

Taxon-specific pollen deposition dynamics in a temperate forest zone, SE Poland: the impact of physiological rhythmicity and weather controls

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Received: 16 February 2014 / Accepted: 27 November 2014 / Published online: 5 December 2014
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Abstract High and low pollen deposition years in the period 1998–2010 were recorded for ten forest-forming trees in Roztocze (SE Poland) using Tauber-style traps. The coincidence of very high/low pollen deposition years recorded in Tauber traps and aerobiological data obtained by volumetric samplers shows that these phenomena occur simultaneously in different places across vast areas of a tree's distribution range. The natural physiological rhythms displayed in abundance of flowering were considered on the basis of the observed data and published sources. The results obtained from applying Spearman's correlation to pollen accumulation rates from Roztocze and the meteorological parameters confirmed several statistically significant correlations between temperature and summer precipitation prior to pollen emission and a negative correlation with the winter temperature before pollen emission. Air temperature, precipitation, growing season duration (its start and end), winter

length and the number of winter days with a daily mean temperature below 0 °C were all considered. The best correlation coefficient results were obtained for the trees most abundant in the vegetation, namely *Abies alba*, *Fagus sylvatica* and *Pinus sylvestris*. Earlier findings on the controlling role of temperature and precipitation during the summer prior to pollen emission were confirmed, and a long period of winter dormancy was stressed as a factor favouring high pollen production. The examples from Roztocze reflected situations when a strong weather signal overrode the natural flowering rhythm. This was observable in the case of *P. sylvestris*, where pollen production reflected the air temperature of the previous summer or in the case of a mast year, which occurred across the whole distribution range of *F. sylvatica* in 2006.

Keywords Pollen monitoring · Temperate forests · Pollen deposition · Pollen–climate correlations

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1 Introduction

The increase in human pollinosis incidence throughout the world is well documented (Puppi Branzi and Zanotti 1992; Masoli et al. 2004; D'Amato et al. 2007; Shea et al. 2008; WHO Report 2012). Several common temperate tree taxa (e.g. *Betula* and *Alnus*) are recognized as being major causes of allergic

reactions in Europe (Emberlin et al. 1993, 1997, 2007; Hicks et al. 1994; Spieksma et al. 1995, 2003; Dahl and Strandhede 1996; Jäger et al. 1996; Aira et al. 1998; Corden et al. 2000; Janutunen et al. 2012; Puc and Kasprzyk 2013; Rodriguez-Rajo et al. 2006; Smith et al. 2007). Increased public interest in pollen production and dispersal patterns has sparked off numerous investigations into cyclicity, and the causes and triggers of pollen production. The start, duration and intensity of the pollen season have been studied with regard to the phenological events triggered by warming in Europe (Chmielewski and Rötzer 2001; Ahas et al. 2002).

The occurrence of high and low pollen production years is observable for most tree species. Natural physiological rhythms and concurrent weather conditions are considered to be the most important factors, among many, influencing pollen production and dispersal. Mast years triggering increased seed production were already well known and being utilized by farmers far back in time (Sork et al. 1993; Herrera et al. 1998; Koenig and Knops 2000). The enormous flowering efforts of wind-pollinated trees, which increases fertilization success rate have been recognized as being among the major causes of seed masting (Kelly 1994). The rhythm of abundant flowering and seed production is associated with the natural physiological rhythm of the alternate production of an abundant amount of reproductive organs 1 year and the growth of vegetative organs the next (Suszka 1983, 1990; Tomanek 1994; Yamauchi 1996; Spieksma et al. 2003). However, the actual enactment of a high/low pollen year depends on the weather conditions during the period of flower development, as well as pollen production in the anthers and pollen release into the atmosphere (Hicks 2001; Latałowa et al. 2002; van der Knaap et al. 2010 inter alia). In the case of the birch (*Betula*) and alder (*Alnus*), the existence of a biennial rhythm of pollen production has been suggested (Latałowa et al. 2002). In the case of other common European tree taxa with large reproductive organs [the beech (*Fagus*), oak (*Quercus*), fir (*Abies*) and spruce (*Picea*)], somewhat longer rhythms have been suggested. The 4-year rhythm was observed by Tonkov et al. (2001) for beech, oak and other species of the Fagaceae family growing in Bulgaria. In the case of some taxa, including that of pine, no rhythm has been identified (Tomanek 1994). The rare occurrence of years with high *Pinus sylvestris* pollen production

close to the distribution limit of this tree species has been reported by Huusko and Hicks (2009). Tomanek (1994) draws attention to the fact that trees typical of sub-montane zones (*Fagus sylvatica*, *Abies alba* and *Picea abies*) show less regularity in the occurrence of high and low pollen production years due to the severer climate conditions in the mountains. The increasing role of weather control as a major factor influencing pollen production at the limit of species' distribution range has been confirmed by pollen deposition studies (Pidek et al. 2010a, 2013). Disturbances in the regionally or temporarily synchronous occurrence of high/low pollen deposition years within the distribution range of a particular tree species can shed light on weather factors that can sometimes override natural rhythmicity and result in the unexpected shift of a high/low pollen year.

The 13-year-long (1998–2010) pollen trapping data series from the Roztocze region in SE Poland is one of the longest continuous records of annual pollen deposition from the temperate climatic zone. Its potential as a proxy for pollen–climate relationship studies was partly utilized by van der Knaap et al. (2010) in association with other PMP data across the transect in Europe and the Caucasus. On the basis of a large dataset from different climatic regions, the study revealed several very important relationships relating to correlation of the pollen production of the main forest-forming trees and meteorological parameters (air temperature and precipitation).

The present study on pollen deposition and meteorological parameter dynamics in the Roztocze area, SE Poland, aims to determine the pattern of the natural physiological flowering rhythmicity of ten common European tree taxa (*A. alba*, *F. sylvatica*, *Alnus glutinosa*, *Betula pendula*, *Carpinus betulus*, *Quercus robur*, *P. abies*, *Ulmus glabra*, *Fraxinus excelsior* and *P. sylvestris*), as well as identifying weather-induced disturbances in natural rhythm and determining meteorological factors possibly responsible for these disturbances.

1.1 An outline of the physiological, phenological and bioclimatic characteristics of the investigated taxa

All the surveyed tree taxa are native to Europe and typical of the northern temperate zone. Many of these taxa have a wide distribution range and/or are the

dominate forest-forming species in the boreal (*Betula pubescens*, *B. pendula*, *P. sylvestris* and *P. abies*) or nemoral (*F. sylvatica*, *Q. robur*, *Quercus petraea*, *F. excelsior*, *A. alba* and *C. betulus*, *A. glutinosa*) forest zones. The taxonomy of Angiosperms follows Bremer et al. (2009).

The Betulaceae family is represented in Roztocze by the following taxa: birch (*B. pendula* and *B. pubescens*), alder (*A. glutinosa*) and hornbeam (*C. betulus*). Of these, the share of *B. pubescens* is very small (Izdebski et al. 1992). All of these are early-successional trees native to most of Europe and well adapted to warm to cold temperate climates. The flowering of *B. pendula* occurs from the second half of April to the first half of May in Poland, but the flower buds are formed in late spring and early summer in the year before pollen emission (Suszka 1979). Abundant fruiting occurs every 2–3 years (Tomanek 1994). *B. pubescens* flowers 10–12 days after *B. pendula* (Suszka 1979). *A. glutinosa* flowers in March in Poland (Suszka 1980; Tomanek 1994), but the flower buds form in the second half of June of the previous year. Mast seed occurs every 2–3 years, and there is a good correlation between abundant pollen production and abundant seed production (Suszka 1980).

The hornbeam (*C. betulus*) is a broadleaved temperate species, which prefers moderately warm conditions (Zarzycki et al. 2002) and flowers in Poland at the end of April to the first half of May (Tomanek 1994). The factor limiting its distribution in the east is a lack of sufficient warmth for the development of seeds during late spring (Faliński and Pawlaczyk 1993). Successful fruiting occurs every 2 years.

