Dendroclimatological comparison of native *Pinus sylvestris* and invasive *Pinus strobus* in different habitats in the Czech Republic

Dendroklimatologické srovnání původní *Pinus sylvestris* a invazní *Pinus strobus* v různých habitatech v České republice

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Mácová M. (2008): Dendroclimatological comparison of native *Pinus sylvestris* and invasive *Pinus strobus* in different habitats in the Czech Republic. – Preslia 80: 277–289.

Many species of the genus *Pinus* are important forestry trees that escape from plantations and invade natural and seminatural habitats. This study compares the native *Pinus sylvestris* with an invasive alien *P. strobus* in the Czech Republic in terms of their radial growth response to climate. *Pinus strobus* invades sandstone regions, while in areas with another bedrock and soil type it regenerates only sparsely. The research was conducted in six areas differing in abiotic characteristics and the degree of *P. strobus* regeneration. The effect of climate on the diameter growth was studied using moving and evolutionary correlation and response function analyses. Climatic factors affect radial growth of both species; some reactions are species-specific, others are the same for both species but differ in their intensity. *Pinus sylvestris* responded positively to high February/March temperatures, *P. strobus* negatively to high temperatures and low precipitation in the previous September in all study sites. Both species responded to summer rainfall in warm and dry areas, but the response of *P. strobus* was stronger than that of *P. sylvestris*. In sandstone areas, both species responded to specific microsite conditions. The study did not find a clear link between dendroclimatological response of *P. strobus* and its invasive behaviour in sandstone areas of the Czech Republic.

K e y w o r d s: Czech Republic, invasion, pine, precipitation, temperature, tree-ring growth

Introduction

Plant invasions occur in various habitat types and situations (Chytrý et al. 2005, Daehler 2006, Pyšek et al. 2006, Stohlgren et al. 2006, Sádlo et al. 2007) and invaders recruit from various life form groups (Křivánek et al. 2006, Perglová et al. 2006, Moravcová et al. 2006, Essl 2007, Kollmann et al. 2007). Coniferous trees are among the most successful invaders with substantial impact on resident vegetation and their invasions often result in changes in ecosystems functioning (Richardson et al. 2000, Richardson & Rejmánek 2004). Forestry trees are widely planted all over the world, escape from cultivation (Křivánek et al. 2006, Křivánek & Pyšek 2006) and cause changes to biodiversity in many areas, especially in the Southern hemisphere (Richardson & Higgins 1998, Richardson & Rejmánek 2004). However, invasive trees are also a problem in the Northern hemisphere, such as Euroasian species invading in North America and vice versa (e.g., Leege & Murphy 2001, Sykes 2001, Kilgore & Telewski 2004, Broncano et al. 2005, Křivánek & Pyšek 2006). The genus *Pinus* consists of a high number of species, some with very large native ranges, and includes some species most frequently used in forest cultivation (Richardson 1998, 2006). In Europe, four of 12 native pine species are widely planted for timber: *Pinus sylvestris*, *P. pinaster*, *P. nigra* and *P. halepensis*. In the second half of the 18th century and the 19th century, 12 other pine species were introduced to increase timber production and several others as ornamental trees to gardens (Tutin et al. 1990). Among these, only *P. contorta* and *P. strobus* are reported to spread from plantations into the surrounding vegetation (Knight et al. 2001, Hadincová et al. 2007).

Successful naturalization and invasion is determined by a complex suite of environmental factors (see e.g., Pyšek & Richardson 2006), one of them being the response to climate in the region of introduction (e.g., Thuiller et al. 2005). Dendroclimatological comparisons of native and alien invasive species (e.g., Kilgore & Telewski 2004, Mortenson & Mack 2006) can contribute to the explanation of invasive behaviour. Dendroclimatological response of the native *P. sylvestris* is well studied in various parts of Europe, including temperate countries such as Austria, Germany and Poland (Spurk 1997, Oleksyn et al. 1998, Oberhuber et al. 1998, Oberhuber & Kofler 2000, Wilczyński & Skrzyszewski 2002). There is no information on the dendroclimatological response of *P. strobus* in Europe, although this species is widely planted in several countries (Musil 1971). From its native range in North America, where *P. strobus* is very common, there are only a few studies dealing with its dendroclimatology (Lyon 1940, Abrams et al. 2000, Kilgore & Telewski 2004).

