From ornamental to detrimental? The incipient invasion of Central Europe by *Paulownia tomentosa*

Probíhající invaze *Paulownia tomentosa* ve střední Evropě

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Essl F. (2007): From ornamental to detrimental? The incipient invasion of Central Europe by *Paulownia tomentosa*. – Preslia 79: 377–389.

The invasion of *Paulownia tomentosa* (*Paulowniaceae*), a new alien tree species in Central Europe, native to China, is analysed. By using its distribution in Austria, the invasion of this country is analysed in detail. The first reports of *P. tomentosa* in Austria were in the 1960s in Vienna. Since then, the number of sites has increased exponentially, with a total of 151 sites in 27 grid cells of the Floristic Mapping project of Austria. The number of sites per grid cell is strongly positively correlated with the minimum residence time in grid cell, which explains 86% of the deviance in the general linear model (GLM). The localities are confined to warm lowland areas (below 450 m altitude) and are concentrated in cities, with 90% of all localities recorded in cities with > 100,000 inhabitants. *Paulownia tomentosa* typically occurs in small populations of less then 10 individuals (83% of all records) and behaves as a pioneer species colonizing mainly disturbed urban habitats. Near-natural habitats, e.g. forest clearings and riparian shrubberies are rarely colonized. In extremely disturbed areas, the average number of vascular plant species is low (8.9 species), as is total plant cover (17%). As *P. tomentosa* is currently mostly confined to synanthropic habitats in urban areas, the invasion is not yet a nature conservation issue. In the future, predicted climate change might allow *P. tomentosa* to spread beyond its current distribution. The habitat preference in the eastern USA indicates that further spread of *P. tomentosa* in Central Europe might be accompanied by a switch to more natural habitats, e.g. forest clearings and forest margins. Thus, the future spread of this species should be closely monitored.

Keywords: Central Europe, habitat preference, minimum residence time, *Paulownia tomentosa*, plant invasion, urban vegetation

Introduction

Biological invasions are acknowledged as a major threat for global biodiversity (e.g. Williamson 1996, McNeely et al. 2001). Two complementary approaches dominate research in invasion ecology: The first builds on large data sets (e.g. inventories of alien species in a given area) and tries to elucidate factors determining invasion success (e.g. Palmer 2006, Stohlgren et al. 2006). The second approach concentrates on a detailed analysis of the invasion history of one or few alien species (e.g. Pyšek 1991, Lavoie et al. 2003, Williamson et al. 2005, Pyšek et al. 2007).

Such case studies are needed to improve the knowledge of distributional patterns and understanding of the underlying mechanisms (Trepl 1984, Pyšek & Prach 1993). Special attention should be given to the first stages of spread (Pyšek & Hulme 2005), as these are crucial for successful invasions (Williamson 1996, Kowarik 2003a) and eradication is more feasible at the very beginning of spread (Rejmánek 2000, Wittenberg & Cock 2001);

unfortunately, data on incipient invasions of aliens are usually scattered and thus poorly represented in invasion literature (Ricciardi et al. 2000, Mack 2005).

This paper analyses the invasion process of a new alien tree species in Central Europe. In the last 20 years, there has been an increase in the spread of *Paulownia tomentosa* in Central Europe (Nowack 1987, Landolt 1993), but no comprehensive analysis of this phenomenon. Furthermore, *P. tomentosa* is reported for 25 US states (Remaley 1998) and regarded as an invasive tree in E and SE North America (Williams 1983, Simberloff 2000).

This paper summarizes the introduction history and spread of *P. tomentosa* in Central Europe and analyses the invasion process in Austria. By using data for this country, the following questions are addressed: (1) What are the spatio-temporal patterns of spread, (2) which habitats are colonized, and (3) which factors influence the size of invading populations?

Material and methods

Study species

The seven species of the genus *Paulownia* (*Paulowniaceae*) are naturally restricted to E Asia. The native range of the empress tree, *P. tomentosa* (Thunb.) Steud., encompasses central and W China (Zhao-Hua et al. 1986, Roloff & Bärtels 1996). This tree may reach 20 meters in height. The conspicuous cordate leaves are about 40 cm long, the violet, bell-shape flowers bloom from April to May. Fruits are ovate capsules 3.0–4.5 cm long, the 2.5–4.0 mm long winged diaspores (5000 diaspores weigh 1 g, Kiermeier 1977) are easily spread by wind (Kumar et al. 1999).

In its native range, *P. tomentosa* occurs in various habitats, preferring alkaline soils and moist to semi-dry, open forests (Richter & Böcker 2001, Global Invasive Species Database 2006). It is shade intolerant and not found in dense forests. The average annual temperature in its native range (ca 10–16°C, Kiermeier 1977) is higher than in Central Europe (ca 7–10°C). Young plants are extraordinarily fast-growing, the terminal branch often growing more than 1 m/year. Life expectancy is short: most trees die after 60–70 years (Kiermeier 1977, Remaley 1998).

History of introduction in Central Europe

Paulownia tomentosa was introduced into Central Europe as an ornamental plant in 1834 (Kiermeier 1977). In Germany, the first recorded casual occurrence of *P. tomentosa* is at approximately 1925 (Kiermeier 1977). Only in the 1970s and 1980s did the number of recorded localities begin to increase, mainly in Rheinland-Pfalz and Baden-Wurttemberg, the warmest regions of Germany (Kiermeier 1977, Nowack 1987). *Paulownia tomentosa* is there currently established in urban areas, rapidly spreading along railways and on urban-industrial sites (Mazomeit 1995, Richter & Böcker 2001, Schmid 2005).

The spread was delayed in other parts of Germany. In the N Rhineland in W Germany the first escaped young plant was found in 1987; in 1994, only two additional sites were recorded (Adolphi 1995). Although *P. tomentosa* has been cultivated in the Ruhr basin for decades, first escaped young plants were recorded only in the mid-1990s (Keil & Loos 2004, 2005). Recently it has spread significantly, namely in large cities, along railways and locally in the Ruhr basin and remaining North-Rhine-Westphalia (Adolphi 2001, Haeupler et al. 2003, Keil & Loos 2004, 2005). In other parts of Germany, *P. tomentosa* is rare.

