

Spatio-temporal investigation of flowering dates and pollen counts in the topographically complex Zugspitze area on the German–Austrian border

Susanne Jochner · Chiara Ziello · Andreas Böck ·
Nicole Estrella · Jeroen Buters · Ingrid Weichenmeier ·
Heidrun Behrendt · Annette Menzel

Received: 19 August 2011 / Accepted: 20 March 2012
© Springer Science+Business Media B.V. 2012

Abstract Flowering behavior of the major allergenic species *Betula pendula* Roth (silver birch), *Dactylis glomerata* L. (cocksfoot) and *Alopecurus pratensis* L. (meadow foxtail), was examined by phenological observations in 2009 along an altitudinal gradient (from 700 m up to 1,700 m a.s.l.) in the topographically complex Zugspitze area on the German–Austrian border. The results were compared with pollen counts derived from pollen traps located at different altitudes (720 m, 1,503 m, 2,650 m a.s.l.). Phenological onset dates showed a great dependence on altitude and on exposition. Altitudinal gradients of the two grass species showed a delay of between 6 and 7 days $(100\text{ m})^{-1}$ and can be interpreted as a temperature response rate varying between -9 and -10 days $(1\text{ }^{\circ}\text{C})^{-1}$. For birch phenophases, the altitudinal gradients were ca. 3 days $(100\text{ m})^{-1}$, corresponding to temperature response rates of circa -7 days $(1\text{ }^{\circ}\text{C})^{-1}$. Northern and western exposed birch trees at the same altitude showed large differences in flowering dates

(5–7 days). A comparison of phenological and aerobiological data in the phenological survey area revealed good agreement in the start of season dates, especially at lower altitude. Therefore, it was local pollen emissions, not long- or medium-range pollen transport that accounted for the timing of the aerobiological start of the season. Pollen counts at the highest and vegetation-free site were particularly affected by medium-range transport. More pronounced responses to altitude and therefore to temperature for the analyzed grass species indicate a greater temperature sensitivity. This suggests that further temperature increase could result in a remarkably earlier grass pollen season and, in turn, lead to major consequences for human health. Particular wind patterns can contribute to high and medically relevant pollen concentrations even at high elevation sites, implying less favourable conditions for those people allergic to pollen.

Keywords Phenology · Aerobiology · Temperature response · Wind · Medium-range transport · Topography · Altitude

S. Jochner (✉) · C. Ziello · A. Böck · N. Estrella ·
A. Menzel

Department of Ecology and Ecosystem Management,
Ecoclimatology, Technische Universität München, Hans-
Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany
e-mail: jochner@wzw.tum.de

J. Buters · I. Weichenmeier · H. Behrendt
ZAUM Center for Allergy and Environment at the
Department of Dermatology and Allergy Biederstein,
Technische Universität München, Biedersteiner Straße 29,
80802 Munich, Germany

1 Introduction

Studying phenology in mountainous regions increases our understanding of temperature responses and the ecological impacts of global change because climatic—mainly temperature—and therefore phenological

conditions change within a short distance due to altitude and topographical characteristics such as aspect and slope (Defila and Clot 2005; Ziello et al. 2009). With higher elevation, air temperature decreases by, on average, $0.6\text{ }^{\circ}\text{C}\text{ (100 m)}^{-1}$ (Barry 1981). Using this temperature lapse rate, altitudinal responses in phenology can be easily translated into thermal responses.

For people allergic to pollen, high mountain regions might be of particular interest since they are believed to have a more pollen-free environment: the amount of airborne pollen usually decreasing with increasing elevation (Clot et al. 1995; Gehrig and Peeters 2000). However, the opposite behavior was reported by Frei (1997) who found a greater amount of allergenic pollen at a high elevation site (Gütsch 2,300 m a.s.l.) compared to a lower elevation site (Davos 1,600 m a.s.l.) in Switzerland. Moreover, mountainous areas are particularly sensitive to global warming. The Alpine region has experienced a more pronounced temperature increase compared to the adjacent lowlands (Beniston 2006), leading to a deterioration of potentially beneficial situations related to pollen. For Austria, Bortenschlager and Bortenschlager (2005) demonstrated that global warming not only affected the pollen season of lowland ecosystems, but at higher altitudes flowering periods also started earlier and lasted longer, and were associated with higher peak values and greater pollen production.

Several studies have revealed that the start of the airborne pollen season does not necessarily match with the beginning of local flowering. For example, Estrella et al. (2006) demonstrated that the start of the birch pollen season in Germany occurred on average 6 days earlier than local flowering, although the peak of the pollen season coincided with the mean flowering date. The mismatch of local phenological onset dates with the start of the pollen season can be partly explained by long- or medium-range transport of airborne pollen by moving air masses.

Short-range transport is limited to a horizontal distance of 1 km, whereas medium-range transport is defined as transport of air within 1–100 km, with long-range transport defined as longer distances (Rantio-Lehtimäki 1994). Usually, the maximum distance of long-range pollen transport is approximately 500 km (Rousseau et al. 2003; Van de Water et al. 2003). Therefore, pollen of species that are not established in a region could still be present in the air. This is of particular interest when pollen of allergenic plants, for

example, ragweed, is considered and when counts are high enough to induce sensitizations (Zauli et al. 2006; Cecchi et al. 2007). Cambon et al. (1992) and Rousseau et al. (2003) also found pollen of exotic taxa in Canada and Greenland, respectively, which originated at least 1,000 km away. Even pollen transported 3,000 km was found in the Arctic (Campbell et al. 1999). Regarding such long distances, pollen amounts are likely to remain below the plant species-specific threshold at which symptoms are likely to occur and hence do not lead to major medically relevant consequences.

Our study was carried out using a detailed regional set of phenological data obtained from a field survey in 2009 in the topographically complex Zugspitze area. We focused on some of the most allergenic plants which have abundant pollen in the air during the flowering season, that is, *Betula pendula* Roth (silver birch), *Dactylus glomerata* L. (cocksfoot) and *Alopecurus pratensis* L. (meadow foxtail). We also incorporated aerobiological and meteorological data for different altitudinal levels for 2008 and 2009 in the analysis.

Our central aims were:

- To analyse phenological data as a function of altitude and aspect.
- To use temperature lapse rates for assessing temperature response rates in phenology.
- To evaluate the spatial and temporal consistency between phenological and aerobiological data.
- To analyse the pollen content of air masses at the highest and vegetation-free pollen site affected by medium-range transport.