The aim of this study is to evaluate whether there are differences in the response of both pine species to climate and if so, whether they could explain the recent invasion of sandstone regions in the Czech Republic by *Pinus strobus*.

Material and methods

Study species

In Central Europe, *Pinus sylvestris* is a dominant species in open forests on extreme sites such as rock outcrops with various bedrock types, peaty soils and other nutrient-poor habitats (Richardson & Rundel 1998). *Pinus strobus* is native to a large part of the E North America, where it occcurs mainly on dry sandy soils (Nichols 1935, Richardson & Rundel 1998). Both species are very stress-tolerant but *P. strobus* is more shade-tolerant than *P. sylvestris* (Nikolov and Helmisaari 1992).

Pinus strobus was introduced to forest stands in the Czech Republic at the end of the 18th century and intensive planting began in the 20th century (Nožička 1965). It was first reported as an invasive species in the sandstone area of Labské pískovce by F. Čeřovský in 1953 (Härtel & Hadincová 1998). At present, *P. strobus* reproduces naturally in this region, suppresses native vegetation by forming dense monocultural stands and by depositing a thick layer of needle litter (Härtel & Hadincová 1998), and outcompetes the native *P. sylvestris* by crown competition (Mácová 2001). As a consequence, the relic *P. sylvestris* forests on sandstones have become a highly endangered forest community. Contrary to this, in other areas with different bedrock and soil types almost no regeneration of *P. strobus* is observed (M. Mácová & T. Tichý, personal observation). The species is also reported as invasive in Germany and Hungary (Richardson 2006).

Study areas

The research was carried out in six areas in the Czech Republic, with different environmental conditions and different degrees of *Pinus strobus* natural regeneration and spread into forest stands composed of other tree species (Fig. 1, Table 1).

Areas W1 and W2 are in warm and dry regions, especially W1 (SW Moravia), which is very dry because it is in the rain shadow of the Bohemian-Moravian Upland (Českomoravská vrchovina). W2 is less extreme, situated in a flat valley of the Elbe river with a low annual precipitation. S1 and S2 are sandstone areas, S1 (Bohemian Paradise – Český ráj) is warmer and drier than S2 (Elbe River Sandstone Mountains – Labské pískovce) but the stands, from which the samples were collected are on extremely dry rocky sites in both areas. C1 and C2 represent cold and moist regions. C1 is in the SW foothills of the Bohemian-Moravian Upland and is moderate in terms of temperature and moisture. C2 (Bohemian Forest – Šumava) is a cold and very wet mountain area; although not located at the timberline (which is not present in this mountain range, not even at the highest altitudes), the stands at C2 are where *P. strobus* forests reach altitudinal maximum in the Czech Republic.

According to the forest management records, *P. strobus* has been planted continuously since the 1850s at W1 and W2, 1860s at S1, 1790s at S2 (but more frequently after the 1820s), 1830s at C1 and 1880s at C2 (Nožička 1965).

At W1, C1 and C2, *P. sylvestris* is planted in study plots and *P. strobus* rarely regenerates; seedlings are rare and saplings never occur in the study plots. At W2, the regeneration in the planted *P. strobus* stands has increased recently and a dense cover of up to about 25 year old seedlings and saplings is now present there. *Pinus sylvestris* may occur naturally at some sites in this region but not at the study plots. Areas S1 and S2 are extensively invaded by *P. strobus*, which is very fecund and invades natural and seminatural stands of *P. sylvestris*.

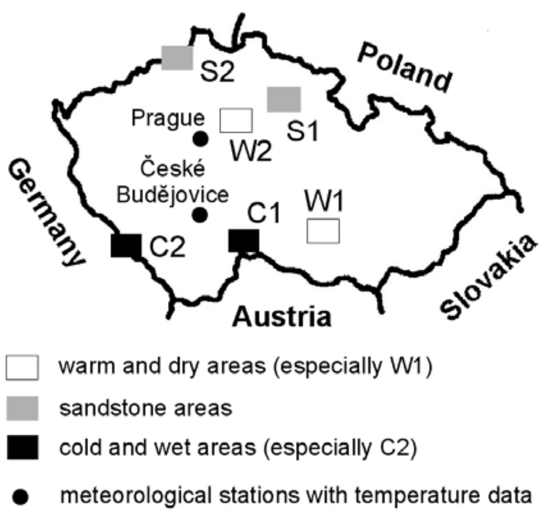

Fig. 1. – Location of the study areas and meteorological stations in Prague and České Budějovice. Local stations with precipitation data are not shown.

