Pollen quality in some representatives of the genus *Pinus*

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Abstract

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During spring 2012 pollen quality of 12 pine species (*P. cembra* L., *P. armandii* Franch., *P. wallichiana* A.B. Jacks., *P. strobus* L., *P. bungeana* Zucc. ex Endl., *Pinus nigra* J.F. Arnold, *P. sylvestris* L., *P. mugo* Turra, *P. coulteri* D. Don, *P. jeffreyi* Balf., *P. ponderosa* Douglas ex C. Lawson, *P. rigida* Mill.) growing in Mlyňany Arboretum was investigated. Pollen germination was tested at 25 °C on medium consisting of 1.5% agar and 10% sucrose. Each sample was triplicated. After 48 hours the number of germinating pollen was recorded from a sample of 100 pollen grains, whereas the pollen tube length in a sample of 30 pollen grains of each Petri dish. Data on average daily temperatures were taken from the local meteorological station in Mlyňany Arboretum. In general, all the analyzed pine species showed high levels of germination ranging from 85% in *P. ponderosa* to 98.89% in *P. cembra*. The pollen tube length averaged between 57.11 µm in *P. bungeana* and 139.2 µm in *P. mugo*. Both these pollen viability parameters were compared by Duncan test and variation analysis (anova). Our results indicate that pollen quality characteristics are more similar in closely related species of pines with pollen shedding in the same period than in systematically distant species with different periods of their pollen shedding. We suppose annual variation in the pollen quality of systematically related species that are shedding their pollen at the same time and which show similar behaviour in several aspects of pollen development. Expected impact of other factors is discussed.

Key words

Pinus species, pollen quality, temperature

Introduction

The genus *Pinus* with 116 species is the largest genus in the family Pinaceae. This genus is divided into subgenus *Strobus* with 43 species and subgenus *Pinus* with 73 species (Businský, 2008). Pines exhibit the greatest diversity of habitat and distribution of the needle-type evergreens, being scattered throughout the Northern Hemisphere from the Arctic Circle to Guatemala, the West Indies, North Africa, and Malayan Archipelago (Dirr, 1975). Only one species, *P. merkusii* Jungh et de Vriese, 1845 in Sumatra, has crossed the equator (Everett, 1981). The processes of introduction and acclimatization of exotic woody plants are often investigated in the arboretums including those pine species which does not occur together naturally.

Pollen size, its germination and pollen tube length are the variable characters of pollen which are sometimes used in studies an introduction (Skogsmyr and Lankinen, 2002). Although they depend in a large degree on the environmental factors (Young and Stanton, 1990; Quesada et al., 1995; Delph et al., 1997; Travers, 1999; Parantainen and Pulkkinen, 2002) the decisive role of the genotype is undeniable (Skogsmyr and Lankinen, 2002). This implies that pollen quality parameters depend primarily on the species. However, this aspect of pollen biology is not investigated enough. Chira´s works (1963, 1964, 1964b, 1965, 1967a, 1967b) are rather descriptive, referring to relationship of the pollen quality and temperature. It is ledged generally that changes in environmental conditions may affect the reproductive process of plants.

Based on the assumptions given above we tried to describe the relationship between pollen quality of pine species growing on common area and systematic position of the tested species. By comparing the observed results with average daily temperatures, we tried to answer the question how the increase of temperature can affect the reproductive process of woody plants.