2 Materials and methods

2.1 Study area

The phenological sites (Fig. 1) were located along an altitudinal gradient up to 1,700 m a.s.l. in the topographically complex Zugspitze area, the highest mountain in Germany (2,962 m a.s.l.), located in the Wetterstein Mountains in the Northern Limestone Alps. Phenological observations were recorded in Garmisch-Partenkirchen (720 m a.s.l.), north-east of the Zugspitze, and followed an altitudinal gradient up to the lake Eibsee (1,000 m a.s.l.) and Ehrwald in

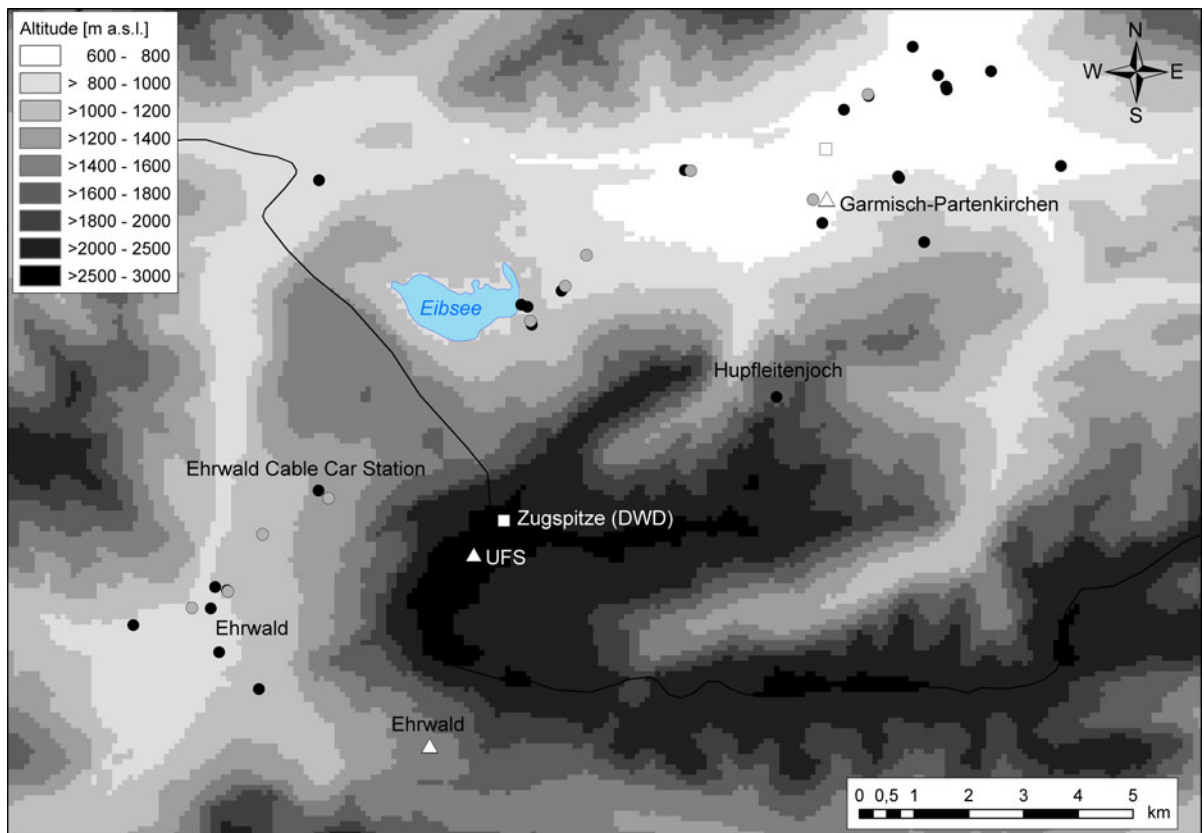


Fig. 1 Location of the study area, the Zugspitze region, located on the German–Austrian border (black line). Black dots: observation sites for birch ($n = 26$), grey dots: observation sites for grass ($n = 10$), white triangles: pollen sampling sites,

Austria (1,000 m a.s.l.), ending with the highest observation sites at 1,200 m a.s.l. (Ehrwald Cable Car Station) and 1,700 m a.s.l. (Hupfleitenjoch). At the lower sites, land use is mainly meadows and some small villages; spruce is the dominant tree species at higher altitudes. The tree line in the northern Alps is found at 1,800 m a.s.l. (Ellenberg 1996).

2.2 Phenology

2.2.1 Phenological data and species characteristics

Phenological observations in 2009 were conducted according to the BBCH code (Meier 2001) and focused on flowering and leaf unfolding of silver birch, cocksfoot, and meadow foxtail, one tree species and two grass species, respectively (Table 1; Fig. 1). Worldwide, grass pollen is the major cause of pollinosis. The most abundant grass pollen originates

white squares: German Weather Service (DWD) climate stations, background: SRTM 90-m digital elevation model (Jarvis et al. 2006)

inter alia from cocksfoot and meadow foxtail (D'Amato et al. 2007). Additionally, these two grass species are monitored within the phenological network of the German Meteorological Service (DWD). The altitudinal limits of meadow foxtail and cocksfoot do not exceed 1,500 and 2,000 m, respectively, in the northern Alps (DWD 1991). We also observed phenological phases of birch, since its pollen is the most allergenic tree pollen in northern, central, and eastern Europe (D'Amato et al. 2007). It is limited to below approximately 1,800 m (DWD 1991); this altitude also corresponds to the tree line.

2.2.2 Phenological observation methods and statistical analysis

Phenological observations were carried out in 2009 using two different methods: the synchronous method (Zacharias 1972) and the method of pooled pre/post

Table 1 Summary of analysed species phenophases: number of individuals and sites, altitudinal range (m a.s.l.), observation method according to BBCH (Meier 2001), PSD: method of pooled pre/post stage development (Cornelius et al. 2011), see text for details

Species	Common name	Phenophases	No. of individuals/no. of sites	Altitudinal range (m a.s.l.)	Observation method (BBCH)
<i>Betula pendula</i> Roth	Birch	Flowering, leaf unfolding	115/26	696–1,709	Synchronous
<i>Dactylis glomerata</i> L.	Cocksfoot	Flowering	120/10	710–1,233	PSD
<i>Alopecurus pratensis</i> L.	Meadow foxtail	Flowering	108/9	710–1,233	PSD

stage development (PSD, Cornelius et al. 2011). For birch, the synchronous method with periodic observations on every third day was used. This method allows calculation of the onset date (day of year; DOY) for flowering/leaf unfolding and their respective substages quite accurately. For grass we applied the PSD method that is based on weekly recording of development indices and linear interpolation to estimate the onset dates of phenological stages. For further information about the PSD method see Cornelius et al. (2011).

We calculated the absolute first observed flowering date (FFD) and the mean date of beginning of flowering (MFD) for each site.