A similar picture can be drawn for other Central European countries. In the list of alien plant species of Switzerland, *P. tomentosa* is classified as casual (Wittenberg 2005). In urban Basel, it occurs "on many places escaped" and is thus classified as "established, although not growing into large trees" (Brodtbeck et al. 1999). In Zurich, the spread started in 1985, and shortly thereafter the species was listed as fast spreading (Landolt 1993). In N Italy in the province of South Tyrol, populations of *P. tomentosa* have only recently been observed. Nevertheless, the species has been recorded several times and some of the largest populations are already classified as established (Wilhalm et al. 2002). In the Czech Republic, *P. tomentosa* is a rare casual alien (Pyšek et al. 2002). In SW Slovenia, young plants were recorded growing near planted trees recently (N. Jogan, personal communication). In Hungary, the species is included in the list of casual alien plants (Botond & Botta-Dukát 2004).

Data and statistical analysis

Distribution data on *P. tomentosa* in Austria have been gathered from many different sources: Database of the Floristic Mapping project of Austria, herbaria, floristic literature and unpublished records (for list of sources see Fig. 2). Localities have been assigned to grid cells of the Austrian floristic mapping. This data was used to produce grid distribution maps (5 longitudinal minutes × 3 latitudinal minutes, approximately 30 km^2, Niklfeld 1998) and to analyse the cumulative number of sites and of occupied grid cells per 5 years as a measure of invasion rate. Altitudes of every population were extracted from the original data sources or by using the digital topographic map of Austria (BEV 2006). Altitudinal distribution in Austria was analysed using altitudinal classes of 100 m (ALTI). Data on colonized habitats was extracted from original data sources and assigned to habitat types; habitat classification is based on a modified version of the Austrian habitat type catalogue (Umweltbundesamt 2005). Data on population size (assigned to three classes: 1–10, 11–100, >100 individuals) and age of oldest plants were recorded for each population; the latter were extracted from original sources or during field work, either by counting the annual shoots of the terminal branch or, for older populations, by taking core samples and counting tree rings (Loacker et al. 2006). Age of oldest plants was used as a proxy for reconstructing the date of establishment of the respective population. Populations were deliminated by assuming that plants separated by > 250 m belong to different populations. This is the maximum distance seeds of wind-dispersed plants regularly travel (Richter & Böcker 2001, Dullinger et al. 2004).

All known sites (n = 69) were visited systematically from 2000–2005 in order to analyse vegetation composition. Accompanying vascular plant species (presence / absence) and total plant cover were recorded on plots of standardized size (10 m^2); the plots were located in the centre of the respective population. The taxonomy and nomenclature of vascular plants follow Fischer et al. (2005), the definition of invasion status is that used by Richardson et al. (2000) and Pyšek et al. (2004).

Some case studies have shown, that the introduction date or minimum residence time (MRT, time since the first record) can be used to predict the abundance of alien species on a (sub)national scale (Wu et al. 2003, Castro et al. 2005). To test the influence of MRT on the abundance at finer scales, the influence of time on numbers of sites (S) within the grid cells was analysed.

A generalised linear model (GLM) with a Poisson-error distribution (McCullagh & Nelder 1989) was used to model the relationship of S with MRT and ALTI. Significance was tested by dropping terms from the full model (S~MRT+ALTI) assuming a chi square distribution. Statistical analyses were carried out in Splus 7.0.

Results

Spread and distribution

The first record of self-sown *P. tomentosa* plants in Austria is in the mid-1960s in Vienna (Forstner & Hübl 1971). Since then, the species has spread markedly within the city (Adler & Mrkvicka 2003). In other lowland areas of Austria, a significant spread started in the 1980s, e.g. in Salzburg the first record was reported in 1986 (Strobl 1995) and in Graz in the early 1980s (Melzer 1991). The number of sites has increased exponentially in Austria, with a total of 151 in 2005 (Fig. 1). The number of occupied grid cells of the Floristic Mapping project of Austria has also grown exponentially; currently 27 grid cells (1% of a total of 2612) are occupied in six of the nine Austrian provinces (Fig. 2). The number of sites per grid cell is strongly positively correlated with MRT per grid cell (Fig. 3), MRT explains 86% of the deviance in the GLM ($P < 0.001$).

The localities of *P. tomentosa* are confined to lowland areas, showing a strong negative correlation with increasing altitude (Fig. 3); 81% of the records are for the lowest parts of Austria (100–300 m a.s.l.), which accounts for only 20.5% of the area of Austria. Nevertheless, the number of sites per grid cell is only moderately correlated with altitude, deviance in the GLM explained by ALTI is 2.6% ($P < 0.01$).

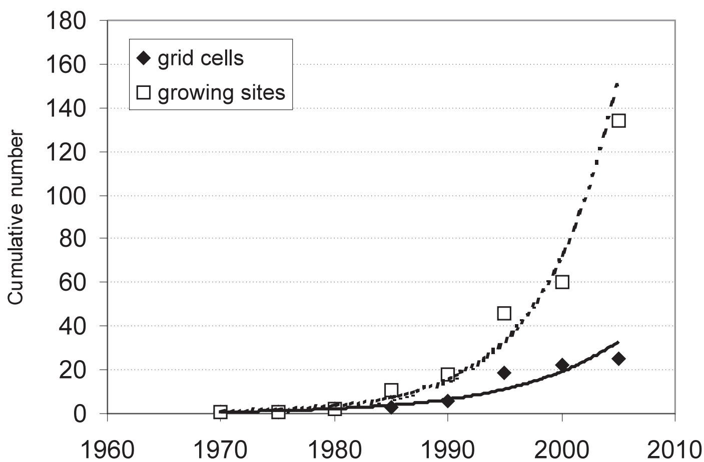

Fig. 1. – Cumulative increase in numbers of sites and grid cells of the Floristic Mapping project of Austria occupied by *Paulownia tomentosa*, recorded at 5-year intervals. Regression lines depict exponential relationship between cumulative numbers of sites ($r^2 = 0.96$; $p < 0.001$) and of grid cells respectively ($r^2 = 0.95$; $p < 0.001$).