Material and methods

The study on pollen viability has included 12 species of pines growing in Arboretum Mlyňany SAS and belonging to the two subgenera of the genus *Pinus*. The species of the subgenus *Strobus* were represented by *P. cembra, P. armandii, P. wallichiana, P. strobus* and *P. bungeana*, whereas those of the subgenus *Pinus* by *Pinus nigra, P. sylvestris, P. mugo, P. coulteri, P. jeffreyi, P. ponderosa* and *P. rigida* (Businský, 2008). The pollen samples of analyzed species were collected in spring 2012 using three individuals of each species. The only exception was *P. ponderosa* represented by two individuals. Pollen was extracted from dessiccated microstrobili on May 4 in *P. sylvestris* and *P. nigra*, on May 10 in *P. rigida* and *P. ponderosa*, on May 11 in *P. mugo* and *P. cembra*, on May 21 in *P. jeffreyi, P. wallichiana, P. strobus* and *P. bungeana* and on May 30 in *P. armandii* and *P. coulteri*. Mature but still unopened compact microstrobili of individual trees were harvested shortly before shedding of pollen and transferred to the laboratory. The dry pollen was stored in a desiccator over silica gel at 4 °C for the period of 3 weeks and then used in germination test. Pollen germination was tested at 25 °C on medium consisting of 1.5% agar and 10% sucrose. Each sample was triplicated. After 48 hours the number of germinating pollen was recorded from a sample of 100 pollen grains, whereas the pollen tube length in a sample of 30 pollen grains of each Petri dish. The differences in pollen size and in pollen tube length and percentage between trees and individuals were tested by nested anova. Because the percentages were bimodally distributed, the germination data were transformed using the arcsin transformation ($p' = \arcsin \sqrt{p}$). All calculations were done using the GLM procedure of SAS (SAS 1988).

Results

We have revealed a high level of pollen germination in all the analyzed pine species (Table 1). The variability between trees is manifested in the pollen tube length rather than in the pollen germination percentage (Table 2). Our results showed that species from the subgenus *Strobus* were characterized by a higher pollen germination rate, whereas species from the subgenus *Pinus* by longer pollen tubes. There were only two exceptions to this finding (*P. mugo* in value of pollen germination and *P. ponderosa* in the length of pollen tubes).

Table 1. Pollen germination percentage in individual trees of pine species

Species	Tree	N	Mean ± SD [%]	Duncan test
Pinus cembra	1	3	98.67 ± 0.58	
Pinus cembra	2	3	98.33 ± 0.58	
Pinus cembra	3	3	99.67 ± 0.58	
Pinus cembra	Sum	9	98.89 ± 0.78	A
Pinus mugo	1	3	98 ± 2	
Pinus mugo	2	3	97.33 ± 1.15	
Pinus mugo	3	3	99.67 ± 0.58	
Pinus mugo	Sum	9	98.33 ± 1.58	AB
Pinus bungeana	1	3	99 ± 1	
Pinus bungeana	2	3	96.33 ± 2.08	
Pinus bungeana	3	3	97 ± 1	
Pinus bungeana	Sum	9	97.44 ± 1.74	BC
Pinus strobus	1	3	96 ± 2.65	
Pinus strobus	2	3	98 ± 1	
Pinus strobus	3	3	98 ± 1	
Pinus strobus	Sum	9	97.33 ± 1.8	C
Pinus wallichiana	1	3	96 ± 2	
Pinus wallichiana	2	3	98 ± 1	
Pinus wallichiana	3	3	95 ± 1	
Pinus wallichiana	Sum	9	96.33 ± 1.8	CD
Pinus armandii	1	3	95 ± 3	
Pinus armandii	2	3	96.67 ± 1.53	
Pinus armandii	3	3	94.67 ± 2.08	
Pinus armandii	Sum	9	95.44 ± 2.19	DE
Pinus nigra	1	3	96.67 ± 0.58	
Pinus nigra	2	3	90 ± 5	
Pinus nigra	3	3	97.33 ± 1.15	
Pinus nigra	Sum	9	94.67 ± 4.36	DE

Table 1. Pollen germination percentage in individual trees of pine species – continued

Species	Tree	N	Mean ± SD [%]	Duncan test
Pinus sylvestris	1	3	93.33 ± 2.89	
Pinus sylvestris	2	3	95 ± 0	
Pinus sylvestris	3	3	95 ± 0	
Pinus sylvestris	Sum	9	94.44 ± 1.67	DEF
Pinus coulteri	1	3	96.67 ± 1.53	
Pinus coulteri	2	3	94 ± 2	
Pinus coulteri	3	3	91 ± 1	
Pinus coulteri	Sum	9	93.89 ± 2.8	EF
Pinus rigida	1	3	91 ± 1.73	
Pinus rigida	2	3	91.33 ± 5.51	
Pinus rigida	3	3	94 ± 1	
Pinus rigida	Sum	9	92.11 ± 3.26	F
Pinus jeffrey	1	3	86.67 ± 1.53	
Pinus jeffrey	2	3	77 ± 2.65	
Pinus jeffrey	3	3	95 ± 2	
Pinus jeffrey	Sum	9	86.22 ± 8.01	G
Pinus ponderosa	1	3	89.67 ± 3.06	
Pinus ponderosa	2	3	80.33 ± 6.81	
Pinus ponderosa	Sum	6	85 ± 6.96	G

SD, standard deviation.