To determine altitudinal gradients, linear regressions were calculated with the mean onset date averaged for each site as the response and altitude as the explanatory variable. Positive coefficients indicate a delay of the phenophase in days $(100 \text{ m})^{-1}$. Temperature response rates were calculated using the adiabatic lapse rates of air temperature that incorporate the mean daily temperatures at the climate station in Garmisch-Partenkirchen (719 m) and at the Schneefernerhaus (UFS, 2,650 m), a research station directly below the summit of the Zugspitze (see Fig. 1). For birch phenophases, we applied the mean temperature lapse rate of March and April in 2009 $(-0.48 \text{ }^\circ\text{C} (100 \text{ m})^{-1})$ and for grass phenophases the mean of May and June 2009 $(-0.68 \text{ }^\circ\text{C} (100 \text{ m})^{-1})$. Negative temperature response rates depict the advancement of a phenophase for a warming of $1 \text{ }^\circ\text{C}$.

To evaluate the effects of aspect, we selected different birch individuals located at almost the same altitude in Ehrwald (aspect: west, mean altitude: 998 m a.s.l.) and Eibsee (aspect: north, mean altitude: 990 m a.s.l.). To test whether the phenological onset dates differed between aspects, we used a two-sample

t test. Where data were non-normal, a Mann–Whitney U -test was used.

2.3 Aerobiology

Airborne pollen was collected using Burkard volumetric traps (Hirst 1952). The samplers were calibrated to handle an air flow of 10 l min^{-1} to mimic human breath. Daily values were presented as number of pollen grains of *Betula* spp. (birch) and *Gramineae* (grass) per cubic metre of air. Note that *Gramineae* records consist of several grass species since it is not possible to distinguish between different grass species from the pollen that are captured on the slides. Pollen traps were located at three different sites: at 720 m a.s.l. in Garmisch-Partenkirchen, at 1,503 m a.s.l. at the Ehrwald alp, and at 2,650 m a.s.l. at the UFS (white triangles in Fig. 1). Straight-line distance between the pollen traps in Garmisch-Partenkirchen and UFS is ca. 9 km, between Garmisch-Partenkirchen and Ehrwald ca. 12 km and between Ehrwald and UFS ca. 4 km.

For birch, we calculated the starting date of airborne pollen season using the method of Galán et al. (1995). This is defined as the date from which the cumulative sum of daily mean pollen concentration reaches 1 % of the total annual sum. The end of the pollen season is in turn defined as the day when the cumulative sum reaches 99 % of the total annual sum.

A common method for defining the pollen season of grass is the threshold 30 method (Sánchez Mesa et al. 2003). The start and the end dates of the pollen season are defined as the first and the last day, respectively, when pollen counts are $\geq 30 \text{ grains m}^{-3}$. However, in high alpine regions, daily pollen counts are not as abundant as at lower altitude. Therefore, we decided to use a definition proposed by the German Pollen Information Service (PID, Polleninformationsdienst):

Table 2 Missing values of daily pollen counts during the flowering period for *Betula* spp. and *Gramineae* in 2008 and 2009 at Garmisch-Partenkirchen, Ehrwald, and UFS

	Garmisch-Partenkirchen		Ehrwald		UFS	
	2008	2009	2008	2009	2008	2009
<i>Betula</i>	0	0	0	0; delayed start (12.05.)	3	2; Delayed start (15.04.)
<i>Gramineae</i>	1	0	2	4	17	11

on three consecutive days or on 3 days within 1 week the pollen concentration of grass pollen has to exceed 6 grains m^{-3} since this is the supposed threshold to induce medically relevant risks. In turn, we defined the end of the pollen season as when this criterion was last reached in the year.

Additionally, we determined the peak (maximum) of the daily pollen concentration and the total amount of pollen grains m^{-3} for each year and pollen station. Pollen sums were also available for the two halves of a day (0:00–12:00 and 12:00–24:00). Two-sample *t* tests were used to identify significant differences in pollen amounts in these periods.

However, the data set is not complete because of temporary technical problems with the traps. For Ehrwald and UFS, continuous pollen trapping in 2009 started only after the beginning of the pollen season of birch. However, calculating the grass pollen season was not affected by the delayed start in sampling. Icebound instruments, dust or delayed replacement of sampling slides caused a few missing values for the traps at higher elevations (see Table 2). After 29, September 2009, snowfall inhibited sampling of grass pollen at the UFS. However, the pollen season was likely to have already ended by this date.

2.4 Aerobiology and phenology/meteorology

A comparison between pollen seasons defined from aerobiology and phenology was made for 2009 by visual interpretation of temporal pollen curves and phenological dates (FFD, MFD) for different altitudinal levels.

Besides altitudinal temperature lapse rates (see Sect. 2.2.2), we analyzed the wind direction for 2008 and 2009 of two climate stations (white squares in Fig. 1) operated by the German Meteorological Service (DWD) which are located at Garmisch-Partenkirchen (719 m a.s.l.) and Zugspitze (2,962 m a.s.l.) in order to examine associations between prevailing

winds and airborne pollen amounts at the vegetation-free pollen station UFS. Wind rose plots visualize not only the prevailing wind direction but also show the sum of pollen counts at the UFS station that were associated with specific wind directions. We did not restrict these analyses to the pollen season since it can be relatively short in duration at sites where no local vegetation exists. Therefore, we included the time period between the days of first and last occurrence of pollen at the UFS.

3 Results

3.1 Phenological data

3.1.1 Altitudinal trends 2009

Results of linear regression models for the selected phases for birch, cocksfoot and meadow foxtail are shown in Table 3. For all birch phases, the altitudinal gradients were highly significant ($P < 0.001$) and ranged between 3.1 and 3.2 days delay per 100-m increase in altitude. High R^2 -values (65.1–75.7 %) confirm that a high fraction of the variation in onset dates can be explained by altitude. For the two grass species, regression coefficients (6.3–7.1 days $(100 \text{ m})^{-1}$) for the beginning of flowering and full flowering were even higher with R^2 -values ranging between 71.8 and 83.5 %. However, the latter results were based on only 9 and 10 samples, respectively. Accordingly, temperature responses varied between $-6.5 \text{ days } (1 \text{ }^\circ\text{C})^{-1}$ and $-6.7 \text{ days } (1 \text{ }^\circ\text{C})^{-1}$ for birch phenophases and between $-9.3 \text{ days } (1 \text{ }^\circ\text{C})^{-1}$ and $-10.4 \text{ days } (1 \text{ }^\circ\text{C})^{-1}$ for grass phenophases.