Table 1. – Description of the research areas. MAT – approximate mean annual temperatures for the period 1961–1990; according to the map of mean annual temperatures, internet pages of the Czech Hydrometeorological Institute (http://www.chmi.cz/meteo/ok/tr6190w.jpg); MSP – mean annual sums of precipitation from the local meteorological stations in the period of analyses (1928–1996). However, study plots S1 and especially S2 are on extreme sandstone sites with permeable bedrock, so the amount of water available for tree growth is much less than can be expected from the precipitation. Furthermore, for C2, the series from a distinctly drier place was used due to lack of a long enough local series; in these short local series the mean annual sums of precipitation can reach more than 1000 mm.

Area code	Latitude Longitude	Altitude (m a.s.l.)	Area characteristics	Bedrock and soils	Level of *Pinus strobus* invasion	Year of sampling
W1	49°06'–49°10' 16°14'–16°19'	250–420	warm and dry area in rain shadow; MAT 8–9 °C, MSP 520 mm	gneiss cambisols	increasing regeneration in recent years	2004
W2	50°11'–50°15' 14°34'–14°44'	145–200	warm and relatively dry; flat river valley; MAT 8–9 °C, MSP 471 mm	river sediments arenic cambisols	no invasion	2000–2001
S1	50°28'–50°33' 15°04'–15°16'	300–450	warm and dry area with rocky stands; MAT 8–9 °C, MSP 667 mm	sandstone podsols	massive invasion to surrounding forests	2002–2003
S2	50°51'–50°52' 14°22'–14°27'	300–360	moderately warm and wet area with dry rocky stands; MAT 7–8 °C, MSP 901 mm	sandstone podsols	massive invasion to surrounding forests	1996–1999
C1	49°02'–49°07' 14°51'–15°00'	480–670	relatively cold and wet upland area; MAT 6–7 °C, MSP 622 mm	granite cambisols	no invasion	2000
C2	48°53'–49°08' 13°27'–13°52'	730–960	cold and wet mountain area; MAT 4–5 °C, MSP 602 mm	migmatites podsols	no invasion	2003

Sample collection

Between 25–50 trees were selected at three study plots in each area (Table 2). Usually two increment cores were taken from opposite sides of each tree at a height of 1.3 m above the ground. The cores were sanded, scanned and the width of the annual rings measured using the WinDENDRO™ program (Guay 1995). The ring-width series were checked using the COFECHA correlation program (Grissino-Mayer 2001) and series, which could not be dated unambiguously, were excluded. Mean ring-width chronologies for each plot were developed using the ARSTAN program (Grissino-Mayer et al. 1992). The series were detrended in two stages; first, using a negative exponential function, and second, a cubic smoothing spline with a 50% frequency response cut-off of 70% series length, with a minimum spline rigidity of 50 years (Cook et al. 1990). From these three chronologies (Standard, Residual and Arstan), residual chronologies with the strongest common high-frequency variation were used (see Table 2 for statistical characteristics).

Data analysis

Relationships between ring-width chronologies and climate variables were studied using correlation and response function analyses (Briffa & Cook 1990). Mean monthly temperatures were taken from meteorological stations in České Budějovice (388 m a.s.l.; mean an-

Table 2. – Descriptive statistics of the residual chronologies of *Pinus sylvestris* and *Pinus strobus*: MS – mean sensitivity; SD – standard deviation.