Table 2. Pollen tube length in individual trees of pine species

Species	Tree	N	Mean ± SD [µm]	Duncan test
Pinus mugo	1	90	115.03 ± 39.83	
Pinus mugo	2	90	162.88 ± 37.78	
Pinus mugo	3	90	139.68 ± 33.57	
Pinus mugo	Sum	270	139.2 ± 41.87	A
Pinus jeffrey	1	90	101.98 ± 41.32	
Pinus jeffrey	2	90	131.47 ± 52.16	
Pinus jeffrey	3	90	152.73 ± 52.67	
Pinus jeffrey	Sum	270	128.73 ± 53.08	B
Pinus coulteri	1	90	127.12 ± 41.36	
Pinus coulteri	2	90	127.12 ± 38.15	
Pinus coulteri	3	90	127.6 ± 41.14	
Pinus coulteri	Sum	270	127.28± 40.09	B
Pinus sylvestris	1	90	89.9 ± 40.62	
Pinus sylvestris	2	90	89.42 ± 41.43	
Pinus sylvestris	3	90	129.53 ± 39.11	
Pinus sylvestris	Sum	270	102.95 ± 44.44	C
Pinus nigra	1	90	111.17 ± 41.81	
Pinus nigra	2	90	86.03 ± 31.26	
Pinus nigra	3	90	108.75 ± 36.45	
Pinus nigra	Sum	270	101.98 ± 38.34	C

Table 2. Pollen tube length in individual trees of pine species – continued

Species	Tree	N	Mean ± SD [µm]	Duncan test
Pinus rigida	1	90	87.97 ± 32.59	
Pinus rigida	2	90	95.7 ± 42.36	
Pinus rigida	3	90	96.18 ± 34.81	
Pinus rigida	Sum	270	93.28 ± 36.88	D
Pinus cembra	1	90	105.37 ± 36.29	
Pinus cembra	2	90	83.62 ± 34.65	
Pinus cembra	3	90	89.9 ± 34.99	
Pinus cembra	Sum	270	92.96 ± 36.36	D
Pinus armandii	1	90	51.38 ± 21.32	
Pinus armandii	2	90	133.92 ± 31.19	
Pinus armandii	3	90	90.48 ± 33.6	
Pinus armandii	Sum	270	91.93 ± 44.57	D
Pinus wallichiana	1	90	86.52 ± 31.43	
Pinus wallichiana	2	90	98.6 ± 31.14	
Pinus wallichiana	3	90	87.97 ± 34.49	
Pinus wallichiana	Sum	270	91.01 ± 32.71	D
Pinus strobus	1	90	73.95 ± 30.2	
Pinus strobus	2	90	89.42 ± 37.1	
Pinus strobus	3	90	73.62 ± 28.04	
Pinus strobus	Sum	270	78.97 ± 32.72	E
Pinus ponderosa	1	90	39.29 ± 22.02	
Pinus ponderosa	2	90	89.34 ± 37.07	
Pinus ponderosa	Sum	180	64.32 ± 39.42	F
Pinus bungeana	1	90	36.83 ± 14.25	
Pinus bungeana	2	90	65.54 ± 14.54	
Pinus bungeana	3	90	68.94 ± 25.66	
Pinus bungeana	Sum	270	57.11 ± 23.73	G

SD, standard deviation.

The species *P. mugo, P. sylvestris* and *P. nigra* represent in the experiment taxonomic section *Pinus.* The longest pollen tubes were found in *P. mugo* (Table 2). Duncan tests confirmed greater similarity between pollen quality parameters of *P. sylvestris* and *P. nigra* than between *P. sylvestris* and *P. mugo* or *P. nigra* and *P. mugo*.