3.1.2 Influence of aspect on single birch trees

Table 4 shows the effects of aspect on phenological phases of selected birch individuals located at Ehrwald

Table 3 Altitudinal gradients (days (100 m)⁻¹) and temperature response rates (days (1 °C)⁻¹) for selected phenophases of birch, cocksfoot and meadow foxtail in the Zugspitze region;*N* number of sites, *P* significance, *R*² goodness of fit; temperature response rates were calculated using different altitudinal lapse rates (see Sect. 2.2.2)

Species	Phenological phase	<i>n</i>	Gradient (days (100 m) ⁻¹)	<i>P</i>	<i>R</i> ² (%)	Temperature response (days (1 °C) ⁻¹)
Birch	Leaf unfolding	26	3.1	<0.001	75.7	-6.5
	Beginning of flowering	25	3.2	<0.001	70.5	-6.7
	Full flowering	26	3.2	<0.001	65.1	-6.7
Cocksfoot	Beginning of flowering	10	7.1	0.002	71.8	-10.4
	Full flowering	10	6.3	<0.001	83.5	-9.3
Meadow foxtail	Beginning of flowering	9	6.8	0.001	82.9	-10.0
	Full flowering	9	6.4	0.001	81.1	-9.4

(aspect: west) and Eibsee (aspect: north). The findings demonstrated that the onset dates of all phases were earlier at the Ehrwald site. The mean differences ranged between 5 days (leaf unfolding) and 7 days (full flowering); all were significant. In relation to altitudinal gradients and temperature response rates (Table 3), the effect of different aspects equates to an altitudinal difference of 161, 184 and 213 m and a temperature difference of 0.8, 0.9 and 1.0 °C for leaf unfolding, beginning of flowering and full flowering, respectively.

3.2 Temperature data in 2008 and 2009

The different monthly mean temperatures in 2008, 2009 and for the standard reference period 1971–2000 recorded at the DWD climate station at Garmisch-Partenkirchen are listed in Table 5. The annual average of mean air temperature was only 0.1 °C higher in 2008 (7.9 °C) compared to 2009. However, single months revealed major differences between the analyzed years: temperatures in January to March 2009 were colder than the corresponding temperatures of the previous year, especially in February (2008: 4.5 °C, 2009: -1.4 °C). Particularly outstanding were the high temperatures in April 2009 (10 °C). June and October in 2009 were associated with lower temperatures than in 2008; however, all other months relevant for the grass pollen season (May, July, September) showed higher temperatures in 2009.

3.3 Aerobiological data

Table 6 summarizes the pollen seasons 2008 and 2009 for birch and grass at the three pollen stations. A comparison between the two study years revealed that the birch pollen season in Garmisch-Partenkirchen in 2009 was not only associated with very high April temperatures (+3.4 °C compared to 2008) but also started 2 weeks earlier (8 April) compared to the previous year (22 April). However, the duration of the pollen season was almost identical (2008: 42 days; 2009: 40 days). The total amount of pollen was 8 % higher in 2008 (about 1,600 grains m⁻³) than in 2009 (about 1,480 grains m⁻³). The pollen traps located at Ehrwald and UFS were characterized by a slightly later start (by 4 days) of the birch pollen season in 2008 compared to the lower site in Garmisch-Partenkirchen, but the end of the pollen season was only 1 day later. At the higher elevation sites, the total pollen amounts were only 40 % (Ehrwald) and 24 % (UFS) of the Garmisch-Partenkirchen value. Peak values were also reached later at the higher locations. The largest delay was at UFS, where the peak was 8 days later than in the valley. The birch pollen season in Ehrwald and UFS between the 2 years could not be directly compared due to the later start of pollen trapping in 2009. However, there were indications that the pollen season duration in 2009 was longer at UFS (>47 days), associated with a higher peak amount (ca. 80 grains m⁻³) and recorded 3 weeks earlier compared to the previous year. The difference between the

Table 4 Onset dates (DOY) for leaf unfolding, beginning of flowering and full flowering in 2009 for birch trees located on westerly (W) and northerly (N) exposed sites at Ehrwald (meanaltitude: 998 m a.s.l.) and Eibsee (mean altitude: 990 m a.s.l.), respectively, and their temporal difference (days); *n* number of sites, *P* significance

	Leaf unfolding	Beginning of flowering	Full flowering
Ehrwald (W); <i>n</i> = 23	1 May (117.8)	20 April (110.5)	24 April (114.0)
Eibsee (N); <i>n</i> = 17	6 May (122.8)	26 April (116.4)	1 May (120.8)
Difference (days)	5.0	5.9	6.8
<i>P</i>	0.003	<0.001	<0.001
Test	<i>t</i> test	Mann–Whitney <i>U</i> -test	Mann–Whitney <i>U</i> -test

Table 5 Mean temperatures (°C) measured at the climate station Garmisch-Partenkirchen (DWD) for 2008, 2009 and for the standard reference period 1971–2000

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
2008	0.2	4.5	2.7	6.6	13.6	16	16.2	16.4	11.4	8.4	2.9	−1.4	7.9
2009	−0.4	−1.4	2	10	13.8	14.3	16.8	17.6	13.9	7.6	4.5	−1.7	7.8
1971–2000	−2.5	−1.0	2.6	6.1	11.3	13.9	16.0	15.5	12.0	7.5	1.6	−1.7	6.8

end of the season at UFS and in the valley may also have been greater in 2009 than in 2008.

The duration of the grass pollen season in Garmisch-Partenkirchen in 2009 was 50 % longer than in 2008 (101 days in 2008, 152 days in 2009) and lasted till the beginning of October. The 2009 grass pollen season was also associated with a 3.6 times higher

total pollen amount (ca. 9,540 grains m^{−3}). However, the location of the pollen trap was changed in 2009 when it was repositioned from a roof (10 m above ground level) to 2 m above ground level in a small meadow. For the higher elevation sites, the pollen season duration and also the peak amounts were lower in both years than in the valley: Total pollen amounts

Table 6 Features of the birch and grass pollen seasons in 2008 and 2009 for Garmisch-Partenkirchen, Ehrwald, and UFS: start, end, and duration of the pollen season, peak date and amount and total amount (grains m^{−3})

Species	Station	2008					2009				
		Start	End	Duration (days)	Peak (amount grains m ^{−3})	Total (grains m ^{−3})	Start	End	Duration (days)	Peak (amount grains m ^{−3})	Total (grains m ^{−3})
<i>Betula</i>	Garmisch-Partenkirchen (720 m)	22.04.	02.06.	42	27.04. (248)	1,602	08.04.	17.05.	40	16.04. (228)	1,481
	Ehrwald (1,503 m)	26.04.	03.06.	39	30.04. (126)	643	<12.05.	~26.05.	~15	<17.05. (>23)	>75
	UFS (2,650 m)	26.04.	03.06.	39	05.05. (68)	392	<15.04.	~31.05.	~47	<15.04. (>77)	>344
<i>Gramineae</i>	Garmisch-Partenkirchen (720 m)	23.05.	31.08.	101	10.06. (265)	2,645	10.05.	08.10.	152	11.06. (969)	9,535
	Ehrwald (1,503 m)	24.05.	11.08.	80	21.06. (32)	621	13.05.	16.08.	96	14.07. (68)	1,249
	UFS (2,650 m)	20.06.	04.08.	46	23.06. (28)	246	13.05.	01.08.	81	13.06. (40)	399

at Ehrwald and UFS were 24 and 9 % of that in Garmisch-Partenkirchen in 2008 and 13 and 4 % in 2009, respectively.

