questionnaire, where the final score indicates the probability of invasion. These schemes are successfully used especially in countries with high levels of invasion, though in Central Europe they are not used at all.

Generally, there are two ways of applying risk assessment schemes to the analysis of invasive potential of any alien species in a new area. The first one constitutes new risk assessment schemes developed specially for an area or country. Testing existing risk assessment schemes and choosing the most appropriate one represents the second way. The advantage of testing existing models lies in the fact that they have already been tested successfully somewhere else. Finally, with an increasing number of successful tests, the effectiveness of the scheme becomes evident. By this approach, a general template for widely applicable risk assessment schemes could be found.

In the Czech Republic, no risk assessment scheme has been used successfully so far. In general, no successful risk assessment scheme has been developed for Central Europe. The main question of this chapter is: does any risk assessment scheme well applicable to the conditions of Central Europe already exist, or will it be necessary to develop a new one? If one exists, which model fits best to the region?

To find the best-fitting scheme and assess its validity, we chose from the large number of schemes available (Křivánek 2006b) and then tested three previously developed models: 1) Australian Weed Risk Assessment Scheme (WRA; Pheloung 1995, Pheloung et al. 1999), 2) WRA with additional analysis for species requiring further evaluation (Daehler et al. 2004), and 3) North American decision tree scheme (Reichard & Hamilton 1997, Reichard 2001). In total, 180 alien woody species planted in the Czech Republic for at least 60 years were selected as the reference group. The group was represented by all 28 alien species planted in forests for timber production (see *Chapter 2*) and 152 species commonly planted in gardens and parks. All 17 woody species invasive in the area of the Czech Republic (Pyšek et al. 2002) have been included. The accuracy and reliability of the schemes tested were calculated after Smith et al. (1999). Accuracy indicates the probability of correct classification of species – invasive assessed as invasive (A_i), non-invasive as non-invasive (A_n) and overall accuracy including both components (A_o). Reliability indicates the probability that accepted species would have been an invader (P_{ai}), and that rejected species would have been an invader (P_{ri}) (Smith et al. 1999).

Although the North American risk assessment scheme (Reichard & Hamilton 1997, Reichard 2001) was primarily developed for testing woody species in temperate regions, the scheme proved to be the least successful in Central Europe. The model rejected only 35% of invasive species and accepted 18% of them for cultivation. On the other hand, the scheme rejects 18% of species that have never escaped from cultivation. The overall accuracy of the model

was only 61.6%, whereas its accuracy in the area of origin of the scheme, North America, was much higher with 76% (Smith et al. 1999). At the other end of success lays the WRA with additional analysis after Daehler et al. (2004). The scheme rejected all invasive species, but only 1% of non-escaping species. The overall accuracy of the scheme was 85.5%. The basic WRA model (Pheloung 1995, Pheloung et al. 1999) had a lower accuracy overall, 67.9%, while the accuracy during Australian testing was 85% (Smith et al. 1999).

Although the Australian Weed Risk Assessment scheme consists of 49 questions, only 10 answers represent a minimum for a species to be evaluated (Pheloung et al. 1999). The scheme is not the easiest one to use, but it provides the most exact fit. In the end, the Australian model was more successful than the “home-made” European, Swiss scheme which yielded an overall accuracy of only 65% (Weber & Gut 2004). The results indicate that the WRA with additional analysis appears to be a promising template for developing a widely applicable system for screening invasive plant introductions.

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Chapter 1 ~ Database DAWIS

Křivánek, M., Pyšek, P. 2007: Forestry and horticulture as pathways of plant invasions: a database of alien woody plants in the Czech Republic. In: B. Tokarska, J.H. Brock, G. Brundu, L.E. Child, C.C. Daehler, P. Pyšek (eds.): Plant Invasions: human perception, ecological impacts and management. Backhuys Publishers, Leiden, Netherlands, pp.: 19-36.

Conclusions

The studies presented focus on the historical and ecological traits corresponding with the successful invasion process of alien woody plants in Central Europe. In regard to invasion biology, woody plant species are among the most problematic plant life forms and constitute a high proportion of the World's worst invasive species. The irreversible changes in ecosystems often caused by invasion of these species constitute one good reason for study. The second is the large amount of data available, especially on human influence and activity (such as the intensity of planting, residence time). The reason for studying alien woody species is also reflected in their ambivalence: on the one hand, the group is represented by the most serious invasive species, while on the other hand, there is still strong pressure to plant these species for timber, food and ornamental purposes.

The native woody flora of the Czech Republic contains about 280 species. The exact number of alien woody species is not known. Based on different approaches and datasets, it has been estimated to be in the order of 4,300 species. Exact data is available for a representative sample of frequently-planted alien woody species that contains 1,691 species. An estimated 128 alien species have escaped from cultivation, of which about 17 are currently invasive in the Czech Republic. What factors influence success in the invasion process? Why are these 17 species invasive and the remaining 1,674 species are not? Is it possible to predict which species will be invasive and which will not be? What roles do human activity and species traits play in the invasion process? These are only some of the questions to which we tried to find answers. To attempt to answer these questions, a large number of woody species and their traits were tested and analysed. The main results could be interpreted as follows: success during the invasion process not only depends on a species' biological and ecological traits, but human influence also plays a very important role. This role can be presented as propagule pressure *sensu lato*. It means early introduction, repeated planting in a wide range of conditions, in gardens and parks as well as in the open landscape. The example of forest engineering shows how important this role can be. Moreover, strong propagule pressure and long residential time can compensate for the lack of ecological adaptation of a species to the conditions in the new area. For its successful escape from cultivation, intensive planting, ideally in a wide range of conditions, are entirely sufficient. Those species that have been planted for a long time are even more successful.

Data is available for about 1,691 alien woody species planted in the Czech Republic, however, only a negligible percentage of this group invade natural ecosystems. It is very difficult to predict which species will be invasive because of the disproportion in numbers in both groups. The results of testing risk assessment schemes proved that prediction is nonetheless possible. The most successful model yielded an overall accuracy of 85.5%, which represents quite a high success rate in the field of risk assessment modelling. The question is how high would the accuracy be if the propagule pressure and residential time variables were included in the calculation?

Although human factors were found to influence the results greatly, the importance of species traits was also not negligible. The comparisons of alien and native woody congeners showed a strong correlation between both groups. It was demonstrated that the alien species escaping from cultivation are more similar in their traits to native species than to aliens that have never escaped. In a general sense, this result contributes to the discussion about the validity of Darwin's naturalization hypothesis. In a particular sense, the result is only part of a mosaic composed of other previous results. The full mosaic can be presented as a memorandum for landscape protection and nature conservation as well as for forestry and ornamental gardening: human activity very strongly facilitates the escape, naturalization and invasion of alien woody species. The impact of these species on the occupied habitats is often irreversible. Naturalized alien woody species compete for space and nutrients with native species, compete for niches occupied by native species (aliens do not colonise unoccupied niches as Darwin's hypothesis suggests). The planting of alien species with

similar bio-ecological traits to native ones necessarily leads to eradication of our native, and not only woody, flora. Although a few successful risk assessment schemes exist, their accuracy of prediction is not absolute and there is still the probability, however low, that strong transformer species that have been introduced and planted will escape and finally invade natural habitats.