The species *P. ponderosa*, *P. jeffreyi* and *P. coulteri* represent section *Pseudostrobus* (Businský, 2008). With this group of species similar values of pollen germination were observed between the species *P. jeffreyi* and *P. ponderosa*. On the other hand, *P. jeffreyi* and *P. coulteri* showed a great similarity in pollen tube length. Individuals of *P. jeffreyi* and *P. ponderosa* showed the greatest variability in pollen germination of all the analyzed species (Table 1).

The species *P. wallichiana*, *P. strobus*, *P. armandii* and *P. cembra* represent section *Strobus* (Businský, 2008). Almost all these species were characterized by comparable levels of pollen germination (Table 1) and length of their pollen tubes (Table 2). The species *P. cembra* was an exception exhibiting other character value of pollen germination. Likewise, *P. strobus* was exceptional by its longer pollen tubes (Tables 1 and 2).

P. bungeana from the section *Gerardiae* and *P. rigida* from section *Trifoliae* were heavier compared to other analyzed pine species. Our results showed that pollen quality parameters of *P. rigida* are more similar to species from the subgenus *Pinus* and pollen quality parameters of *P. bungeana* are more similar to species from the subgenus *Strobus*.

Discussion

Among factors affecting pollen quality parameters external factors influencing pollen development during maybe mentioned on the first place microsporogenesis (Chira, 1965).