3.4 Comparison of season parameters determined from phenological and aerobiological data in 2009

3.4.1 *Betula*

The relationship between phenology and airborne pollen counts can be explored in Fig. 2a in which the temporal course of birch pollen counts in Garmisch-Partenkirchen in 2009 and phenological onset dates for different altitudinal levels are shown. The first vertical line indicates the day when the first birch tree emitted pollen (FFD) in the valley of Garmisch-Partenkirchen (9 April). This date coincides very well with the start of the birch pollen season (8 April) calculated from aerobiological data. The second vertical line represents the mean date for the beginning of flowering (MFD) in Garmisch-Partenkirchen and exactly corresponds with the peak of the pollen season (16 April). The MFD in Ehrwald (line 3) and Eibsee (line 4) almost match a local peak observed at the Garmisch-Partenkirchen pollen station. The MFD of locations above 1,200 m (lines 5 and 6) do not correspond directly with higher pollen levels in the valley.

Figure 2b shows first and mean dates of the beginning of flowering (FFD and MFD) at different birch sites within the study area in 2009 compared with pollen amounts counted at Ehrwald and UFS. In contrast to Garmisch-Partenkirchen, the start of trap recording in 2009 was delayed, and thus, pollen counts were not recorded before 15 April (UFS) or 12 May (Ehrwald), respectively. However, distinctive characteristics, especially for the UFS site, where no birches occur, can be derived. Within 1 week of the first flowering date (line 1) and the start of the pollen season (line 2) in Garmisch-Partenkirchen, pollen was transported to the 2,650 m site. The corresponding daily pollen amount of 77 grains m^{-3} was the highest within the total pollen season of 2009, declining distinctively until 7 May. A few days after the MFD in Ehrwald (line 5) (1,200–1,300 m), pollen amounts increased again, but did not again exceed 30 grains m^{-3} . The last small peak (8 grains m^{-3}) was observed on 29 May. The local peaks at Ehrwald matched those of UFS but were associated with higher pollen amounts.

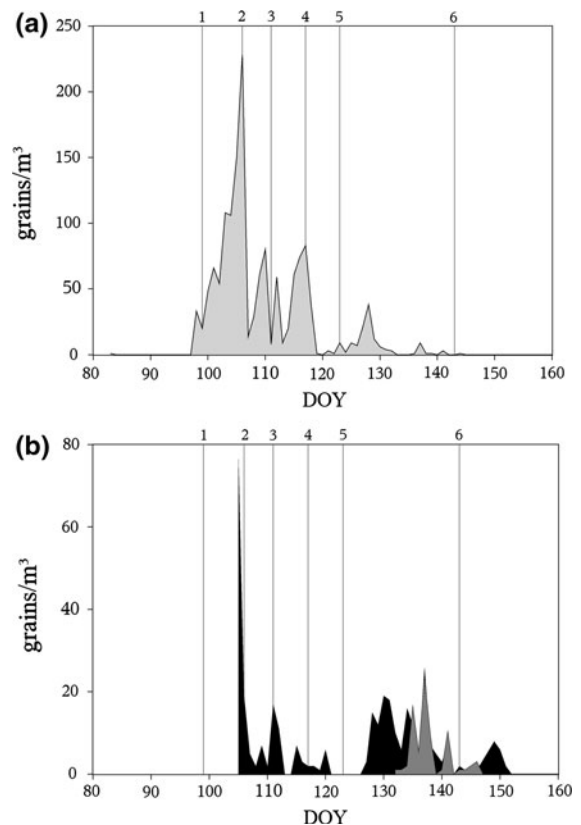


Fig. 2 Temporal course of birch pollen amount (grains m^{-3}) in 2009 for **a** Garmisch-Partenkirchen and **b** Ehrwald (grey) and UFS (black); vertical black lines (1–6) indicate the first flowering date (FFD, 1) and mean flowering date (MFD, 2–6) for different altitudinal ranges, n number of individuals: (1) FFD 9 April Garmisch-Partenkirchen (700–800 m, $n = 1$); (2) MFD 16 April Garmisch-Partenkirchen (700–800 m, $n = 57$); (3) MFD 21 April Ehrwald (900–1,100 m, $n = 24$); (4) MFD 27 April Eibsee (800–1,020 m, $n = 24$); (5) MFD 3 May Ehrwald (1,200–1,300 m, $n = 5$); (6) MFD 23 May high level sites (1,700 m, $n = 3$)

3.4.2 *Grass*

The temporal course of grass pollen amount in Garmisch-Partenkirchen in 2009 is shown in Fig. 3a. For a comparison with phenology, we selected the mean dates for the beginning of flowering (MFD) for cocksfoot and meadow foxtail averaged for three of the lowest locations in the valley of Garmisch-Partenkirchen (700–800 m) and for two of the highest locations in Ehrwald (1,100–1,300 m). The start of the grass pollen season was on 10 May (Table 6) and therefore only 2 days before the MFD for meadow foxtail (line 1) in the valley. During the next few days,

there was a continuous increase in pollen amounts and cocksfoot (line 2) started to flower 2 weeks after meadow foxtail in Garmisch-Partenkirchen. Almost 3 weeks later (16 June), the mean flowering date for meadow foxtail (3) occurred at the highest observation sites; however, pollen amounts had already decreased remarkably and did not again exceed $200 \text{ grains m}^{-3}$. The mean flowering date for cocksfoot (4) at high level sites was recorded on 30 June, but pollen grains remained under 50 grains m^{-3} until the end of the pollen season.