The Pinaceae family is mainly represented by fir (*A. alba*), pine (*P. sylvestris*) and spruce (*P. abies*). Izdebski et al. (1992) mentioned a sporadic occurrence of *Pinus strobus*, *P. rigida* and *P. banksiana*, but their contribution to the *Pinus* pollen sum is negligible. *P. sylvestris* and *P. abies* are native to northern and central Europe and Asia, well adapted to continental conditions and tolerant of cold temperate climates with low winter temperatures and a short growing season. The pine flowers in May in Poland, and the seed mast occurs every 2–3 years, and every 5–6 years in the mountains (Tomanek 1994). The spruce flowers at the end of April or in May, usually 2 weeks before the pine, and abundant seed production occurs every 4–10 years (Tomanek 1994). *A. alba* is native to central and south European mountains and

favours cool temperate maritime climates with high humidity and low summer and high winter temperatures. The fir flowers from April to the beginning of May in Poland (Tomanek 1994), and abundant seed production occurs every 3–4 years, and every 5–8 years in the mountains (Suszka 1983).

The Fagaceae family is represented in Roztocze by an abundant population of *F. sylvatica*, frequent *Q. robur*, infrequent *Q. petraea* and sporadic *Q. rubra*. Of the three oak species, it is *Q. robur* that mostly contributes to the pollen spectra. All these trees are adapted to the moderately warm temperate climates of south and central Europe and are sensitive to late spring frosts (Suszka 1990). The distribution range of *F. sylvatica* in north and east Europe is restricted by the winter temperature and the range in the south by moisture deficiency. The beech flowers from the end of April to the beginning of May and produces fruits abundantly every 5–8 years in Poland (Tomanek 1994). Oaks flower in May and abundant fruiting occur every 4–6 years (Tomanek 1994). Years of abundant flowering do not always coincide with abundant seed production.

The Ulmaceae family. *U. glabra* and *U. minor* are represented in the Roztocze flora. Of these, only *U. glabra* sporadically occurs close to the pollen trapping sites. It tolerates a moderately warm climate, flowers in Poland from March to the beginning of April and produces fruits every year or every 2 years (Tomanek 1994).

The Oleaceae family. *F. excelsior* prefers the warm temperate climate of the European sub-oceanic area (Zarzycki et al. 2002). It flowers in the second half of April to the beginning of May, but flower buds start to form the previous summer. Abundant fruiting occurs every second year (Tomanek 1994).

2 Materials and methods

2.1 Study area

The Roztocze region forms an elevation up to 28 km wide at the border between Poland and Ukraine in south-eastern Poland (Fig. 1). The area is characterized by high solar radiation (ca. 3,600 MJ/m² annually) and low cloudiness, especially in late summer and early autumn. The characteristic features of this area are high annual precipitation totals (up to

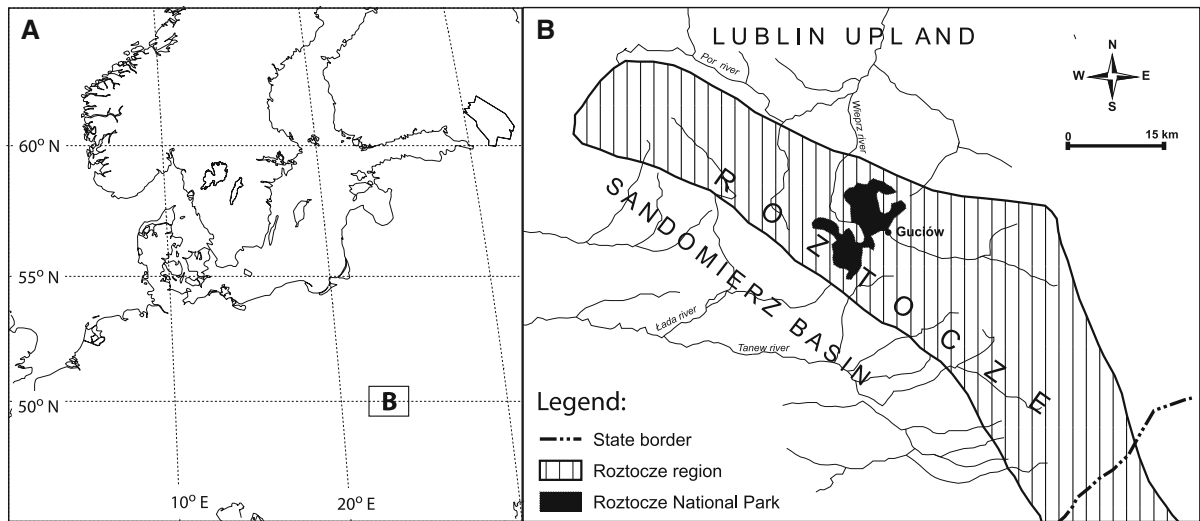


Fig. 1 Situation of the study area

700 mm), the number of rainy days (up to 172), and the high number (up to 56) of frost days ($t_{\max} < 0^{\circ}$), especially in the lower parts of the terrain (Kaszewski et al. 2002).

The Roztocze landscape is distinctive for its rich forest cover. Forests of different types cover more than 60 % of its surface. In the central part of Roztocze, there is a national park (the Roztocze National Park), which protects the most natural parts of forests incorporating nineteen different forest associations (Izdebski et al. 1992). The uplandic relief and the lowering of the Wieprz River Valley dictate the zonal distribution of the forest associations. Fir-tree woods (*Abietetum polonicum*) cover the lower and middle parts of slopes, and Carpathian beech forests (*Dentario-glandulosae-Fagetum*) cover the summits of the hills (Izdebski et al. 1992). Both forest types are typical of the lower submontane zone of the Carpathian Mountains. Alder carrs occur in the valley bottom. Large patches representing different pine communities occur on dunes and plains.

2.2 Pollen monitoring

Nine pollen traps are located around the village of Guciów (50° 34' N; 23° 04' E), situated in the protected zone of the Roztocze National Park (Fig. 1). The annual pollen accumulation rates (PARs) have been monitored using Tauber-style traps constructed according to the description given by Hicks and Hyvärinen (1986). A

trap is a 5-litre plastic container with an opening 5 cm in diameter that is covered with a large wire mesh (vide Pidek 2004). The trap is buried so that the opening is on the ground surface. The placement of the traps from closed forest through the forest edge to open situations follows the recommendations of the Pollen Monitoring Programme (PMP; Hicks et al. 1996; www.pollentrapping.net). The pollen deposited in the trap over a year is treated in a laboratory using *Lycopodium* tablets (Stockmarr 1971), filtering, Erdtman's standard acetolysis technique and, finally, microscopic analysis. The number of pollen grains of each taxon deposited annually across a surface area of 1 cm² is calculated (PARs). The counting is continued until a minimum of 500 pollen grains from trees and shrubs (AP) and a minimum of 100 *Lycopodium* spores are obtained. The average annual PAR was calculated for each tree species based on pollen accumulation data from all the traps in the Roztocze area. The median PAR for each species over the period from 1998 to 2010 and the annual deviations from the median were calculated thereafter. The observed pollen deposition over 13 years was treated as an indicator of pollen production (i.e. flowering intensity) during each year between 1998 and 2010.

2.3 Meteorological data

The meteorological data used in the present study cover the period 1997–2010 and were obtained at the

Meteorological station of the Roztocze National Park in Zwierzyniec—7 km NW from the village of Guciów. In the period 1997–2008, observations were made three times a day (at 7 a.m., 1 p.m. and 9 p.m.). In 2009 and 2010, the data were collected by the automatic weather station. The average daily temperature and precipitation sums were used to calculate the monthly mean temperature and precipitation.