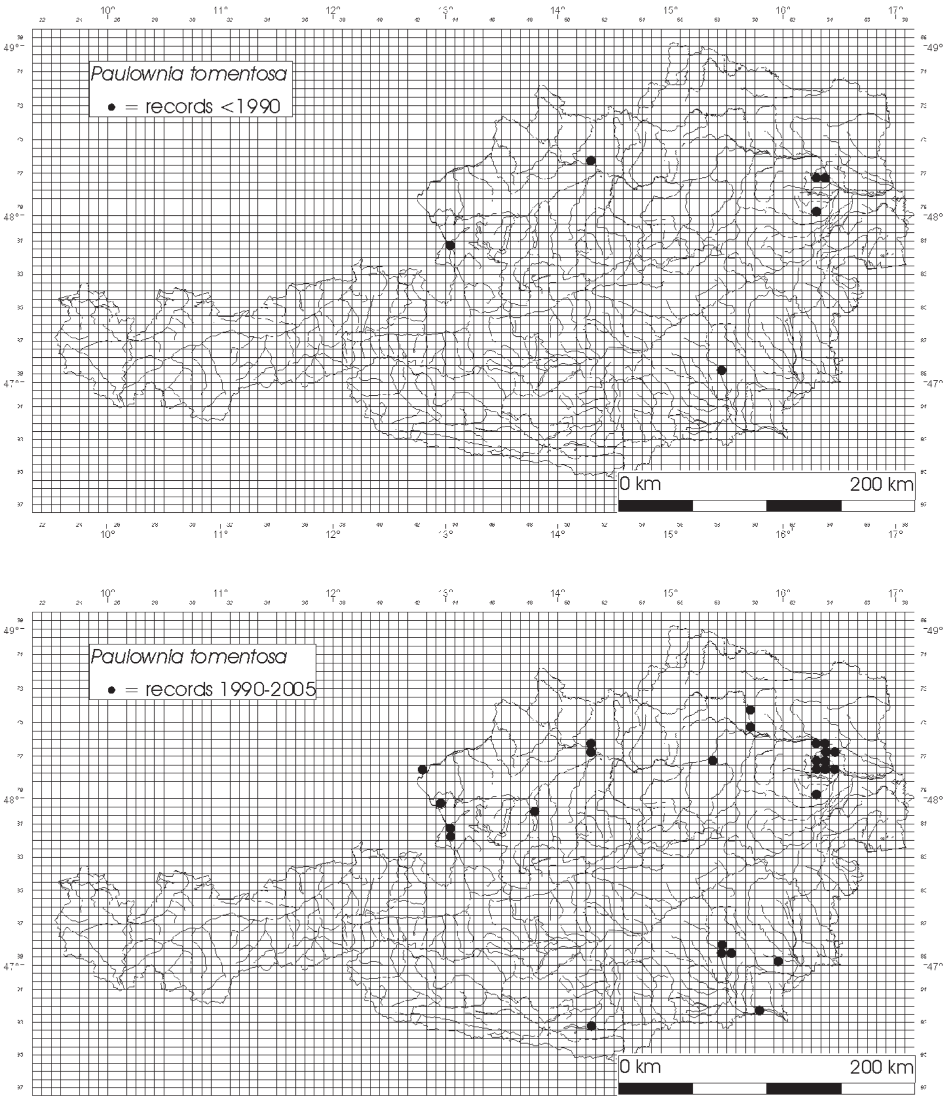

Fig. 2. – Grid distribution maps of *Paulownia tomentosa* in Austria based on the grid of the Floristic Mapping project of Central Europe (Niklfeld 1998). Data sources: Herbaria GJO, GZU, LI, NHM, SZB, WU, Adler & Mrkvicka (2003), Essl (2003, 2004, 2005), Essl & Stöhr (2006), Forstner & Hübl (1971), Hohla et al. (1998), Melzer (1991, 1999, 2000), Melzer & Barta (1995, 1996), Strobl (1995), Zechmeister & Grabherr (1998), and unpubl. data.

The species is mostly confined to urban areas in Austria; 90% of all localities were recorded in cities > 100,000 inhabitants. *Paulownia tomentosa* typically occurs in small populations of less than 10 individuals (83% of all records); only 2% of the populations consist of more then 100 individuals.