Area	Plot	Trees	Cores	Chronology span (with signal strength > 0.85)	MS	SD
Pinus sylvestris						
W1	1	28	54	1913–2003	0.26	0.23
	2	30	58	1901–2003	0.22	0.19
	3	32	64	1918–2003	0.18	0.17
W2	1	34	66	1897–1999	0.23	0.19
	2	31	57	1924–1999	0.26	0.23
	3	31	57	1926–2000	0.24	0.20
S1	1	25	49	1868–2002	0.18	0.16
	2	28	56	1901–2002	0.17	0.16
	3	31	62	1893–2003	0.20	0.20
S2	1	31	53	1855–1996	0.16	0.16
	2	34	63	1851–1998	0.17	0.16
	3	33	62	1827–1998	0.16	0.15
C1	1	31	58	1879–1999	0.19	0.17
	2	27	54	1924–1999	0.17	0.16
	3	30	58	1917–1999	0.14	0.12
C2	1	29	56	1900–2002	0.15	0.15
	2	35	64	1895–2002	0.16	0.16
	3	30	58	1921–2002	0.14	0.15
Pinus strobus						
W1	1	30	59	1918–2003	0.29	0.25
	2	32	63	1932–2003	0.23	0.20
	3	31	58	1915–2003	0.18	0.17
W2	1	31	60	1928–2000	0.26	0.24
	2	30	59	1926–2000	0.29	0.25
S1	1	25	51	1902–2002	0.18	0.16
	2	30	60	1926–2002	0.17	0.14
	3	25	47	1924–2003	0.17	0.14
S2	1	50	50	1916–1997	0.14	0.13
	2	45	62	1917–1999	0.14	0.13
	3	40	47	1915–1998	0.16	0.14
C1	1	30	60	1919–1999	0.17	0.15
	2	30	58	1902–1999	0.20	0.18
	3	29	57	1916–1999	0.16	0.14
C2	1	30	55	1935–2002	0.15	0.13
	2	26	44	1928–2002	0.14	0.12
	3	30	58	1918–2002	0.15	0.14

nual temperature 8.2°C over the analysed period 1928–1996; used for C1 and C2) and Prague (191 m a.s.l.; mean annual temperature 9.4°C in 1928–1996; used for all the other areas). Monthly sums of precipitation were taken from local stations (up to 30 km from the study plots) except for C2 where data from České Budějovice (45–80 km from the study plots) were used because the local series were too short or had large gaps in the 1940s. Mean annual sums of precipitation are given in Table 1. Climate data from July of the previous year to September of the year in which a tree-ring was developed were included.

Moving, as well as forward evolutionary and backward evolutionary correlation and response function coefficients (Biondi 1997) were computed by the DendroClim 2002 program (Biondi & Waikul 2004). The method of response function analysis is based on stepwise multiple regression, where climatic variables (monthly mean temperatures and monthly sums of precipitation) are used after their transformation into principal components. The significance of climatic variables is tested using bootstrap techniques (Guiot 1990). Moving response function is based on a fixed number of years shifted in time. Forward and backward evolutionary response functions use an increasing number of years with a fixed beginning and ending year of the interval, respectively. The chronologies were used in their maximum common period 1928–1996 except for short chronologies for plot 2 from W1 (only 1932–1996) and plot 1 from C2 (only 1935–1996). For these two chronologies, forward evolutionary correlation and response functions were not computed.

Results

A summary of results from the moving correlation analysis is shown in Fig. 2. Each cell represents a reaction to climate in a particular month in a 53-year time window (the first time window is 1928–1981, the last 1943–1996). Similar results were obtained using forward and backward evolutionary correlation analyses, and response function analyses, where the coefficients were similar but slightly lower than in the correlation analyses (results not shown here).

Response to temperature

Warm and dry September in the previous year negatively affected the radial growth of *P. strobus* in all six areas and that of *P. sylvestris* in warm and dry areas W1 and W2. Above-average temperatures in February and/or March of the current year had a strong positive effect on the radial growth of *P. sylvestris* in all areas, but for *P. strobus* only in sandstone areas S1 and S2 (Fig. 2).

Response to precipitation

Both species showed a positive response to high precipitation in summer. This was very strong for *P. strobus* in all areas (only slightly weaker in the cold areas C1 and C2). *Pinus sylvestris* from warm and dry areas W2 and W1 responded very strongly to precipitation, but very weakly in the sandstone areas S1 and S2; its reaction was even weaker than in cold and wet areas C1 and C2 (Fig. 2).

Discussion

Effect of climate on growth

The study showed distinct responses of two pine species to climate in all the regions studied. Some of these responses are in good agreement with the results for *Pinus sylvestris* or other conifers in Central Europe or other areas with similar ecological conditions (e.g., Schichler et al. 1997, Spurk 1997, Dittmar & Elling 1999, Wilczyński & Skrzyszewski