In order to determine the extremal values, deviations were calculated from the mean monthly temperature and precipitation over the period 1998–2010 and for each season: winter (December of the previous year, January and February), spring (March, April and May), summer (June, July and August) and autumn (September, October and November). The start, end and duration of the dormancy period were determined using the incidence of chill days, frequently referred to as “winter days”, i.e. days with a temperature below 0 °C ($T_{\text{mean}} < 0$ °C), as a proxy.

The start, end and duration of the growing season (days with a mean daily temperature above 5 °C) were determined for each year. The beginning of the growing season was defined as the first day featuring continuous occurrence of the temperature typical of that particular season. The date concluding the vegetation season was defined as the last day of a series of days with a mean temperature above 5 °C (Kaszewski and Bilik 2009).

2.4 Numerical data handling

2.4.1 Time–frequency analysis

Wavelet analysis was used to decompose our taxon-specific observation series into time and frequency space in order to obtain information on the “periodic” signals within the dataset and variation of these signals through the observation time.

The continuous wavelet transform for time-series analysis (Farge 1992; Torrence and Compo 1998) was used to obtain information on both the amplitude of the “periodic” signals within the observation series and also on how this amplitude varies with time by decomposing a one-dimensional time series into a two-dimensional time–frequency space. The web-based Interactive Wavelet Plot tool (<http://ion.researchsystems.com/>) was used for the calculations and plotting. The Morlet wavelet was applied and wavelet number was set to six. Padding with zeroes

was used to avoid wrapping of the signal at one end of the time series to the other end.

The PAR data were converted into a series of wavelet coefficients [power (PAR)] by wavelet transform. Each of the coefficients represents the amplitude of the wavelet function at a particular point in time within the data series. A larger value implies higher correlation (Table 1).

2.4.2 Correlation analysis

Spearman’s correlation coefficient was used to estimate the influence of air temperature and precipitation on the pollen production and deposition of each tree taxon in turn (Table 3). This coefficient is used in cases defined as “small samples”, where the number of observations (N) is < 30 (Łomnicki 1995). Correlations were considered significant when $p < 0.05$. The mean values for the meteorological parameters (mean air temperature and mean precipitation sum), which were taken for the calculations, covered the months and seasons both during the year of pollen emission and during the preceding year (Table 3). These included:

1. during the year prior to pollination
 - a. the 6 months from May to October
 - b. the whole summer (June, July and August) and autumn (September, October and November)
2. during the year of pollination.
 - a. the 5 months from January to May
 - b. the whole winter (December, the previous year, and January and February), spring (March, April and May) and summer (June, July and August)

Additionally, Spearman’s correlation coefficients were calculated between the annual PARs of each taxon and the duration of each year’s dormancy period. The dormancy period was calculated as the total number of chill days. Separate coefficient calculations were also made between the annual PARs and the number of chill days in each month, in which chill days occurred (from January to April and from October to December).

Spearman’s correlation coefficient was also calculated between the PARs and duration of the growing

Table 1 Main meteorological characteristics of the Roztocze area in the period under investigations (1997–2010)

	Min (year)	Max (year)	Mean
Annual temperature (°C)	7.0 (1997)	8.7 (2008)	7.8
Annual precipitation (mm)	603 (2003)	875 (1998)	739
Winter season temperature (°C)	−6.0 (2003)	1.3 (2007)	−2.0
Winter season precipitation (mm)	83 (2008)	174 (2004)	127
Spring season temperature (°C)	6.4 (2005)	9.4 (2007)	7.8
Spring season precipitation (mm)	127 (2007)	235 (2000)	184
Summer season temperature (°C)	16.6 (2000)	19.0 (2010)	17.7
Summer season precipitation (mm)	167 (2003)	397 (2000)	272
Autumn season temperature (°C)	5.9 (1998)	9.4 (2006)	7.7
Autumn season precipitation (mm)	55 (2000)	222 (2008)	156
Beginning of the growing season	07.03 (2007)	24.04 (1997)	01.04
End of the growing season	06.10 (2010)	25.11 (2000)	28.10
Duration of the growing season (days with mean daily temperature above 5 °C)	174 (1997)	245 (2000)	211
First winter day	22.10 (1997)	01.12 (2000)	
The last winter day	26.02 (2007)	13.04 (1997)	
Number of winter days (days with mean daily temperature below 0 °C)	43 (2008)	97 (2010)	73

season (the number of days with a mean air temperature above 5 °C) during the year prior to pollination and between the PARs and the end of the growing season during the year prior to pollination and the start of the growing season during the pollination year.

3 Results

3.1 The dynamics of the meteorological characteristics during the investigation period (1997–2010)

3.1.1 Intra-seasonal variability

Great intra-seasonal variability, both in temperature and precipitations, was observed for the period 1997–2010 (Table 1; Fig. 2). The deviations from the mean temperatures were largest for the winter (−4 to +3 °C) and autumn (−2 to +2 °C) seasons and lowest (± 1 °C) for the spring and summer seasons. The precipitation pattern has no clear connection to the observed temperature dynamics. The largest deviations from the mean values were observed for the summer season (−20 to +40 mm), and the lowest for the winter season (± 10 mm).

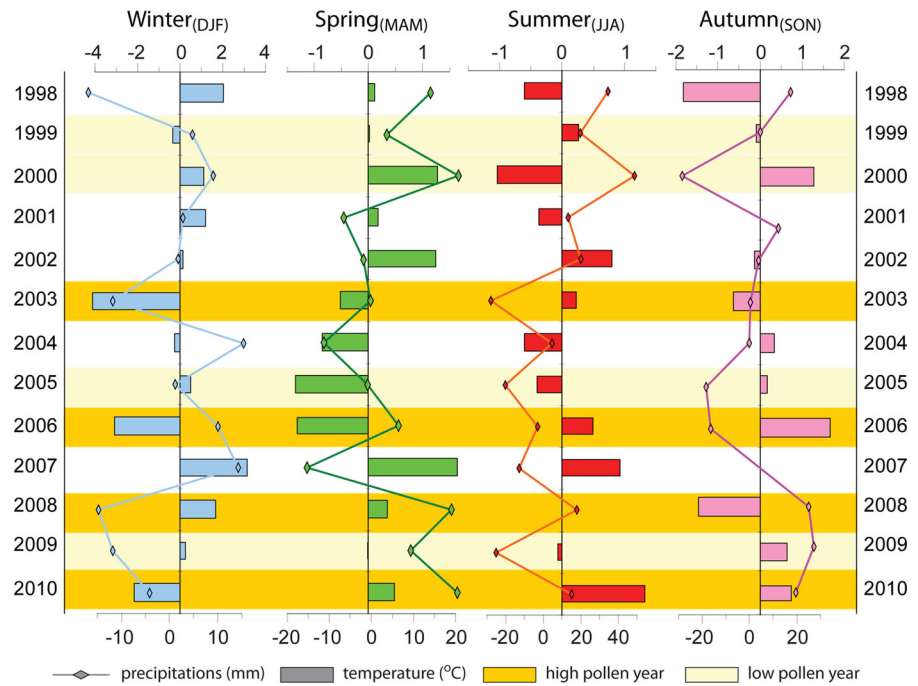
3.1.2 The start and duration of the growing and winter seasons

There are considerable variations in the growing and winter seasons' start, end and length (Table 2). The growing season generally starts in March and continues to October, a mean duration of about 200 days. However, both the start and end of the growing season vary considerably (Table 2). Winter days occurred from October to April with the highest frequency in January (20 days on average), December (17 days) and February (15 days). In certain years, winter days also occurred sporadically in April and October.