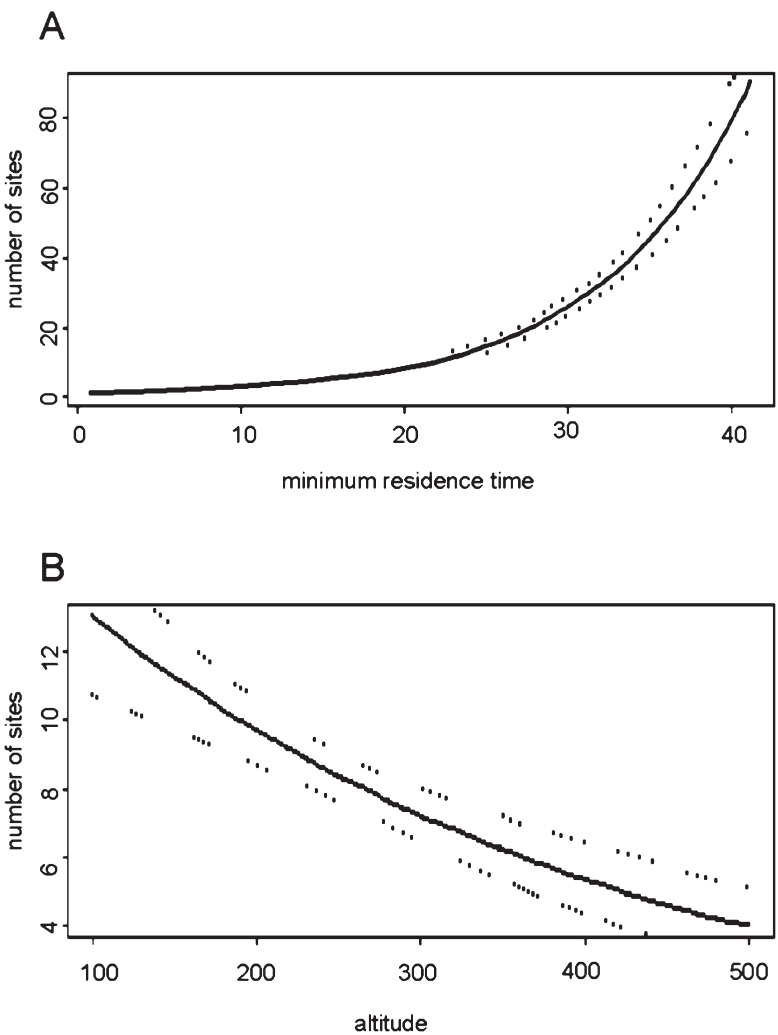

Fig. 3. – Response curves of number of sites (S) per grid cell of *Paulownia tomentosa* with altitude (A) and minimum residence time (B) derived from GLM using Poisson error distribution. Altitude was held constant at 250 m, minimum residence time at 20 years. Standard errors of the predicted values are represented by the dotted lines.

Habitats

Paulownia tomentosa is a pioneer species, which colonizes mainly disturbed urban habitats in Austria. It was most frequently recorded growing in crevices between paving stones (49% of all populations), followed by xerophytic ruderal vegetation (20%), wall crevices (14%), and railway habitats (10%); these four habitat types account for 93% of all records. Natural habitats like forest clearings including early reforestation stages and riverbanks are rarely colonized (7% of all records). It successfully invades extremely dry, disturbed sites on initial soils. Accordingly, 43% of the 69 investigated populations form monospecific stands without any accompanying species.

Table 1. – Plant species associated with invading *Paulownia tomentosa*, ranked according to decreasing constancy (n = 69 plots of 10 m^2). Only taxa with constancy > 5% are shown, neophytes (according to Essl & Rabitsch 2002) are marked by asterisks. The vegetation types for which the species is indicative are given (after Mucina et al. 1993).

Species	Vegetation type	Constancy (%)
Taraxacum officinale agg.	ruderal fertilized mesic grassland	29.0
*Ailanthus altissima**	perennial synanthropic vegetation of mesic habitats	24.6
Poa annua	vegetation of trampled habitats	21.7
Polygonum aviculare agg.	vegetation of trampled habitats	20.3
*Conyza canadensis**	annual ruderal vegetation	15.9
Plantago major	vegetation of trampled habitats	15.9
Salix caprea	pioneer forests	14.5
Sonchus oleraceus	annual ruderal vegetation	14.5
Betula pendula	pioneer forests	11.6
Artemisia vulgaris	perennial synanthropic vegetation of xeric habitats	10.1
Clematis vitalba	–	8.7
Epilobium tetragonum	perennial synanthropic vegetation of mesic habitats	8.7
Senecio vulgaris	annual ruderal vegetation	8.7
Stellaria media	annual ruderal vegetation	8.7
Achillea millefolium agg.	ruderal fertilized mesic grassland	7.2
*Buddleja davidii**	perennial synanthropic vegetation of mesic habitats	7.2
Dactylis glomerata	ruderal fertilized mesic grassland	7.2
Tussilago farfara	perennial synanthropic vegetation of xeric habitats	7.2
Acer pseudoplatanus	–	5.8
Arenaris serpyllifolia	–	5.8
Bromus sterilis	perennial synanthropic vegetation of xeric habitats	5.8
Calamagrostis epigejos	–	5.8
Chenopodium album	annual ruderal vegetation	5.8
Cirsium arvense	annual ruderal vegetation	5.8
Cirsium vulgare	perennial synanthropic vegetation of xeric habitats	5.8
Daucus carota	perennial synanthropic vegetation of xeric habitats	5.8
*Erigeron annuus**	perennial synanthropic vegetation of xeric habitats	5.8
Hordeum murinum	annual ruderal vegetation	5.8
Lolium perenne	ruderal fertilized mesic grassland	5.8
Populus alba	–	5.8
Sagina procumbens	vegetation of trampled habitats	5.8

The most frequent of the 133 accompanying species found is *Taraxacum officinale* agg., followed by *Ailanthus altissima, Poa annua, Polygonum aviculare* agg., *Conyza canadensis* and *Plantago major* (Table 1). Average species number at a site is low (8.9 species), as is total plant cover (17%). In total, 24.1% of the accompanying species are neophytes, but as most of them are rare, they only contribute 6.3% in terms of cover; the most common neophytes are *Ailanthus altissima, Conyza canadensis* and *Buddleja davidii.*

Discussion

Generality and limitations of the results

The data analysed are not based on a constant sampling effort due to variation in floristic surveys. This is seen as a possible significant error in documentations of spread (Delisle et al. 2003, Pyšek & Hulme 2005). Nevertheless, in the present case it seems unlikely that recording bias significantly affected the results. First, the integration of all available data sources should partly level out varying recording intensities (Rich et al. 2006). Second, *P. tomentosa* is a very conspicuous and well-known species making even young plants easily recognizable; thus, even single specimens are frequently recorded (e.g. Melzer & Barta 1995, 1996, Strobl 1995, Hohla et al. 1998). Previous studies have shown that floristic data are suitable for reconstructing the pattern of invasion of conspicuous alien plants (e.g. Pyšek 1991, 1995, Pyšek et al. 2007). Third, there are few records in the comprehensive older inventories of alien plants in Austrian cities, whereas the species is found in cities regularly today (e.g. Vienna – Forstner & Hübl 1971, Graz – Hamburger 1948). Furthermore, the invasion history of *P. tomentosa* in Austria is rather short, making strong variations in sampling effort less likely.

Spread and distribution

In Austria, *P. tomentosa* has shown an exponential spread since the 1970s, with no sign of a decrease in the number of new records. Thus, the saturation phase of its invasions – when the invasion rate slows down (Pyšek & Hulme 2005) – has apparently not been reached. This spatio-temporal pattern of spread seems to be valid for other parts of Central Europe (Richter & Böcker 2001).