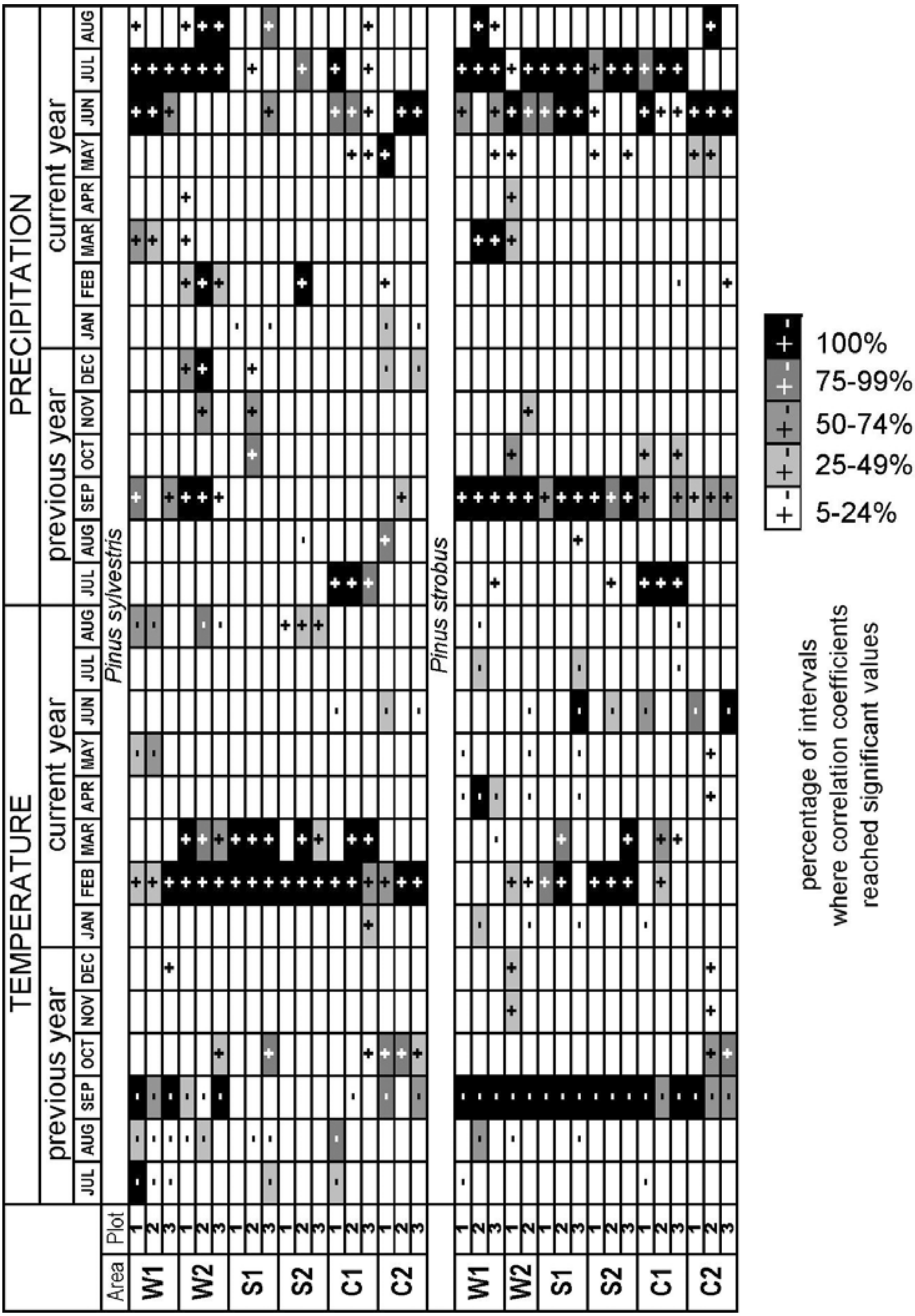

Fig. 2. – Summary of results of the moving correlation analysis. Each "cell" represents the growth response to climate in a particular month within the sixteen 53-year periods from 1928–1981 to 1943–1996. Signs show the type of the response (positive/negative), the shade of grey indicates the percentage of the periods in which the correlation is significant ($P < 0.05$).

2002). There is, however, lack of similar studies on *P. strobus* in Europe and a low number of such studies of this species in its native distribution range (Lyon 1940, Abrams et al. 2000, Kilgore & Telewski 2004).