The temporal development of grass pollen amount in Ehrwald and at UFS in 2009 is shown in Fig. 3b. It can be seen that MFD in the valley for meadow foxtail

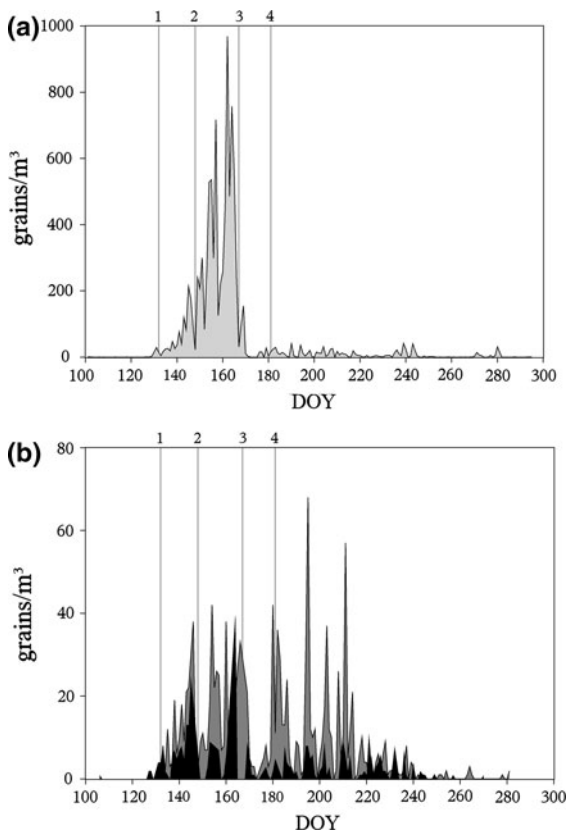


Fig. 3 Temporal course of grass pollen amount (grains m^{-3}) in **a** Garmisch-Partenkirchen and **b** Ehrwald (grey) and UFS (black) in 2009; vertical black lines (1–4) indicate mean flowering dates (MFD) for the lowest and the highest altitudinal level, n number of individuals: (1) meadow foxtail MFD 12 May Garmisch-Partenkirchen (700–800 m, $n = 3$); (2) cocksfoot MFD 28 May Garmisch-Partenkirchen (700–800 m, $n = 3$); (3) meadow foxtail MFD 16 June Ehrwald (1,100–1,300 m, $n = 2$); (4) cocksfoot MFD 30 June Ehrwald (1,100–1,300 m, $n = 2$)

(1) prompted an increase in pollen amounts, both in Ehrwald and at UFS, and that phenological dates of cocksfoot (2) corresponded well with local peaks. The onset of meadow foxtail (3) at higher altitudes did not seem to affect aerobiological data very much since it was followed by a decrease in pollen amounts. However, grass pollen amounts, especially for Ehrwald, were higher again after the mean flowering date of cocksfoot (4) at higher altitudes.

3.5 Wind conditions and pollen amount at UFS in 2008 and 2009

Pollen that is released by the anthers of plants is suspended by turbulent vertical mixing and transported by wind (D'Amato et al. 2007). Wind is therefore a major factor that influences the dispersion of pollen after release into air (Laaidi 2001), and it is especially important for pollen traps located in vegetation-free areas, such as at UFS. Figure 4 shows an example of the prevailing wind direction during the 2008 birch pollen season measured at the climate station in Garmisch-Partenkirchen (grey) and at the Zugspitze climate station (white).

The Zugspitze site is characterized by northerly, westerly, and southerly/south-easterly winds. Wind from the south can be attributed to the foehn, a wind system that results in higher temperatures on the northern slope of the Alps.

Garmisch-Partenkirchen is characterized by a mountain-valley wind system with daytime up-valley winds (NE, E) and nocturnal down-valley winds (SW, WSW). It can be assumed that this diurnal regime contributes to higher pollen amounts during the daytime since pollen from the valley is transported up to the high mountain site. The necessary wind for this pollen transport originates from the north-east and accounted for almost 50 % of the measured wind directions during 2008 and 2009 birch pollen seasons. Since diurnal pollen sums were only split at midnight and at noon, it is not possible to attribute the diurnal wind regime to these aerobiological data. Figure 5 shows the prevailing wind directions for different times of the day and demonstrates that a separation at midnight and noon (Fig. 5a, b) does not coincide with the diurnal change of wind direction at Garmisch-Partenkirchen. A better discrimination is achieved when the wind direction is separated for the time before and after sunrise (Fig. 5c, d).

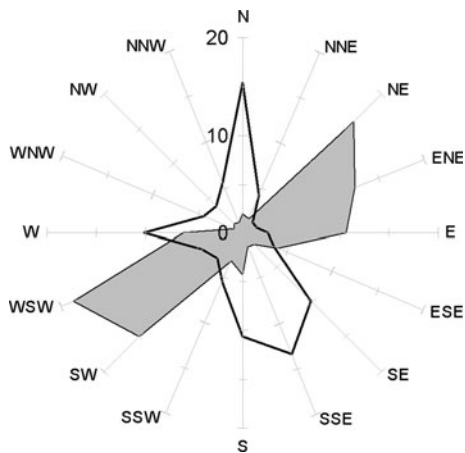


Fig. 4 Prevailing wind directions (hourly values) at Garmisch-Partenkirchen (grey) and Zugspitze (white) during pollen flight of birch 208 at the Schneefernerhaus (UFS)

In Garmisch-Partenkirchen, pollen sums were higher during the 0:00–12:00 period with the only exception being birch pollen in 2009 (Table 7). In Ehrwald, the picture was the reverse with most of pollen counted between 12:00 and 24:00, except for birch pollen in 2009. At the UFS, most of the pollen was recorded between 12:00 and 24:00; however, birch pollen in 2008 showed the opposite pattern. A *t* test for comparison of means showed, however, that differences in pollen amounts for these two daily subperiods were only significant for grass pollen amounts in Garmisch-Partenkirchen in 2009.

Figure 6 a–d shows the sums (%) of birch and grass pollen in 2008 and 2009 that were transported with a specific wind direction. Since we only had two pollen counts per day, the data can merely be associated with the most frequent wind direction during the corresponding time period. Of the total birch pollen amount in 2008 recorded at the UFS, 40.9 % was associated with north-easterly winds at Garmisch-Partenkirchen. Winds from the south-west and west–south-west contributed 11.3 and 33.5 % of the pollen amount, respectively. When wind at the Zugspitze came from the north, 19.5 % of the pollen sum was recorded. South-easterly, south–south-easterly, and westerly winds at the Zugspitze each contributed approximately 15 % of the pollen sum. In 2009, westerly winds at Garmisch-Partenkirchen contributed more than 60 % of the pollen amount at the UFS and southerly wind directions at the Zugspitze were

associated with the highest percentage of pollen registered (41.4 %).