Spread is clearly visible at different spatial scales, as expressed by exponentially growing number of sites and of occupied grid cells of the Austrian floristic mapping scheme (Fig. 2). Different processes are operating at these two scales: Whereas local spread depends on increasing seed input from adjacent source populations, long-distance dispersal is probably only mediated by planting trees in new regions. This finding is underlined by the high explanatory value of MRT in the GLM (Fig. 3). This indicates that MRT effectively predicts the distribution of alien species both at (sub)national scales (McKinney 2001, Pyšek & Jarošík 2005) and finer scales (Müllerová et al. 2005).

Occurrences of *P. tomentosa* in Central Europe are almost exclusively confined to urban areas. More than 99% of all records in SW Germany (Richter & Böcker 2001) and 90% of Austrian records have been made in urban areas. Cities offer specific "urban niches" with characteristic patterns of disturbance (Kowarik 1995, Wittig 2002) and are especially rich in alien species in Central Europe (Kühn et al. 2004, Pyšek et al. 2004, Walter et al. 2005). The concentration of preferred habitats in urban areas probably contributes to the relative success there. The significantly warmer climate in cities (up to 2°C warmer than adjacent rural areas) and higher minimum winter temperatures of 1–3°C in large cities allow the plants to survive otherwise extreme low temperature events (Wittig 2002). But even in cities, *P. tomentosa* strongly prefers microclimatically favoured sites, e.g. crevices in walls or the gravelled areas along railway tracks (Richter & Böcker 2001). However, the low predictive value of ALTI in the GLM shows that within climatically favourable regions increasing altitude only moderately slows down the invasion process.

Although more favourable temperature regimes might explain the preference for urban areas, note that *P. tomentosa* is mainly cultivated in cities and that diaspore availability is therefore strongly biased towards cities (Taylor & Irwin 2004). Currently, populations are usually small and consist mainly of young sterile plants; accordingly, populations depend on diaspore input from nearby planted mature trees. Propagule availability from planted trees is thus one key factor limiting spread (Kiermeier 1977, Křivánek et al. 2006). As populations grow older, they will become increasingly autonomous of diaspore input from planted trees. Empirical evidence shows that young individuals of *P. tomentosa* are frequently observed up to ca 200 m from the parental tree (Richter & Böcker 2001). Long-distance dispersal up to 3–4 km is recorded rarely in the E USA (Langdon & Johnson 1994). Moreover, frequent planting greatly fosters naturalization and population expansion of alien plant species. This is mainly due to propagule pressure and their ability to overcome barriers to spread (Kowarik 2003b, Lockwood et al. 2005).

In the future, predicted climate change might allow *P. tomentosa* to spread beyond its current distribution limits, pushing altitudinal limits upwards and making areas outside cities more accessible. The altitudinal limit in SW Germany lies below 300 m a.s.l. (Richter & Böcker 2001), which is somewhat lower than in Austria, where it is at 450 m; this altitudinal limit corresponds with an annual mean temperature of 7.5–8.0 °C (ZAMG 2006). Strong negative correlations between invasion success and annual mean temperature are known for many neophytes in Central Europe (Chytrý et al. 2005, Walter et al. 2005). Key limiting factors for the invasion success of *P. tomentosa* are winter minimum temperatures and early and late frosts. Old specimens survive winter minimum temperatures of down to –25°C without damage, but young, fast-growing individuals are damaged by –10°C (Richter & Böcker 2001).

The invasion pattern of *P. tomentosa* ressembles the early invasion phase of *Ailanthus altissima* in Central Europe (Adolphi 1995, 2001), which is the second-most frequent accompanying plant species in Austria and also grows syntopically in the native range of *P. tomentosa* (Kiermeier 1977). *Paulownia tomentosa* must currently be classified as casual. However, if the recent spread continues and escaped plants increasingly produce seed, this species will probably soon sustain self-replacing populations and will have to be reassessed as naturalized (sensu Richardson et al. 2000, Pyšek et al. 2004) in urban areas of the warmest regions in Central Europe, e.g. E and SE Austria (Vienna, Graz), S and N Switzerland (Tessin, Zurich – Landolt 1993) and SW Germany (Rhine valley and surroundings – Richter & Böcker 2001).

Habitats

In Central Europe, invasion of *P. tomentosa* is currently limited to urban ruderal habitats. Although the relative importance of habitats differs in SW Germany (40% in wall crevices, 16% in gravel, and 14% in crevices between paving stones, Richter & Böcker 2001), the general picture corresponds well with the Austrian data. Accompanying plant species are ubiquitous species typical of synanthropic vegetation. Low total plant cover and species numbers are due to extreme site conditions, e.g. partly sealed surfaces, trampling, extremely high summer temperatures and low water availability during periods of drought. *Paulownia tomentosa* is extraordinarily resistent to these stress factors.

Surprisingly, habitat preference in North America is different and natural habitats are invaded more frequently than in Central Europe (Williams 1983, 1993), although the species was introduced there in the same decade as in Central Europe (Remaley 1998) and is planted regularly in urban areas in both regions. In the E USA, the invasion of forests is strongly promoted by disturbance, e.g. forest clearings or gaps caused by hurricanes. It is a pioneer species in gaps of nemoral forests, at forest margins and along roadsides (Williams 1993, Simberloff 2000). In the Great Smoky Mountains National Park it is invading rock habitats and replacing native pine species in dry forests, after natural fire cycles are restored (Langdon & Johnson 1994). Similarily, intensive logging could promote the spread of *P. tomentosa* in forests, as is indicated by several records from forest clearings in Central Europe (Landolt 1993). The ability of *P. tomentosa* to spread to near-natural habitats in Central Europe is rarely reported (Landolt 1993, Brodtbeck et al. 1999). Successful colonization of these habitats, as already seen in the invasion by *Ailanthus altissima* (Kowarik & Säumel 2007), is a potential future scenario.

Habitat change of alien plants is not an uncommon phenomenon and usually makes less disturbed habitats colonizable (e.g. Trepl 1984, Kowarik 1995, 2003a). The future spread of *P. tomentosa* should be closely monitored. Furthermore, factors limiting the spread to natural areas should be investigated in order to assess future spread and associated risks to nature conservation.