The negative correlation between the width of tree-rings and temperature in the September prior to the growing season is surprising. Similar results are reported for *P. sylvestris* and *Picea abies* but mostly for August instead of September (e.g., Lindholm et al. 2000, Miina 2000, Mäkinen et al. 2001, Mäkinen et al. 2002, Rigling et al. 2003, Rolland & Lemperiere 2004). These studies were carried out at higher latitudes or altitudes (Alps, S Fennoscandia), where the growing season is shorter and, therefore, the end of the growing season occurs earlier. In locations closer to the Czech Republic, the same response was reported for *Abies alba* in Slovenia (Schichler et al. 1997) and *Picea abies* from middle altitudes in Germany (Dittmar & Elling 1999). However, the majority of studies do not include data for September of the previous year in their analyses (e.g., Grace & Norton 1990, Wilczyński & Skrzyszewski 2002, Feliksik & Wilczyński 2004) or do not find any significant reaction to temperature in September of the previous year (e.g., Spurk 1997, Strumia et al. 1997). Fritts (1974) and Chhin et al. (2004) report a relationship between narrow tree-rings and high temperatures in combination with low precipitation in the autumn of the previous year in areas where the growth of tree is limited by moisture availability. They account for this by accounting that in hot summers/early autumns net photosynthesis is reduced due to increased evaporation and transpiration, which may lead to a depletion of food reserves the following year. LaMarche (1974) reports a negative relationship between temperatures in the period prior to the growing season and the length of needles near the arid lower forest border in the SW USA. It is likely that the same mechanism influences *Pinus strobus* and *P. sylvestris* on dry and warm sites in Central Europe.

A positive relationship between tree-ring width and mean temperature in February and/or March is reported for *P. sylvestris* growing in low and middle altitudes of Central Europe (Spurk 1997, Oleksyn et al. 1998, Wilczyński & Skrzyszewski 2002). This may be due to an early start of the vegetation period in warm years or, more likely, to frost damage in cold years.

Summer precipitation influenced the tree-ring growth of both species at all the study stands, although with different intensities. This positive response is common in pines at low and middle altitudes throughout Central Europe, especially on dry sites, but is reported also for less extreme sites (Spurk 1997, Strumia et al. 1997, Wilczyński & Skrzyszewski 2002). The response of *P. sylvestris* to precipitation on dry rocky sites at S1 and S2 was weaker than that of *P. strobus*, which agrees with the results of other studies from the same region (Mácová 2001, Mácová & Tichý 2007). The weak response of *P. sylvestris* to summer precipitation in the sandstone areas may be due to differences in microsite conditions and root architecture of both species, which enables *P. sylvestris* to better utilize small water reserves (Rundel & Yoder 1998). The strong response of *P. strobus* to February/March temperatures in the sandstone areas may be because extremely dry and nutrient-poor sites enhance the effect of frosts on trees growing in open forests (Tranquillini 1979).

Response to climate and invasive behaviour

The relationships between tree-rings and climate are used to predict the behaviour of trees under climate change (e.g., Wilmking et al. 2004, Andreu et al. 2007, Di Filippo et al. 2007). In Central Europe, it is predicted that there will be an increase in temperature and extreme weather events such as periods of drought combined with sudden floods (Watson et al. 1997). As both pine species studied respond to climatic factors in a complex way, it is unknown which factors might be important determinants of future growth as global climate changes. Both species are tolerant of stress induced by climatic extremes. However, studies of *P. sylvestris* in the Alps (Rigling et al. 2003, Bigler et al. 2006) indicate a high mortality due to drought. In addition, Oleksyn et al. (1998) reports earlier cessation of growth of *P. sylvestris* at high temperatures. Potential changes in the geographical distribution of *P. sylvestris* provenances with climate change in the former USSR are described by Rehfeldt et al. (2002). However, it needs to be borne in mind that short-term climatic fluctuations also influence regeneration and invasion of alien species on a local scale (Richardson & Bond 1991).

Mortenson & Mack (2006) suggest that alien conifers planted in the northern USA have a weak potential to become naturalized; the only two exceptions are *P. sylvestris* and *P. thunbergii*. One of the reasons for the invasion success of *P. sylvestris* in that region is its broad ecological amplitude; for *P. thunbergii* it is its ability to outcompete native woody species. This study found no differences in the climatic responses of pairs of native and introduced species (Mortenson & Mack 2006). A low invasion potential of introduced conifers in the North America is also reported from California (Burns & Sauer 1992). As regards Europe, Peterken (2001) discusses potential risks associated with several introduced tree species (not including *P. strobus*) in Great Britain. Sykes (2001) reports *P. contorta* as a potentially problematic alien pine in Sweden (see Richardson & Rejmánek 2004, Richardson 2006 for the list of other potentially invasive species).