As shown by Chira (1964a), the development of pollen is most profoundly affected by ambient temperature. Each stage of pollen development exhibits different sensitivity to external temperature fluctuations (Chira, 1964a). Mitotic division of PMCs in archesporial tissue begins in July last year. This stage is less sensitive to low temperatures (Konar, 1960; Chira, 1965). Cold reduces activity of the cells in the archesporial tissue to a minimum. PMCs are further divided, when temperature rises above 2 °C (Chira, 1965). Archesporial tissues are resistant to cold, unless temperature does not fall below –20°C (Chira, 1965). Chira (1965) reported that low temperatures are particularly harmful to PMCs of *P. jeffreyi* and *P. coulteri*. When heterotypic prophase of PMCs starts, the period of development associated with increased sensitivity of dividing cells to temperature fluctuations begins (Chira, 1963, 1965). If the temperature rises above 5 °C, heterotypic prophase of PMCs starts. The process of prophase observed in PMCs of pine species lasted from 2 to 14 days as compared with several hours duration of homeotypic prophase (Chira, 1965). The period from the heterotypic metaphase to the tetrad formation lasted 2–6 days. Subsequent formation of complete pollen lasted from 4–13 days. After this division mature pollen is released from microstrobili in sunny days (Chira, 1965). Expect for microsporogenesis variation considerable interannual variability of the pollen quality parameters was detected (Chira, 1963). While in 1961 the average daily temperature has not fallen below 6 °C during the critical months leaving unaffected the course of pollen development and germination percentage of mature pollen ranging from 25% in *P. edulis* to 85% in *P. wallichiana, P. coulteri, P. nigra* ssp. *Pallasiana* in 1963 a sudden temperature drop below 0 °C for more than 15 days during meiosis caused an absolute sterility of *P. nigra* pollen and 83% sterility of *P. sylvestris* pollen (Chira, 1963). The temperatures below 5 °C adversely affect the course of pollen development in *P. sylvestris* and *P. nigra* during prophase provided the temperature decline is longer (2 °C for 3 days does not affect the course of meiosis) (Chira, 1965). In other of pines species normal development of pollen was detected. This finding is explained by a sufficiently high temperature (above 0 °C) during the relevant period. Therefore, the author believes that low temperature is a major cause of abnormal development of pollen in studied pine species. Curiously, the high temperatures can also affect adversely the pollen development (Chira, 1965). The author writes that the increase in temperature to 18 °C during tetrad development in *P. bungeana* caused a strong plasmolysis and significant deformation of the cells nuclei (Chira, 1965). Inhibition, resulting from lower average daily temperature (below –1 °C) as well as accelerating pollen development by higher temperatures (above 18 °C) during the initial division of the heterotypic prophase after the third mitotic division in PMCs cause reduction percentage of pollen germination and in some cases its complete sterility (Chira, 1965). Temperatures from 5 °C to 15 °C are optimal conditions for pollen development of most pine species (Chira, 1965). Some interspecies variation may be expected in the range of these temperatures. For example, *P. edulis* pollen germination in 1961 was 25% only, while for other pine species was significantly higher (up to 85% in *P. wallichiana, P. coulteri* and *P. nigra* ssp. *pallasiana*) (Chira, 1963). However, meiosis in *P. edulis* begins when exposed to the temperatures of 10–15 °C for 5–6 days (Chira, 1967a). Therefore, we assume that the temperatures above 5 °C may have a negative impact on the pollen development of this species. The species *P. sylvestris* and *P. nigra* may represent a similar example. These two species have shed their pollen about the same time but their germinations were 17% and 0% only. Our results indicate that pollen quality characteristics are more similar in pine species with pollen shedding in the same period than in pine species with different periods of their pollen shedding. This assumption is supported by Chira´s (1963) findings. When we compare the author´s observations in 1961 and 1962, we see that percentage of pollen germination of pine species that shed their pollen in the same period show the same direction of changes (increase or decrease). We assume that the process of meiosis of pine species that shed pollen in the same period is synchronized. By comparing the average daily temperature in 2012 with that given by Chira (1963, 1965), we can conclude that temperatures during the spring months of 2012 were optimal for pollen development of pines (Fig. 1). Although high percentages of pollen germination in all analyzed species were observed, Duncan test revealed differences between them. These results indicate that percentages of pollen germination are more similar in closely related species of pines than in systematically distant species (*P. strobus* and *P. wallichiana*, *P. nigra* and *P. sylvestris*, *P. jeffreyi* and *P. ponderosa* are typical examples). Synchronization of pollen shedding was observed in the first two pairs of these species. Shedding of *P. jeffreyi* and *P. ponderosa* pollen was not synchronous. This result indicates that under optimal weather conditions, they react similarly. The species *P. cembra* and *P. mugo* are the exceptions. They shed their pollen during the same period of time, but more closely related pine species shed in different periods. The variability in the pollen tube length is relatively high, but Duncan's test revealed a similar dependence as in pollen germination. Our results indicate that length of pollen tubes are more similar in closely related species of pines with pollen shedding in the same period than in systematically distant species with different periods of their pollen shedding. According to some authors (Kelly et al., 2002; Dufay et al., 2008) the size of pollen serve as an indicator of its viability. Some authors (van Breukelen, 1982; Lord and Eckard, 1984; Perez and Moore, 1985; Gore et al., 1990; Manicacci and Barrett, 1995) found a positive correlation between the length of pollen and length of pollen tubes, but other researchers (Cruzan, 1990; Pietarinen and Pasonen, 2004) did not confirm this dependence. We can compare one results with those presented by Chira (1964c). The above mentioned dependence is valid for the species *P. coulteri*, *P. jeffreyi* and *P. ponderosa* of the section *Pseudostrobus*. The author has found a relatively large size of pollen in *P. coulteri* and *P. jeffreyi* (112.4 µm and 102.1 µm) as compared with the reduced pollen size in *P. ponderosa* (84.4 µm). We have not measured pollen size in our experiment but pollen tube length parameters correlate well with the data given by Chira (1964). The pollen tube length in *P. ponderosa* has accordingly deviated statistically from the corresponding parameter of pollen in *P. jeffreyi* and *P. coulteri* the same applies for *P. strobus* and *P. wallichiana* of the section *Strobus* the pollen tube length of which has not deviated significantly from each other. Also pollen size of these species was nearly identical with the data published by Chira (1964) (81.4 µm resp. 83.3 µm). On the contrary, such a tendency has not been proved for the species *P. mugo*, *P. nigra* and *P. sylvestris* of the section *Pinus*. Both *P. nigra* and *P. sylvestris* shoved similar pollen size exhibiting simultaneously non significant difference in their pollen tube length as compared with *P. mugo* which has differed in both pollen characteristics from the pair of species given above.

Presented results indicate similarity of the pollen viability characteristics in taxonomically related species of pines growing on the same locality and shedding their pollen in the same period of time as compared with the corresponding characteristics of pollen in taxonomically distant species shedding their pollen in different periods of the flowering time. Annual variation in pollen quality of taxonomically related species shedding their pollen in the same period of time is expected to exhibit the same tendency. There exist a correlation between pollen size and pollen tube length in *Pinus* species belonging to the same section (*Pseudostrobus* and *Strobus*). However, this correlation has not been proved for the species of the section *Pinus*. Under conditions of a global warming, we expect increase in pollen quality of the species indigenous for the warmer regions of the world.