Acknowledgements

R. May has made available distribution data kept at the database of the Floristic Mapping project of Germany. I am also obliged to H. Niklfeld, L. Schratt-Ehrendorfer and T. Englisch for access to the data of the project "Mapping the Flora of Austria". Valuable unpublished distribution data was provided by G. Heber, M. Hohla, W. Kabas, H. Kammerer, A. Mrkvicka, P. Pilsl, N. Sauberer, C. Schröck and H. Wittmann. I thank T. Dirnböck for statistical advice and W. Rabitsch, P. Pyšek and an anonymous reviewer for valuable comments. For the distribution data from Slovenia I am grateful to N. Jogan. Linguistic revision was done by M. Stachowitsch, final version of the manuscript was edited by Tony Dixon. This work was funded by the EU 6th FWP project DAISIE (SSPI-CT-2003-511202).

Souhrn

Práce analyzuje probíhající invazi *Paulownia tomentosa* (*Paulowniaceae*) v Rakousku. První lokality tohoto druhu byly zaznamenány v 60. letech minulého století ve Vídni, poté začal počet lokalit exponenciálně narůstat. V současnosti je druh zaznamenán na 151 lokalitách v 27 mapovacích polích. Počet lokalit v mapovacím poli je korelován s rokem prvního výskytu v poli, který v analýze pomocí zobecněných lineárních modelů vysvětluje 86% deviance. *Paulownia tometosa* je vázána na narušovaná stanoviště ve městech ležících v teplých nížinných oblastech v nadmořské výšce do 450 m n.m; 90% lokalit je udáváno z měst s více než 100 tis. obyvateli. Do polopřirozených stanovišť (lesní světliny, pobřežní křoviny) proniká zřídka. Invadované porosty se vyznačují nízkým počtem druhů (v průměru 8.9) i pokryvností bylinného patra (17%). Zatím druh nepředstavuje hrozbu z hlediska ochrany přírody, to se však může změnit s předpovídaným zvyšováním teplot. Ze stanovištní vazby *P. tometosa* ve východní částí USA, kde druh také invaduje, lze usuzovat, že pokračující invaze by mohla zasáhnout přirozenější stanoviště, jako jsou lesní světliny a okraje.

References

Adler W. & Mrkvicka A. C. (2003): Die Flora Wiens – gestern und heute. – Verlag des Naturhistorischen Museums Wien.

Adolphi K. (1995): Neophytische Kultur- und Anbaupflanzen des Rheinlandes. – Nardus 2: 1–271.

Adolphi K. (2001): In jüngster Zeit entdeckte Neophyten und Überlegungen über ihre mögliche Einbürgerung. – Braunschw. Geobot. Arb. 8: 15–24.

BEV (2006): Austrian Map. – URL: http://www.austrianmap.at/index-ie.html [accessed 14 Jan 2006].

Botond M. & Botta-Dukát B. (2004): Biologai invaziok magyaroszaragon Özönnövenyek. – Alapitavany Kiadó, Budapest.

Brodtbeck T., Zemp M., Frei M., Kienzle U. & Knecht D. (1999): Flora von Basel und Umgebung 1980–96. – Sonderdruck der Mitteilungen der Naturforschenden Gesellschaften bei der Basel 2: 543–1003.

Castro S. A., Figueroa J. A., Munoz-Schick M. & Jaksic F. M. (2005): Minimum residence time, biogeographical origin, and life cycle as determinants of the geographical extent of naturalized plants in continental Chile. – Diversity Distrib. 11: 183–191.

Chytrý M., Pyšek P., Tichý L., Knollová I. & Danihelka J. (2005): Invasions by alien plants in the Czech Republic: a quantitative assessment across habitats. – Preslia 77: 339–354.

Delisle F. C., Lavoie M. J. & Lachance D. (2003): Reconstructing the spread of invasive plants: Taking into account biases associated with herbarium specimens. – J. Biogeog. 30: 1033–1042.

Dullinger S., Dirnböck T. & Grabherr G. (2004): Modelling climate change driven tree-line shifts: relative effects of temperature increase, dispersal and invasibility. – J. Ecol. 92: 241–252.

Essl F. (2003): Bemerkenswerte floristische Funde aus Wien, Niederösterreich, dem Burgenland und der Steiermark. – Linzer Biol. Beitr. 35: 935–956.

Essl F. (2004): Floristische Beobachtungen aus dem östlichen Oberösterreich und dem angrenzenden Niederösterreich, Teil III. – Beitr. Naturk. Oberösterreichs 12: 131–183.

Essl F. (2005): Bemerkenswerte floristische Funde aus Wien, Niederösterreich, dem Burgenland und der Steiermark, Teil II. – Linzer Biol. Beitr. 37: 1207–1230.

Essl F. & Rabitsch W. (eds.) (2002): Neobiota in Österreich. – Umweltbundesamt, Wien.

Essl F. & Stöhr O. (2006): Bemerkenswerte floristische Funde aus Wien, Niederösterreich, dem Burgenland und der Steiermark, Teil III. – Linzer Biol. Beitr. 38: 121–163.

Fischer M. A., Adler W. & Oswald K. (2005): Exkursionsflora für Österreich, Liechtenstein und Südtirol. – Biologiezentrum Oberösterreich, Linz.

Forstner W. & Hübl E. (1971): Ruderal-, Segetal- und Adventivflora von Wien. – Notring Verlag, Wien.

Global Invasive Species Database (2006): *Paulownia tomentosa*. – URL: http://www.issg.org/database/species/ecology.asp?si=440&fr=1&sts [accessed 3 Feb 2006].

Haeupler H., Jagel A. & Schumacher W. (2003): Verbreitungsatlas der Farn- und Blütenpflanzen in Nordrhein-Westfalen. – LÖBF Nordrhein-Westfalen, Recklinghausen.

Hamburger I. (1948): Zur Adventivflora von Graz. – Doctoral Thesis, Univ. Graz.

Hohla M., Kleesadl G. & Melzer H. (1998): Floristisches von den Bahnanlagen in Oberösterreich. – Beitr. Naturk. Oberösterreichs 6: 139–301.

Keil P. & Loos G. H. (2004): Ergasiophygophyten auf Industriebrachen des Ruhrgebietes. – Flor. Rundbr. 38: 101–112.