For grass pollen in 2008, the amount was almost equally distributed between winds from the north-east and south-west at Garmisch-Partenkirchen. About half of the pollen sums were associated with westerly winds at the Zugspitze. The highest percentage of pollen (26 %) in 2009 could be linked to westerly winds at the summit. Pollen sums were also higher at the UFS when north-easterly winds were prevalent in Garmisch-Partenkirchen.

4 Discussion

4.1 Influence of topography on phenology

Altitudinal gradients (Table 3) for all species and phases were statistically significant and associated with high R^2 -values, indicating that altitude was able to explain a high percentage of the variance in phenological onset dates. The magnitudes of the regression coefficients were higher for grass phenophases (6.3–7.1 days $(100 \text{ m})^{-1}$) than for birch phenophases (3.1–3.2 days $(100 \text{ m})^{-1}$). Since temperature is the most important factor explaining phenological onset dates (Menzel and Fabian 1999; Badeck et al. 2004; Defila and Clot 2005), we conclude that the decrease in temperature with an increase in altitude is the main factor responsible for a delay of entry dates. Additionally, temperature response rates in phenology showed that phenological phases are delayed by almost 7 (birch) and 10 (grass) days per $1 \text{ }^\circ\text{C}$ decrease in temperature. Our findings suggest a discernible temperature sensitivity in the grasses and indicate that further temperature increases relating to climate change could lead to a notably earlier start of the grass pollen season, associated with major consequences for people suffering from pollen allergies.

Note that our study does not incorporate temperature data measured directly at the 36 phenological observation sites but temperature lapse rates calculated from two climate stations whereas the altitude of the highest situated station (2,650 m) by far exceeds the altitude of our highest phenological observation site (1,233 m). Besides, phenological observations were only conducted in one single year and should therefore be interpreted with caution. This makes it

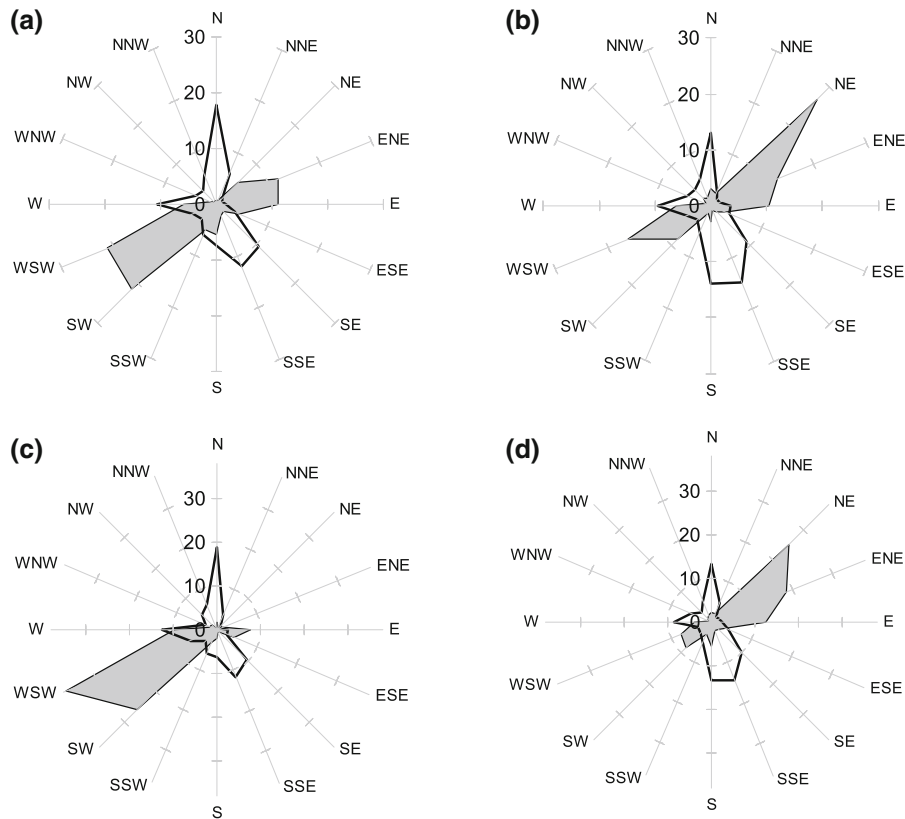


Fig. 5 Prevailing wind directions (hourly values) at Garmisch-Partenkirchen (grey) and Zugspitze (white) during pollen flight of birch 2008 at the Schneefernerhaus (UFS) separated for

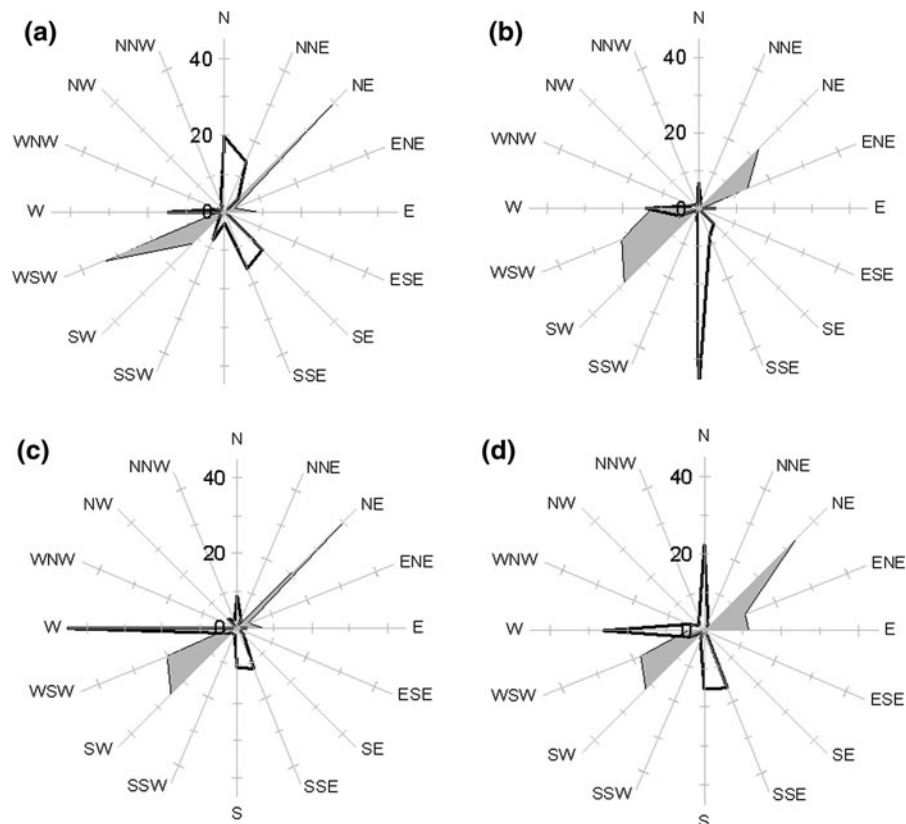
different times of the day; **a** 0:00–12:00, **b** 12:00–24:00, **c** 0:00–7:00 and 22:00–24:00, **d** 7:00–21:00

Table 7 Sums of birch and grass pollen amounts (grains m⁻³) in 2008 and 2009 for the sites Garmisch-Partenkirchen, Ehrwald, and UFS, divided into two daily subperiods (0:00–12:00; 12:00–24:00).