3.2 Annual variations in pollen accumulation rates

Large year to year variation in PARs was observed for all the taxa included in the pollen data series (Fig. 3). The total average annual tree pollen PAR was about 18,000 grains $\text{cm}^{-2} \text{year}^{-1}$ in the study area. The highest median values of PARs were recorded for *Pinus* and *Betula* (ca. 6,000 and 5,000 pollen grains $\text{cm}^{-2} \text{year}^{-1}$, respectively), and they are somewhat lower for *Alnus*, *Fagus* and *Carpinus* (ca. 1,300–1,400, respectively). However, a deviation of over $\pm 2,000$ pollen grains $\text{cm}^{-2} \text{year}^{-1}$ from the

Fig. 2 Deviations from the mean values of precipitation (dotted line) and air temperature (bars) in seasons of the period 1998–2010 in Roztocze. Winter months—December of the previous year, January and February; Spring—March, April and May; Summer—June, July and August; Autumn—September, October and November



median values was observed for all the above-mentioned species during the investigation period (Fig. 3). Low PARs were recorded for *Abies* (860), *Quercus* (502), *Fraxinus* (150), *Picea* (81) and *Ulmus* (65) with a deviation of over ± 100 pollen grains $\text{cm}^{-2} \text{year}^{-1}$ from the median values. The highest PAR for major forest-forming trees in Roztocze was recorded in the following years: pine—in 2010 ($\sim 11,000$ pollen grains cm^{-2}), beech—in 2006 ($\sim 4,200$) and fir—in 2004 ($\sim 2,100$). The lowest PARs were recorded for pine in 2000 ($\sim 2,900$), for beech in 2001 (~ 100) and for fir in 1999 (~ 60).

More than 130 % of the median PARs (1998–2010) were recorded in more than 75 % of traps and for ≥ 4 of 10 observed taxa during 2003 (for *Pinus*, *Quercus*, *Betula* and *Ulmus*), 2006 (for *Picea*, *Carpinus*, *Fagus*, *Fraxinus*, *Ulmus*, *Betula* and *Alnus*), 2008 (for *Alnus*, *Betula*, *Ulmus* and *Abies*) and 2010 (for *Pinus*, *Fagus*, *Abies*, *Fraxinus*, *Alnus* and *Betula*). Lower than 70 % of the average value in at least 75 % of pollen traps and for ≥ 4 of 10 observed taxa was recorded during 1999 (for *Fagus*, *Abies*, *Quercus* and *Betula*), 2000 (for *Pinus*, *Carpinus*, *Alnus* and *Quercus*), 2005 (for *Pinus*, *Picea*, *Alnus* and *Carpinus*) and 2009 (for *Fagus*, *Abies*, *Carpinus*, *Ulmus*, *Alnus*, *Betula* and *Fraxinus*).

3.3 Suggested flowering rhythms

Although the taxon-specific annual variation in PARs is large, the years of high and low deposition do not follow the same pattern for all the observed taxa, suggesting the existence of taxon-specific flowering rhythms. The time–frequency analysis results (Fig. 4) may suggest four types of rhythmicity patterns based on the observed PAR dynamics of ten major forest-forming taxa and a 13-year (1998–2010) observation series from the Roztocze area:

1. 2-year flowering rhythm (*Betula*, *Abies* and *Fraxinus*);
2. 4-year flowering frequency (*Quercus* and *Carpinus*);
3. shifting from 2- to 4-year (*Fagus*) or from 4- to 2-year flowering frequency (*Alnus* and *Ulmus*) during the observation period; although 13 years is too short to support either the 2- or 4-year rhythm.
4. no rhythmicity detectable in flowering frequency (*Pinus* and *Picea*).

The above listed results could be affected by the short observation period used for the current study (only 13 years). This factor makes it relatively easy to detect high-frequency (2 years) flowering rhythmicity,

Table 2 Start, end and duration of the dormancy period and number of chill days with temperature <0 °C, and start, end and duration of the growing season in the years 1997–2010

Year	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	Average	SD ^b
<i>Dormancy period</i>																
Start ^a	292	308	310	330	293	304	292	314	297	299	304	317	317	324	306	11.66
End ^a	102	88	79	79	88	95	98	91	90	83	55	86	85	76	87	10.99
Duration	156	131	129	129	118	162	154	159	136	146	116	142	128	119	136	15.58
<i>No. of chill days ($\Sigma T < 0$ °C)</i>																
January	28	11	15	22	22	17	19	26	15	28	8	12	24	31	20	6.85
February	10	6	20	10	15	4	28	19	21	24	14	9	18	18	15	6.71
March	10	17	9	10	9	3	14	9	19	21		5	8	10	5.69	
April	3					2	6	1	1						1	1.66
October	6				1		6		2	1					1	2.06
November	13	20	14		11	4	4	7	9	2	14	6	3	6	8	5.45
December	14	23	17	11	31	28	9	12	18	6	18	11	15	29	17	7.52
Total	84	77	75	53	89	58	86	74	85	82	54	43	68	97	73	15.30
<i>Growing season</i>																
Start ^a	113	90	85	85	91	99	103	93	92	98	66	92	87	78	92	10.79
End ^a	283	298	307	324	292	297	284	312	296	298	303	309	281	275	298	13.00
Duration	170	208	222	239	201	198	181	219	204	200	237	217	194	197	203	18.66

^a Number of days from first of January^b SD standard deviation

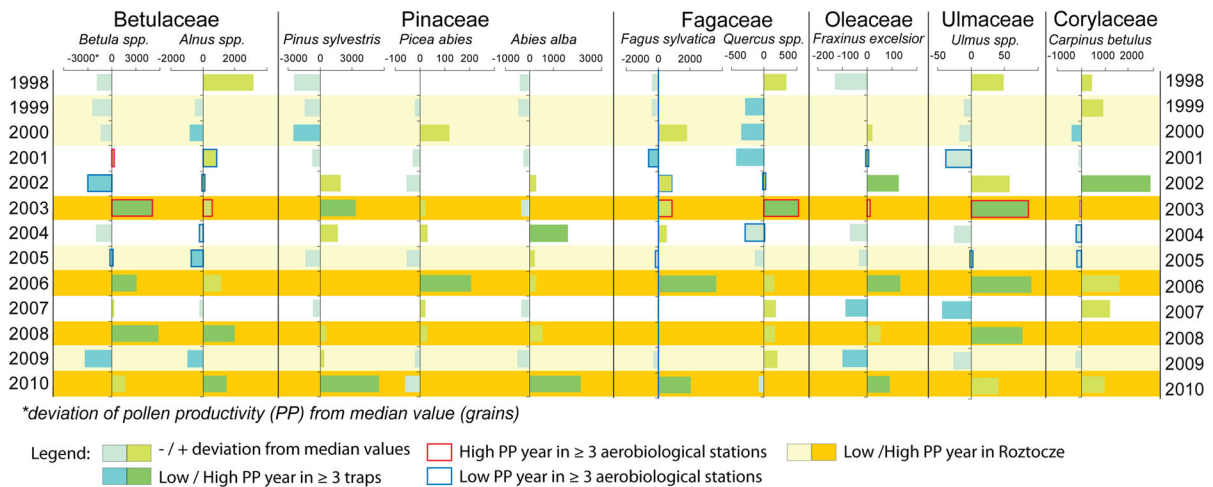


Fig. 3 Deviations from the mean values of pollen accumulation rates (PARs) for investigated tree taxa in Roztocze in the period 1998–2010. High and low pollen production years are marked

by dark colouring. A coincidence with at least three aerobiological station records are indicated by black contour

but the period is too short to detect lower frequency (4–6 years or longer).