Keil P. & Loos G. H. (2005): Preliminary account of ergasiophygophytic and xenophytic trees, shrubs and subshrubs in the Central Ruhrgebiet (Germany). – Electronic Publications of the Biological Station of Western Ruhrgebiet 3: 1–12.

Kiermeier P. (1977): Erfahrungen mit *Paulownia tomentosa* (Thunb.) Steud. im Rheingau. – Mitt. Deutschen Dendrol. Ges. 69: 11–22.

Kowarik I. (1995): On the role of alien species in urban flora and vegetation. – In: Pyšek P., Prach K., Rejmánek M. & Wade M. (eds), Plant invasions: general aspects and special problems, p. 85–103, SPB Acad. Publ., Amsterdam.

Kowarik I. (2003a): Biologische Invasionen: Neophyten und Neozoen in Mitteleuropa. – E. Ulmer Verlag, Stuttgart.

Kowarik I. (2003b): Human agency in biological invasions: secondary releases foster naturalisation and population expansion of alien plant species. – Biol. Inv. 5: 281–300.

Kowarik I. & Säumel I. (2007): Biological flora of Central Europe: *Ailanthus altissima* (Mill.) Swingle. – Persp. Plant Ecol. Evol. Syst. 8: 207–237.

Křivánek M., Pyšek P. & Jarošík V. (2006): Planting history and propagule pressure as predictors of invasion by woody species in a temperate region. – Conserv. Biol. 20: 1487–1498.

Kühn I., Brandl R. & Klotz S. (2004): The flora of German cities is naturally species rich. – Evol. Ecol. Res. 6: 749–764.

Kumar P. P., Rao C. D., Rajaseger G. & Rao A. N. (1999): Seed surface architecture and random amplified polymorphic DNA profiles of *Paulownia fortunei, P. tomentosa* and their hybrid. – Ann. Bot. 83: 103–107.

Landolt E. (1993): Über Pflanzenarten, die sich in den letzten 150 Jahren in der Stadt Zürich stark ausgebreitet haben. – Phytocoenologia 23: 651–663.

Langdon K. R. & Johnson K. D. (1994): Additional notes on invasiveness of *Paulownia tomentosa* in natural areas. – Nat. Areas J. 14: 139–140.

Lavoie C., Jean M., Delisle F. & Létourneau G. (2003): Exotic plant species of the St Lawrence River wetlands: a spatial and historical analysis. – J. Biogeogr. 30: 537–549.

Loacker K., Kofler W., Pagitz K. & Oberhuber W. (2006): Spread of walnut (*Juglans regia* L.) in an Alpine valley is correlated with climate warming. – Flora 202: 70–78.

Lockwood J. L., Cassey P. & Blackburn T. (2005): The role of propagule pressure in explaining species invasions. – Trends Ecol. Evol. 20: 223–228.

Mack R. N. (2005): Assessing biotic invasions in time and space: the second imperative. – In: Mooney J. A., Mack R. N., McNeely J. A., Neville L. E., Schei P. J. & Waage J. K. (eds), Invasive alien species: a new synthesis, p. 179–208, Island Press, Washington, D.C.

Mazomeit J. (1995): Zur Adventivflora (seit 1850) von Ludwigshafen am Rhein – mit besonderer Berücksichtigung der Einbürgerungsgeschichte der Neophyten. – Mitt. Pollichia 82: 157–246.

McCullagh P. & Nelder J. A. (1989): Generalized linear models. – Chapman & Hall, London.

McKinney M. (2001): Effects of human population, area, and time on non-native plant and fish diversity in the United States. – Biol. Conserv. 100: 243–252.

McNeely J. A., Mooney H. A., Neville L. E., Schei P. J. & Waage J. K. (2001): Global strategy on invasive alien species. – IUCN, Gland.

Melzer H. (1991): Neues zur Flora von Steiermark, XXXII. – Mitt. Naturwiss. Ver. Steiermark 121: 183–193.

Melzer H. (1999): Neues zur Flora der Bahnanlagen Kärntens. – Wulfenia 6: 21–28.

Melzer H. (2000): Neues zur Flora von Steiermark, XXXIX. – Mitt. Naturwiss. Ver. Steiermark 130: 107–120.

Melzer H. & Barta T. (1995): *Orobanche bartlingii* Grisebach, die Bartling-Sommerwurz, – neu für das Burgenland und andere Neuigkeiten zur Flora dieses Bundeslandes sowie von Nieder– und Oberösterreich. – Linzer Biol. Beitr. 27: 1021–1043.

Melzer H. & Barta T. (1996): Neues zur Flora des Burgenlandes, von Niederösterreich, Wien und Oberösterreich. – Linzer Biol. Beitr. 28: 863–882.

Mucina L., Grabherr G., Ellmauer T. & Wallnöfer S. (1993): Die Pflanzengesellschaften Österreichs. Vol. 3. – G. Fischer, Stuttgart.

Müllerová J., Pyšek P., Jarošík V. & Pergl J. (2005): Aerial photographs as a tool for assessing the regional dynamics of the invasive plant species *Heracleum mantegazzianum*. – J. Appl. Ecol. 42: 1042–1053.

Niklfeld H. (1998): Mapping the flora of Austria and the eastern Alps. –Rev. Valdot. Nat. 51: 53–62.

Nowack R. (1987): Verwilderungen des Blauglockenbaums (*Paulownia tomentosa* (Thunb.) Steud.) im Rhein-Neckar-Gebiet. – Flor. Rundbr. 21: 25–32.

Palmer M.W. (2006). Scale dependence of native and alien species richness in North American floras. – Preslia 78: 427–436.

Pyšek P. (1991). *Heracleum mantegazzianum* in the Czech Republic: the dynamics of spreading from the historical perspective. – Folia Geobot. Phytotax. 26: 439–454.

Pyšek P. & Prach K. (1993): Plant invasions and the role of riparian habitats: a comparison of four species alien to central Europe. – J. Biogeogr. 20: 413–420.