Previous studies on the genus *Pinus* (Rejmánek & Richardson 1996, Richardson 2006) found that among the most important characteristics of an invasive species is short juvenile period, short interval between large seed crops and small seed mass. With the exception of the last parameter, it is also true when *P. strobus* and *P. sylvestris* are compared. Furthermore, the ability of the alien to outcompete the native species is also a crucial factor (Härtel & Hadincová 1998). This study found relationship between *P. strobus* tree-ring growth and climate in areas where the species is and is not invading. The most distinct difference is the positive response to February/March temperatures, which is quite strong in invaded sandstone areas but weak or absent in other regions. *Pinus strobus* was also found to be more sensitive to water stress in summer than *P. sylvestris* while in other study areas the response is quite similar. Although *P. strobus* grows in its native range on dry acidic soils (Richardson & Rundel 1998, Kilgore & Telewski 2004) and it is thought to be water stress-tolerant, studies of *P. strobus* from its native range report a high sensitivity to water stress (Lyon 1940, Abrams et al. 2000).

In general, the relationships between tree-ring growth and climate of both species in NE USA and central Europe are similar. The climate matching between both areas is relatively high and the slight differences (longer and cooler winters and higher annual precipitation at American study sites than European ones) have negligible effect on the growth of *P. strobus* in the new range. Although the association between the tree-ring growth and climate in Europe may differ, the propagule pressure is strong enough to trigger an invasion. It is not possible to simply associate the response to climate with invasion, beacause many other factors are involved in invasiveness (Richardson & Pyšek 2006). As for possible change in the growth of both species in response to climate change, the key factor is that both of the species studied are highly tolerant of stress but similarly sensitive to climatic extremes. There is no reason to think that changes in climate are likely to change the competitive species status between these two species.

Acknowledgements

I thank T. Tichý for help with field and laboratory work and J. Dobrý, V. Hadincová, T. Kyncl, P. Pyšek and J. Wild and three anonymous reviewers for their valuable comments on the manuscript. Tony Dixon kindly edited my English. This study was supported by grant projects no. B6005302 of the Grant Agency of the Academy of Sciences of the Czech Republic, no. 526/05/0430 of the Grant Agency of the Czech Republic and no. AV0Z60050516 of the Academy of Sciences of the Czech Republic.

Souhrn

Rostlinné invaze jsou důležitým faktorem ovlivňujícím stav a změny vegetace v celosvětovém měřítku. Druhy rodu *Pinus* patří mezi nejčastěji lesnicky pěstované dřeviny, jež se ve velkém rozsahu stávají invazními druhy. Předkládaná studie se zabývá srovnáním reakce radiálního růstu dvou lesnicky využívaných druhů, autochtonní *Pinus sylvestris* a introdukované *Pinus strobus*, na klimatické podmínky. *Pinus strobus* se v pískovcových oblastech České republiky chová jako invazní druh, zatímco v oblastech s jinými typy podloží a půd ve větší míře nezmlazuje. Výzkum probíhal v šesti oblastech lišících se abiotickými vlastnostmi a mírou zmlazení *P. strobus*. Vliv klimatických faktorů na radiální přírůst byl studován pomocí korelačních analýz a tzv. funkce odezvy (metody založené na mnohonásobné regresi). V rámci studie bylo zjištěno, že některé z klimatických faktorů mají vliv na růst jen u jednoho ze studovaných druhů, zatímco jiné ovlivňují oba druhy, avšak s různou intenzitou. Ve všech studovaných oblastech byl radiální růst *P. sylvestris* pozitivně ovlivněn vysokými teplotami v únoru a/nebo březnu, zatímco *P. strobus* reagovala negativně na vysoké teploty a nízké úhrny srážek v září předchozího roku. Oba druhy reagovaly podobně na letní srážkové poměry především v teplých a suchých oblastech; reakce byla obvykle silnější u *P. strobus* než u *P. sylvestris*. V pískovcových oblastech se u obou druhů projevily specifické reakce na mikrostanovištní podmínky. Studie neprokázala souvislost mezi reakcí *P. strobus* na klima a jejím invazním chováním v pískovcových oblastech České republiky.

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Received 6 December 2007
Revision received 8 April 2008
Accepted 23 April 2008