3.4 Correlation between pollen deposition and the dynamics of the meteorological characteristics

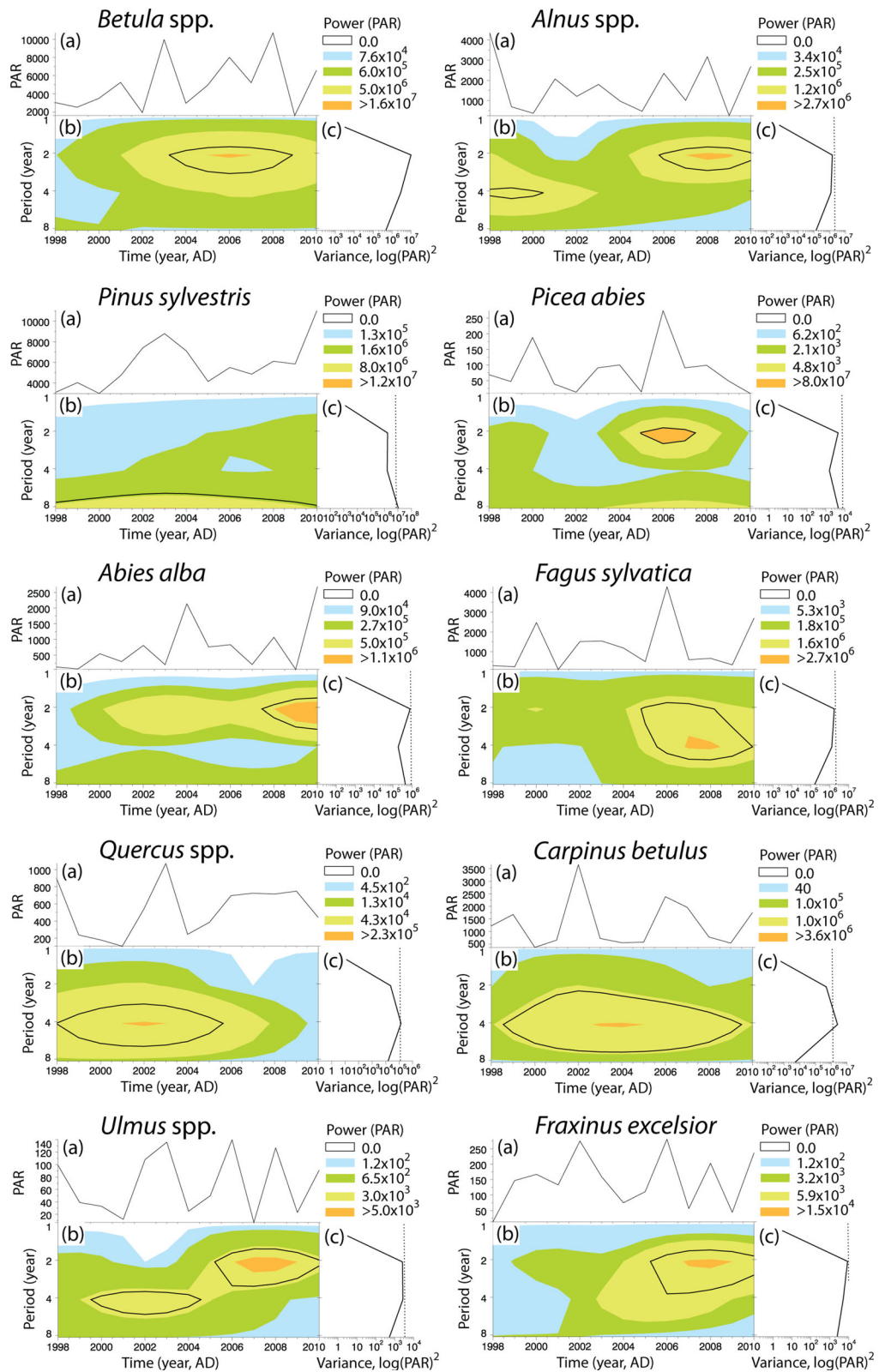
The relationship between the observed pollen production and meteorological conditions during the year prior to the year of pollen emission and during the flowering year was investigated (Table 3). Significant correlations ($p < 0.05$) with meteorological parameters were found for all taxa, with the exception of *Betula*. Generally, the correlations were positive with the summer temperature the previous year (*Pinus*, *Picea*, *Fagus* and *Quercu*) and negative with the winter temperature during the pollen emission year (*Pinus*, *Fagus*, *Fraxinus* and *Ulmus*). Most of the statistically significant correlations with precipitations were also negative. These included three negative results for *Abies* and three for *Quercus*. The correlation with the average temperatures of the season was found to be significant if at least one of the months included in the season had a significant correlation with the pollen deposition. Thus, the averaged summer temperature of the previous year was found to have a significant effect on the pollen deposition of several species, but the different taxa show significant correlations with different months (Table 3). Significant correlations with precipitation were mainly negative,

but even more numerous than those with temperature. The dry summer preceding the year of pollen emission favours pollen production among several tree taxa (*Pinus*, *Abies*, *Quercus* and *Fagus*). Taking all the investigated taxa into account, one negative correlation with the duration of the growing season (*Quercus*) was found, as well as one positive correlation with the growing season starting in the year of pollen emission (*Ulmus*) and one negative correlation with the end of the year prior to pollen emission (*Alnus*). The pollen deposition of two taxa (*Fraxinus* and *Ulmus*) is significantly influenced by a number of chill days in the previous December, whilst *Fagus* is significantly influenced by a number of chill days in January of the year of pollen emission.

In most cases, a combination of several potential meteorological factors acting both in previous and in pollen emission year should be considered as triggering mechanism of high/low pollen production. These include examples of warm and/or dry summer of the previous year and a very cold winter in the year of pollen emission, which resulted in the high PARs for several tree taxa (Table 4).

4 Discussion

The rhythmically alternating low and high flower and seed production in trees, as well as disruptions and changes in frequency, are well recognized (Suszka



◀ **Fig. 4** **a** Data. **b** The wavelet power spectrum using Morlet wavelet. The *left axis* represents the Fourier period (in year). The contour levels are chosen so that 75, 50, 25 and 5 % of the wavelet power is above each level, respectively. *Black contour* is the 20 % significance level, using a white-noise background spectrum. The wavelet coefficients power (PAR) represents the amplitude of the wavelet function with larger values implying higher correlation. **c** The global wavelet power spectrum (*black line*). The *dashed line* is the significance for the global wavelet spectrum, assuming the same significance level and background spectrum as in **(b)**

1983; 1990; Emberlin et al. 1993; Koenig and Knops 2000). Such rhythmicity in the reproductive cycle is widely regarded to have considerable economic impact on the seed or fruit production industries (Bock and Lepthien 1976; Tomanek 1994; Załęski et al. 1999–2007). The steady global increase in the number of people suffering from allergic reactions to airborne pollen (Masoli et al. 2004; D'Amato et al. 2007; Shea et al. 2008) is highlighting the increasing role of pollen production dynamics within a context of healthcare and human well-being today. A firm understanding of flowering dynamics and its major environmental drivers could possibly be used as a basis for long-term airborne allergen concentration predictions.

Regardless of its importance, data on species-specific behaviour, its drivers and the causes of disturbances are scarce (Spieksma et al. 1995; Emberlin et al. 1997; Jato et al. 2000; Peeters 2000; Chmielewski and Rötzer 2001). The long-term monitoring of seed production rather than the pollen production of forest-forming trees important to the human economy is well established (Sork et al. 1993; Isagi et al. 1997; Herrera et al. 1998; Koenig and Knops 2000; Hilton and Packham 2003). Attempts to predict seed crop abundance based on the abundance of flowering have been made (Załęski et al. 1999–2007). However, as the time span between pollen and seed production is usually several months, variations in meteorological phenomena and the activity of herbivorous insects and parasites can disrupt the link between flowering and seed production abundance (Koenig and Knops 2000), making it difficult to make direct use of the gathered long-term seed production data to calibrate the flowering abundance forecasts. Roztocze is a part of the N–S European transect for tracing variability in annual PARs conducted in frame of the Pollen Monitoring Programme (www.pollenmonitoring.net;

www.pollenmonitoring.net; Giesecke et al. 2010; Poska 2013). In the case of *Fagus*, the studies in the N–S European transect revealed temporal irregularity and regional synchronicity in the occurrence of extremely high pollen production years (pollen mast years) and low years, which are often matched by high/low seed production (Pidek et al. 2010b). These studies can serve also for palaeoecological and palaeoclimate reconstructions (Hicks 2001; Hicks and Sunnari 2005; Huusko and Hicks 2009; Kuoppamaa et al. 2009; Gerasimidis et al. 2006).