It is necessary to evaluate critically both the obtained results and conclusions drawn so far. We have subjected to analysis a relatively small number of pine individuals. In the next years, it would be necessary to carry out additional experiments with pine species growing in other localities. The attention would be paid primarily to the related pine species.

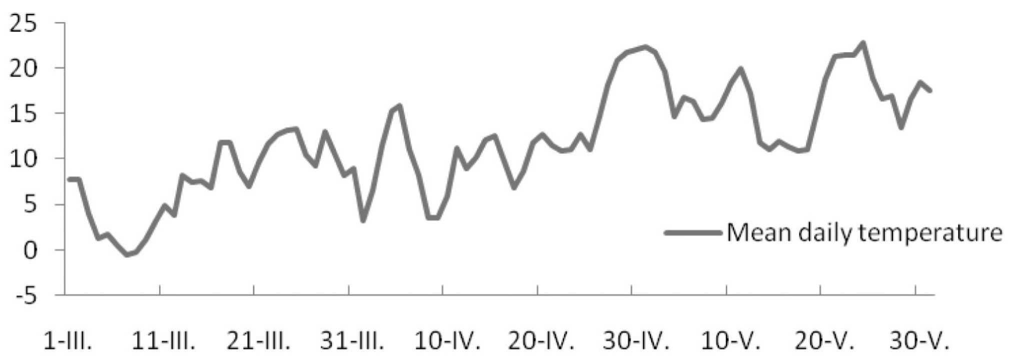

Fig. 1. Mean daily temperature variation in Arborertum Mlyňany during spring months 2012 (Source: Meterological station in Arboretum Mlyňany).

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Kvalita peľu vybraných zástupcov rodu *Pinus*

Súhrn

Počas jari 2012 sme skúmali kvalitu peľu 12 druhov borovíc (*P. cembra* L., *P. armandii* Franch., *P. wallichiana* A.B. Jacks., *P. strobus* L., *P. bungeana* Zucc. ex Endl., *Pinus nigra* J.F. Arnold, *P. sylvestris* L., *P. mugo* Turra, *P. coulteri* D. Don, *P. jeffreyi* Balf., *P. ponderosa* Douglas ex C. Lawson, *P. rigida* Mill.) rastúcich v Arboréte Mlyňany. Klíčivosť peľu bola analyzovaná pri teplote 25 °C na médiu s 1,5 % agaru a 10 % sacharózy. Každá vzorka peľu bola analyzovaná v trojnásobnom opakovaní. Klíčivosť bola hodnotená na vzorke 100 peľových zŕn, kým dĺžka peľových vrecúšok bola meraná iba z 30 peľových zŕn na každej Petriho miske po 48 hodinách kultivácie. Údaje o priemerných denných teplotách boli získané z meteorologickej stanice Arboréta Mlyňany SAV. Vo všeobecnosti všetky analyzované druhy borovíc vykazovali vysoké hodnoty klíčivosti (od 85 % pre *P. ponderosa* do 98,89 pre *P. cembra*). Hodnoty dĺžok peľových vrecúšok sa pohybovali v rozmedzí od 57,11 µm pre *P. bungeana* do 139,2 µm pre *P. mugo*. Hodnoty klíčivosti a dĺžky peľových vrecúšiek boli porovnané Duncanovým testom a variačnou analýzou (ANOVA). Naše výsledky naznačujú, že pokiaľ skúmame na jednej lokalite viaceré príbuzné druhy borovíc, ktoré v danom roku prášia v rovnakom období, tak charakteristiky kvality ich peľu budú podobnejšie ako pri systematicky vzdialených druhoch prášiacich v inom období. Predpokladáme, že medziročná zmena smeru kvality peľu bude pri systematicky príbuzných druhoch prášiacich v rovnakom období prebiehať rovnakým smerom. Predpokladaný vplyv ďalších faktorov je uvedený v diskusii.

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