Pyšek P. & Prach K. (1995): Invasion dynamics of *Impatiens glandulifera*: a century of spreading reconstructed. – Biol. Conserv. 74: 41–48.

Pyšek P., Sádlo J. & Mandák B. (2002): Catalogue of alien plants of the Czech Republic. – Preslia 74: 97–186.

Pyšek P., Chocholoušková Z., Pyšek A., Jarošík V., Chytrý M. & Tichý L. (2004): Trends in species diversity and composition of urban vegetation over three decades. – J. Veg. Sci. 15: 781–788.

Pyšek P. & Hulme P. (2005): Spatio-temporal dynamics of plant-invasions: linking pattern to process. – Ecoscience 12: 302–315.

Pyšek P. & Jarošík V. (2005): Residence time determines the distribution of alien plants. – In: Inderjit (ed.), Invasive plants: ecological and agricultural aspects, p. 77–96, Birkhäuser Verlag, Basel.

Pyšek P., Müllerová J. & Jarošík V. (2007). Historical dynamics of *Heracleum mantegazzianum* invasion at regional and local scales. – In: Pyšek P., Cock M. J. W., Nentwig W. & Ravn H. P. (eds.), Ecology and management of giant hogweed (*Heracleum mantegazzianum*), p. 42–54, CAB International, Wallingford.

Rejmánek M. (2000): Invasive plants: approaches and predictions. – Austr. Ecol. 25: 497–506.

Remaley T. (1998): Plant conservation alliance fact sheet: princess tree. – URL: http://www.nps.gov/plants/alien/fact/pato1.htm [accessed 3 Feb 2006].

Ricciardi A., Steiner W. W. M., Mack R. N. & Simberloff D. (2000): Towards a global information system for invasive species. – BioScience 50: 239–244.

Rich T. C. G. & Karran, A. B. (2006): Floristic changes in the British Isles: comparison of techniques for assessing changes in frequency of plants with time. – Bot. J. Lin. Soc. 152: 279–301.

Richardson D. M., Pyšek P., Rejmánek M., Barbour M. G., Panetta F. D. & West C. J. (2000): Naturalization and invasion of alien plants: concepts and definitions. – Diversity Distrib. 6: 93–107.

Richter M. & Böcker R. (2001): Städtisches Vorkommen und Verbreitungszentren des Blauglockenbaumes (*Paulownia tomentosa*) in Südwestdeutschland. – Mitt. Deutschen Dendrol. Ges. 86: 125–132.

Roloff A. & Bärtels A. (1996): Gehölze. Bestimmung, Herkunft und Lebensbereiche, Eigenschaften und Verwendung. – E. Ulmer Verlag, Stuttgart.

Schmid M. (2005): Untersuchungen zur neophytischen Gehölzflora im Stuttgarter Stadtgebiet. – Jh. Naturkde. Württemberg 161: 187–257.

Simberloff D. (2000): Global change and introduced species in United States forests. – Sci. Tot. Env. 262: 253–261.

Stohlgren T. J., Jarnevich C., Chong G. W. & Evangelista P. H. (2006): Scale and plant invasions: a theory of biotic acceptance. – Preslia 78: 405–426.

Strobl W. (1995): Bemerkenswerte Funde von Gefäßpflanzen im Bundesland Salzburg IX. – Mitt. Ges. Salzburger Landesk. 135: 803–812.

Taylor B. W. & Irwin R. E. (2004): Linking economic activities to the distribution of exotic plants. – Proc. Natl. Acad. Sci. USA 101: 17725–17730.

Trepl L. (1984): Über *Impatiens parviflora* als Agriophyt in Mitteleuropa. – Diss. Bot. 73: 1–400.

Umweltbundesamt (2005): Naturschutzfachliches Informationssystem Austria (NISA). – URL: http://gis.umweltbundesamt.at/austria/natur/nisa/Default.faces [accessed 17 Aug 2005].

Walter J., Essl F., Englisch T. & Kiehn M. (2005): Neophytes in Austria: habitat preferences and ecological effects. – Neobiota 6: 13–25.

Wilhalm T., Stockner W. & Tratter W. (2002): Für die Flora Südtirols neue Gefäßpflanzen (2): Ergebnisse der floristischen Kartierung, vornehmlich aus den Jahren 1998–2002. – Gredleriana 2: 295–318.

Williams C. E. (1983): The exotic empress tree, *Paulownia tomentosa*: an invasive pest of forests. – Nat. Areas J. 13: 221–222.

Williams C. E. (1993): Age structure and importance of naturalized *Paulownia tomentosa* in a central Virginian streamside forest. – Castanea 58: 243–249.

Williamson M. (1996): Biological invasions. – Chapman & Hall, London.

Williamson M., Pyšek P., Jarošík V. & Prach K. (2005): On the rates and patterns of spread of alien plants in the Czech Republic, Britain, and Ireland. – Ecoscience 12: 424–433.

Wittenberg R. (ed.) (2005): An inventory of alien species and their threat to biodiversity and economy in Switzerland. – CABI Bioscience Switzerland Centre, Delemont.

Wittenberg R. & Cook M. J. W. (2001): Invasive alien species: a toolkit of best prevention and management practices. – CAB International, Wallingford.

Wittig R. (2002): Ökosysteme Mitteleuropas aus geobotanischer Sicht: Siedlungsvegetation. – E. Ulmer Verlag, Stuttgart.

Wu S. H., Chaw S. M. & Rejmánek M. (2003): Naturalized *Fabaceae* (*Leguminosae*) species in Taiwan: the first approximation. – Bot. Bull. Acad. Sin. 44: 59–66.

ZAMG (2006): Multi-centennial climate variability in the Alps. – URL: http://www.zamg.ac.at/alp-imp [accessed 14 Jan 2006].

Zechmeister H. & Grabherr G. (1998): Erfassung der Flora des Wiener Stephansdomes. – Verh. Zool.-Bot. Ges. Österreich 135: 323–342.

Zhao-Hua Z., Ching-Ju C., Xin-Yu L., Yao X. (1986): *Paulownia* in China. Cultivation and utilization. – Chinese Acad. Sci., Beijing.

Received 5 April 2007
Revision received 16 June 2007
Accepted 25 July 2007