In this study, an attempt was made to determine the flowering rhythm of the main forest-forming species of a temperate forest zone and to identify the meteorological factors that could have caused disturbances in the natural rhythm on the basis of observed PAR dynamics and meteorological data from the Roztocze area in south-eastern Poland, for the time period 1998–2010.

4.1 Taxa-specific pollen production and deposition

In the period 2001–2005, in most cases, high/low pollen production years in Roztocze can be confirmed by published aerobiological data from Poland (Weryszko-Chmielewska 2006; Pidek et al. 2009, 2010a). PARs from Roztocze were compared to the annual sums of the same tree taxa obtained by volumetric methods in the six Polish cities. The cities were situated in different regions of Poland: in the south (Rzeszów, Kraków and Sosnowiec), east (Lublin) and west (Poznań and Szczecin). The regions differed in terms of climate, from Kraków and Rzeszów in the foreland of the Carpathians, via Poznań in west-central Poland and to Szczecin on the Baltic Sea coast.

Aerobiological results for the period 2001–2005 (Weryszko-Chmielewska 2006) confirmed most of the tendencies towards more or less abundant flowering occurring in the Roztocze data in these years (Fig. 3), in spite of the different methods used and climatic differences among the regions. It has been previously demonstrated that, in spite of essential differences in pollen capture methodology, the results of pollen monitoring using Tauber traps and the volumetric method are well correlated both on a local scale, i.e. when both types of trap are placed at the same site (Levetin et al. 2000; Ranta et al. 2007), and on a regional scale, when the sites are distant from each

Table 3 Spearman's correlation coefficients with monthly and seasonal mean temperature and precipitation, duration of dormancy period and growing season for ten tree taxa under investigations

Taxon	<i>Pinus</i>	<i>Picea</i>	<i>Fagus</i>	<i>Abies</i>	<i>Carpinus</i>	<i>Alnus</i>	<i>Quercus</i>	<i>Betula</i>	<i>Fraxinus</i>	<i>Ulmus</i>
Monthly (seasonal) mean temperature (°C)										
Year prior to pollination										
May	0.46	0.27	-0.01	0.12	0.16	0.47	0.30	0.27	0.07	0.35
June	-0.23	0.46	-0.22	-0.24	-0.58	-0.30	-0.10	0.00	-0.25	-0.29
July	0.40	0.30	0.72	0.28	0.35	-0.30	0.30	0.31	0.46	0.28
August	0.80	-0.25	0.11	0.17	-0.06	0.13	0.48	0.17	0.03	0.20
September	-0.18	0.17	0.45	-0.06	0.32	-0.07	0.08	-0.07	0.21	0.01
October	-0.18	-0.37	-0.23	-0.14	0.17	-0.31	-0.29	-0.15	0.12	-0.34
Summer (JJA)	0.35	0.51	0.37	0.08	-0.12	0.13	0.59	0.35	-0.04	0.13
Autumn (SON)	0.01	-0.26	0.08	0.32	0.39	0.47	-0.06	0.46	0.13	-0.12
Pollination year										
January	-0.52	-0.15	-0.66	-0.39	0.07	0.07	0.12	-0.08	-0.48	-0.28
February	-0.20	0.05	-0.19	0.00	0.05	0.07	0.02	-0.44	-0.17	-0.15
March	0.07	-0.18	-0.09	0.03	0.28	-0.11	-0.23	-0.18	0.14	-0.35
April	-0.52	0.17	-0.13	-0.26	-0.15	0.05	-0.03	-0.18	-0.04	-0.04
May	0.27	-0.31	0.32	0.03	0.36	0.21	0.22	0.22	0.26	0.12
Winter(DJF)	-0.61	0.09	-0.58	-0.22	-0.19	0.06	-0.07	-0.06	-0.56	-0.52
Spring(MAM)	0.00	-0.15	0.06	0.04	0.26	0.12	-0.05	-0.03	0.13	-0.28
Summer (JJA)	0.55	-0.35	0.31	0.17	0.81	0.25	0.26	0.23	0.46	0.23
Monthly (seasonal) mean precipitation (mm)										
Year prior to pollination										
May	0.47	0.01	0.06	0.03	-0.07	0.19	0.49	0.18	-0.39	-0.22
June	0.07	-0.10	0.12	0.08	0.12	0.10	-0.52	0.29	0.55	0.10
July	-0.34	-0.38	-0.69	-0.54	-0.34	-0.12	-0.02	-0.49	-0.48	-0.12
August	-0.50	0.19	-0.36	-0.50	-0.11	-0.36	0.21	-0.24	-0.34	-0.32
September	0.17	-0.20	-0.13	-0.25	0.06	0.12	0.28	-0.27	0.13	0.23
October	0.25	-0.11	0.23	-0.06	-0.15	-0.07	0.14	-0.14	-0.04	0.23
Summer (JJA)	-0.26	-0.14	-0.43	-0.75	-0.22	-0.34	-0.27	-0.22	-0.08	-0.15
Autumn (SON)	0.20	-0.11	0.32	-0.12	0.33	-0.11	0.31	-0.28	0.14	0.07
Pollination year										
January	-0.30	-0.02	-0.28	0.10	-0.08	-0.13	-0.30	-0.03	-0.30	-0.42
February	-0.10	0.07	0.27	0.19	0.02	-0.55	-0.57	-0.47	0.26	-0.13
March	-0.39	0.28	-0.05	-0.03	-0.40	-0.21	-0.02	-0.09	-0.06	-0.08
April	-0.43	0.03	-0.30	-0.23	-0.14	0.20	-0.31	-0.02	0.00	0.13
May	0.66	0.01	0.62	0.32	0.20	0.13	0.51	0.28	0.41	0.40
Winter (DJF)	-0.14	0.35	0.20	0.24	0.07	-0.39	-0.55	-0.15	0.11	-0.40
Spring (MAM)	-0.15	0.10	0.30	0.07	-0.17	0.17	0.07	0.15	0.28	0.37
Summer (JJA)	-0.44	-0.10	-0.09	0.13	0.06	0.18	-0.44	-0.25	0.18	0.07
Dormancy period										
Duration	-0.30	0.12	0.24	-0.49	-0.53	-0.51	0.13	-0.14	-0.53	-0.11
No. of chill days ($\Sigma T < 0$ °C)										
January	0.42	0.05	0.52	0.42	-0.18	-0.10	-0.30	0.03	0.39	0.06
February	0.17	0.14	0.18	-0.04	-0.14	-0.24	-0.01	0.25	0.07	0.16

Table 3 continued

Taxon	<i>Pinus</i>	<i>Picea</i>	<i>Fagus</i>	<i>Abies</i>	<i>Carpinus</i>	<i>Alnus</i>	<i>Quercus</i>	<i>Betula</i>	<i>Fraxinus</i>	<i>Ulmus</i>
March–April	None									
October										
November										
December	0.21	−0.06	0.366	0.04	0.39	0.22	0.11	0.15	0.71	0.79
Total	None									
Growing season										
Start (pollination year)	0.04	0.14	0.26	0.23	0.06	0.19	0.20	0.17	0.33	0.63
End (year prior to pollination)	0.39	0.00	−0.46	−0.36	−0.52	−0.51	−0.31	0.01	−0.20	−0.43
Duration (year prior to pollination)	0.28	−0.17	−0.22	0.05	−0.34	−0.22	−0.53	0.18	0.23	−0.20

Statistically significant values are marked in bold

other (Pidek et al. 2006, 2009). This coincidence points to the climatic factors affecting vast areas, triggering the mechanisms of pollen production.

4.2 Taxa-specific differences in the frequency of abundant flowering

The plant physiology-driven rhythmicity of abundant flowering and subsequent seed production is well known. Observations show that an abundant pollen/seed year should be followed by one of low abundance and is also usually preceded by a low or average one (Tomanek 1994; Dahl and Strandhede 1996; Isagi et al. 1997; Hilton and Packham 2003). However, long-term pollen monitoring studies have shown that area- and taxa-specific differences exist with regard to the amount of low pollen production years between the abundant flowering years (Hicks 2001).

A biannual rhythm of abundant flowering was detected for the *Betula* species. This shows strong agreement with studies using the monitoring results of aerobiological stations in Poland, which suggested an abundant biannual pollen production rhythm for birch and alder (Latałowa et al. 2002; Spieksma et al. 2003). In the case of the birch, a strong correlation between abundant pollen production and abundant seed production has been noted (Suszka 1979), suggesting that disruptions between flowering and seed production caused by external factors are rare for this taxon. A certain shift in abundant flowering frequency was observed for the alder in the Roztocze area. The 4-year rhythm detectable during the first half of the observation period (1998–2003) seemed to change into an almost biannual frequency during the second half of the

observation period, which is more probable for taxa of the Betulaceae family. Our results may have been affected by the short observation period used for the current study (only 13 years). This factor makes it relatively easy to detect high-frequency (2 year) flowering rhythm, but the observation period is too short to detect lower-frequency (4–6 years or longer) flowering rhythm.

The rhythms involved in abundant flowering suggested for tree taxa in Roztocze are not easily interpretable, due to considerable land-use changes during the observation period. A significant number of arable fields were abandoned during the 1990s, inducing the secondary succession process, with birch being the earliest successional species to establish itself on former farmland. Overgrowing of abandoned fields led to a general increase in pollinating birch trees during the observation and also, therefore, to an unexpected increase in the *Betula* PAR values.

Our study could not determine with acceptable certainty any rhythmicity in pollen production for *Pinus*, in spite of the fact that the pine is one of the most abundant tree species in the investigation area, on both a local and regional scale, being well known for its long-distance pollen dispersal capacity (Poska and Pidek 2010). The time–frequency analysis hints at the possible existence of ca. 8-year cycle of abundant flowering for this species (Fig. 4), but the shortness of the observation period in comparison with the suggested rhythm length prohibits us from drawing any definite conclusions. As for *Pinus*, no clear rhythmicity was found in the pollen production of *Picea*, another taxon of the Pinaceae family. As opposed to the pine, this tree species is represented in the region by scattered trees.

Table 4 Possible factors that could have been responsible for the occurrence of high and low years for tree taxa under investigations

Year	Taxa with high/low values	Climatic factors of the year of pollen emission	Climatic factors of previous year
<i>High pollen years</i>			
2003	High PARs for <i>Pinus</i> , <i>Quercus</i> , <i>Betula</i> , <i>Ulmus</i> and also <i>Alnus</i> , <i>Fraxinus</i> , <i>Fagus</i> in Roztocze had average or higher PAR values	One of the shortest growing seasons 185 days extremely cold and dry winter , average temperature and precipitation in spring	In 2002 warm summer and more humid, average temperature and precipitation in autumn with a very mild November
2006	High PARs for <i>Picea</i> , <i>Carpinus</i> , <i>Fagus</i> , <i>Fraxinus</i> , <i>Ulmus</i> , <i>Betula</i> , <i>Alnus</i>	Very low winter temperature , cold and wet spring	Average duration of the growing season dry summer and dry autumn until 27 October temperature >5 °C
2008	High PARs for <i>Alnus</i> , <i>Betula</i> , <i>Ulmus</i> , <i>Abies</i>	Winter very dry and warm, spring very wet but with average temperature	Summer slightly drier and very warm , autumn wet and rather cold, whole October without chill days
2010	High PARs for <i>Pinus</i> , <i>Fagus</i> , <i>Abies</i> , <i>Fraxinus</i> , <i>Alnus</i> , <i>Betula</i>	Very low temperature in winter with average precipitation, very wet spring	Very dry summer , whole October without chill days, slightly higher temperature in autumn
<i>Low pollen years</i>			
2000	Low PARs for <i>Pinus</i> , <i>Carpinus</i> , <i>Alnus</i> , <i>Quercus</i>	Cold March 2000	Slightly wetter summer of slightly higher temperature, average autumn in terms of temperature and precipitation, in November 14 chill days
2001	Low PARs for <i>Fagus</i> , <i>Quercus</i> , <i>Ulmus</i>	Winter temperature slightly higher with average precipitation, spring slightly drier, of average temperature	The longest growing season, very wet summer and of the lowest temperature, very dry autumn and mild November without chill days
2005	Low PARs for <i>Pinus</i> , <i>Picea</i> , <i>Alnus</i> , <i>Carpinus</i>	Winter and spring average precipitation, winter average temperature but very low temperature in spring	Very dry June but followed by very wet July and average August, total summer temperature lower than average, average autumn in terms of precipitation and temperature
2009	Low PARs for <i>Fagus</i> , <i>Abies</i> , <i>Carpinus</i> , <i>Ulmus</i> , <i>Alnus</i> , <i>Betula</i> , <i>Fraxinus</i>	Very dry winter of average temperature, wet spring of average temperature	Wet summer of average temperature, autumn extremely wet with slightly higher temperature

In the case of high pollen years, the cold winters and the dry and/or warm summers of previous year are marked in bold. In the case of low pollen years wet summer of the previous year was marked in bold

As the Roztocze area is situated near the southern limit of its distribution range in Europe, its long-distance dispersal capacity is much lower (Pidek et al. 2010a), and the amount of pollen grains deposited in traps is generally low. It is possible that its physiological flowering rhythm is either longer or frequently disturbed by environmental factors and therefore undetectable. The 4-year rhythm for *Carpinus* and *Quercus* was stable throughout the entire observation period. The same was the case for *Fagus*, during the second part of the observation period. All these taxa represent major forest-forming temperate broadleaved trees of the area. A similar flowering rhythm was detected for *Quercus* and *Fagus* in the Rila Mts, Bulgaria by

Tonkov et al. (2001). The beech and oak forest production of nuts and acorns can reach 1,000–1,500 (or more) kg/ha during the mast year (Janick and Paull 2006). Therefore, the suggested long rest period between prolific flowering and seed production for the above-mentioned hard mast (nut and acorn) producers is explainable by the need to restore resources depleted during a high seed production year.

4.3 Meteorological factors influencing pollen deposition

An impressive number of meteorological factors and/or their combinations have been discussed as possible

drivers of change in flowering frequency and prolificacy by different authors (Andersen 1980; Frenguelli et al. 1992; Emberlin et al. 1993, 1997; Jato et al. 2000; Peeters 2000; Latałowa et al. 2002; Rodriguez-Rajo et al. 2004; Kasprzyk 2009; Nielsen et al. 2010). We used Spearman's rank correlation coefficient to test statistical dependencies between the observed changes in pollen production of studied taxa and a number of meteorological factors, all of which could have an effect on the pollen production intensity. The correlation results suggest that a considerable number of the tested factors had a negligible influence or no influence at all on pollen production. No correlation was found between pollen deposition and temperature or precipitation averages for any of the autumn months (September, October and November), whether they were considered separately and/or the autumn season was taken as a whole. The impact of late spring or early autumn frosts on plants' general well-being and flowering capacity is well recognized (Suszka 1990; Tomanek 1994; Peeters 2000;). We tested this idea using the number of chill days per month as a proxy for frost. The attempt to find correlations between pollen deposition and the number of chill days per month failed to yield correlations for any of the tested taxa for any autumn or spring months, suggesting that the spring or autumn frosts did not have a detectable impact on the pollen production of the studied taxa in the investigated region. On the other hand, a positive correlation was found between the number of chill days recorded during January and December and several temperate broadleaved taxa. The summer temperature and/or winter temperature, when combined with precipitation measurements made during the corresponding seasons of the year prior to pollen production as well as the temperatures and precipitation during the flowering season, was major contributor to the statistically significant correlations that were detected. The data from the observed period (Fig. 3) show that years with unexpectedly high (2003, 2006 and 2010) or low (1999, 2000, 2005 and 2009) pollen deposition frequently co-occurred and this applied to most of the studied tree taxa. The correlation between steady and low winter temperatures preceded by warm and/or dry summer period and high pollen deposition is distinguishable by visual inspection and was confirmed by a number of statistically significant correlations found in our dataset (Table 3, 4). This relationship between pollen deposition and the

above-mentioned meteorological parameters has been recognized as one of the major weather controls influencing pollen production by several other studies (Andersen 1980; Latałowa et al. 2002; Jato et al. 2013; Kasprzyk et al. 2004; Pidek et al. 2009; Myszkowska et al. 2010, 2011). A tentative explanation for the importance of winter temperatures in general and the number of frost days during the winter season could be that a cold winter with a long and uninterrupted dormancy period favours high pollen production as it inhibits an early start to the growing season and therefore prevents any possibility of frost damage.

Numerous recent studies on changes in the start, end and duration of the growing season and interruptions that affect it highlight the importance of changes in the dormancy/growing season to plant life (Rodriguez-Rajo et al. 2004; Menzel et al. 2011; Jato et al. 2013). The suggested dependency was tested by comparing the observed pollen dynamics to changes in the start of the growing season of the pollen emission year; the end and duration of the growing season of the previous year; and the length of the winter season prior to pollen emission. The resultant statistically significant correlations were all negative, suggesting that a late start to the flowering season enhances flowering intensity, although there was one exception, since there was a positive correlation between the start of the growing season and elm pollen deposition. The causes of this difference could be connected to differences in flowering time (with April flowering obviously producing richer deposition than May flowering). However, we must be aware that the obtained correlations need to be confirmed by further studies, as some of the apparently statistically significant correlations could be the inadvertent result of data-related restrictions. A similar concern was expressed by van der Knaap et al. (2010) when studying the relationship between pollen production and climate in Europe and the Caucasus.

The low PAR values obtained in 2005 were also observed in the case of *Carpinus*, *Ulmus* and *Fraxinus*, where rather a high pollen year could have been expected (due to the low 2004). Of the other low years, 2009 was reflected in 7 out of 10 taxa as being a low or very low pollen production year. Although it registers as such in the data from several tree taxa (*Fraxinus*, *Betula* and *Abies*), it is actually frequently expressed as an extremely low or even the lowest pollen year in the whole series. One possible reason for this could

have been the winter–spring wet and mild conditions of 2009 and the scarcity of summer warmth the previous year (Table 4).

Several times, high and low years occurred in parallel for *Fagus* and *Picea*. This was also observed by Tonkov et al. (2001) and potentially points to the same weather triggering factors. This makes sense ecologically, as both species are present in the submontane zone of the mountains.

Pinus is an example of how pollen production is controlled by summer warmth. Its PAR seems to follow the August temperature of the previous summer. Thus, the factor triggering high pollen production in the case of pine was summer temperature. This is confirmed by Hicks (2001) and Huusko and Hicks (2009) in northern Finland, but in their case, it was July not August that was the significant month. Further studies are needed to confirm whether this difference in months results from the much shorter summer period in Finland.

Pollen production in *Fagus* is also favoured by summer warmth, and additionally by summer dryness. This is visible in the high negative correlation coefficients both with the July precipitation of the previous year and with the whole summer period. As rarely as a few times a century, mast years occur in which the beech produces a large amount of both pollen and seeds (Suszka 1990). One of these mast years was observed in 2006 across *Fagus*' distribution range (Pidek et al. 2010b). It is obvious that in Roztocze, the meteorological factors of the previous year (a warm and very dry summer and autumn in 2005, especially in July) promoted high pollen production in beeches in 2006. This correlates with the data published by Suszka (1990 and reference therein).

The exceptional heat wave, which affected Europe in the summer of 2003 (Della Marta et al. 2007; Natali et al. 2013), also influenced Roztocze and resulted in very dry conditions that could have been responsible for a very high pollen year for *Abies* in 2004.

Two years—2000 and 2001—although they exhibit low PARs for 3–4 taxa, are more ambiguous in character. In the case of several other taxa, the pollination rate was average or even high. For example, 2000 was good for *Picea* and *Fagus* and 2001 for *Betula* and *Alnus*. In this case, the difference in plants' reaction to different meteorological conditions can be analysed. The very dry autumn of 2000, or

even the late summer–autumn period (August–November) the same year, may be considered responsible for high pollen production in the alder and birch in 2001 (Table 4). This correlates with observations made by van der Knaap et al. (2010) and Nielsen et al. (2010).

However, the very cold March in 2000 might have stopped pollen production in several trees, but this cold signal did not seem to influence spruce and beech pollen production. *Picea* and *Fagus* are trees inhabiting the submontane zone. Thus, it is obvious that summer warmth promotes high pollen production the following year, so the high pollen deposition in 2000 could have been a response to the warmer summer in 1999. However, these trees seem to be more resistant to the lower temperatures of early spring. Additional examples of a coincidence in abundance of flowering in *Picea* and *Fagus* come from the Bulgarian Rila Mountains (Tonkov et al. 2001).

In the period 2001–2005, in most cases, high/low pollen production years can be confirmed by published aerobiological data. The aerobiological results (Weryszko-Chmielewska 2006) confirmed most trends occurring in the Roztocze data in these years (Fig. 3) in spite of different methods being used and climatic differences among the regions. This coincidence points to weather factors affecting vast areas and triggering the mechanisms of pollen production.

Observations from Roztocze seem to confirm the fact that a weather signal, if strong enough, can override the natural rhythm of abundant flowering and is most pronounced in areas where particular tree species reach their distribution ranges, both longitudinal and altitudinal. This is clearly visible in the far north (Hicks 2001) and in Roztocze, where the fir, beech and spruce are at their distribution limits.

5 Conclusions

The 13-year-long pollen data series from Tauber traps in SE Poland revealed high and low years of pollen deposition for ten tree taxa, which reflected both the physiological rhythms in abundant flowering and weather signals. Of these, the most frequently exhibited was the biannual rhythm known for the *Betula* species. The rhythms lasting around 4 years are detectable in the

case of some broadleaved deciduous trees, but due to data restrictions cannot be fully confirmed.

However, changes of weather conditions can override natural flowering rhythm.

This is observable in the case of *Pinus*, in which pollen production directly reflects the air temperature of the previous summer or in the case of mast years, occurring throughout a tree's distribution range (e.g. *Fagus* in 2006). When compared to aerobiological data obtained in volumetric samplers, it is clear that very high and very low pollen deposition frequently occurs simultaneously in different places across vast swathes of a tree's distribution.

The highest number of correlations between meteorological parameters and PARs were obtained for trees most abundant in the vegetation (i.e. *Abies*, *Fagus* and *Pinus*), and correlations for less common taxa (*Picea*, *Carpinus*, *Fraxinus* and *Ulmus*) were scarce and no correlations were found for *Betula*.

The controlling role of temperature and precipitation on pollen production (and deposition) during the summer prior to pollen emission suggested by earlier studies was confirmed. The meteorological conditions during the year of pollen emission were found to have low impact on pollen deposition. However, the statistically significant correlations with the winter temperature before pollen emission suggest that a sufficiently long dormancy period in the winter promotes the pollen production reflected in the pollen deposition.

Our pollen and meteorological data confirm some pollen weather conditions correlations suggested by other authors as well as exhibit new correlations, which need to be verified in the future by longer data series.

Acknowledgments This study is a contribution to the Pollen Monitoring Programme (<http://www.pollentrapping.net>). The work was partially financed by research funds for the period 2010–2012 granted for a research project entitled “Pollen dispersal and deposition of the main European trees”, as well as scientific cooperation between the Polish and Estonian Academies of Sciences and by research funds granted by the Polish Ministry of Science and Higher Education for the Faculty of Earth Sciences and Spatial Management UMCS, BECC project at Lund University, ESF project 9031 and IUT 1-8.

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