Species	Station	2008			2009		
		0–12	12–24	<i>P</i>	0–12	12–24	<i>P</i>
<i>Betula</i>	Garmisch-Partenkirchen (720 m)	816	776	0.901	650	831	0.512
	Ehrwald (1,503 m)	257	371	0.483	42	33	0.741
	UFS (2,650 m)	219	187	0.701	96	248	0.091
<i>Gramineae</i>	Garmisch-Partenkirchen (720 m)	1,646	999	0.161	6,388	3,147	0.048
	Ehrwald (1,503 m)	274	347	0.226	528	730	0.116
	UFS (2,650 m)	120	126	0.887	176	239	0.272

Bold *P* value (*t* test) indicates significant difference between the two time periods

Fig. 6 Sums of pollen amount (%) associated with wind directions (modal values of two daily subperiods, 0:00–12:00; 12:00–24:00) at Garmisch-Partenkirchen (*grey*) and Zugspitze (*white*) during pollen flight of **a** birch 2008, **b** birch 2009, **c** grass 2008, and **d** grass 2009 at the Schneefernerhaus (UFS)



indispensable to compare our results with other studies. Altitudinal gradients for the Taunus hills, located in the Central German Uplands, were evaluated by Chen (1994). Regression coefficients for leaf unfolding of birch were $4 \text{ days } (100 \text{ m})^{-1}$. In addition, Rötzer and Chmielewski (2001) found a delay of 3 days $(100 \text{ m})^{-1}$ for the beginning of flowering of birch across Europe. For full flowering of cocksfoot and meadow foxtail, Chen (1994) calculated a delay of only 2 days $(100 \text{ m})^{-1}$. Ziello et al. (2009) found an altitudinal gradient of about 4 days $(100 \text{ m})^{-1}$ for cocksfoot in the region of Garmisch-Partenkirchen. Whereas these values for birch almost match our findings, the values for the grass species are far lower. However, the study area of Chen (1994) only comprised a gradient from 100 m to 800 m.

Besides altitudinal effects, we also found discernible differences in phenology with different aspects (Table 4, 5–7 days). Chen (1994) also found that northern and southern exposed birches in the Taunus hills showed differences in onset dates up to 14 days. In our study, birches at the same altitudinal level but with different aspects revealed different onset times that

equate to altitudinal/temperature differences ranging from $161 \text{ m}/0.8 \text{ }^{\circ}\text{C}$ for the beginning of leaf unfolding to $184 \text{ m}/0.9 \text{ }^{\circ}\text{C}$ for the beginning of flowering and $213 \text{ m}/1.0 \text{ }^{\circ}\text{C}$ for full flowering. High temperature variations were also documented by Scherrer et al. (2011) who evaluated surface and soil temperatures in alpine landscapes and found substantial temperature variations of $2\text{--}3 \text{ }^{\circ}\text{C}$ related to slope exposure. Therefore, even locations at the same altitude can have noticeable differences in phenology and consequently in the timing of pollen release. Hence, being less exposed to pollen in high mountain altitudes is not only a question of elevation but also of aspect. However, our analysis only evaluated birch individuals of two different sites located at approximately the same altitude. Micrometeorological influences (e.g. proximity to forests or water bodies) that also alter flowering times (Jochner et al. 2011b) have not been evaluated here. Even though the database of grass ($n = 10$) was not sufficiently large to allow a comparison of effects related to different aspects or microtopographical characteristics, phenology of grass species is believed to be strongly influenced by microclimate (Defila

2007) and might therefore show even higher differences than those that were detected for birch. The study of Scherrer et al. (2011), for example, found not only soil temperature differences for different slopes but also noticeable variations within slopes (3–4 °C) due to microtopography and even within a small plot (1 m²) resulting from plant cover effects.

4.2 Shifts in pollen seasons 2008 and 2009

The comparison between phenological and aerobiological data in Garmisch-Partenkirchen revealed a good agreement with respect to the start of the pollen season. Since phenology is responsive to the temperature of the preceding months (Menzel et al. 2006), this meteorological parameter is widely applied using mean temperatures or temperature sums in models for forecasting the start of the pollen season (e.g. Galán et al. 2001; Laaidi et al. 2003; Smith and Emberlin 2005). The 2-week earlier start of birch pollen season in 2009 compared to 2008 is probably related to the high mean April temperature (2009 10 °C; 2008 6.6 °C) that was among the six highest mean values since the start of temperature measurements in Garmisch-Partenkirchen in 1889. The average April temperature (1971–2000) was, however, only 6.1 °C, and the highest value was recorded in 2007 (11.1 °C). As shown by Bruns (2009) and Jochner et al. (2011a), who described the phenological impacts of high temperatures in spring 2009 for other parts of Germany, it can be assumed that the abrupt temperature increase in early April after a relatively cold winter and late spring also led to a much earlier and more rapid plant development in Garmisch-Partenkirchen, implying an earlier but also shorter birch pollen season compared to 2008. The same can be seen in the grass pollen season that also started almost 2 weeks earlier in 2009.

4.3 Synchronization between aerobiological and phenological data

Local emissions of birch pollen matched closely the timing of the start of the pollen season in 2009, defined by aerobiology. The peak of the pollen season also coincided with the mean flowering date of birch in the valley. Evidence that the pollen trap of Garmisch-Partenkirchen was affected by medium-range transport of pollen can be derived from Fig. 2 where the mean

flowering dates of birch in Ehrwald and Eibsee, including Griesen, corresponded to local peaks of the temporal birch pollen concentration. Besides local influence, these peaks could be supplemented by a downward movement of pollen from higher locations. This movement can be attributed to the mountain-valley wind system that is characterized by down-valley winds during the night.

Pollen counts in Garmisch-Partenkirchen were not affected by mean onset dates of higher locations (>1,200 m, see Fig. 2a) where birch tree abundance and therefore pollen production were generally lower. This also indicates that the end of the pollen season cannot be described and explained by phenological data as accurately as the start of the pollen season since a wide range of flowering times within a small area—as a consequence of the variety of temperature conditions characteristic of mountainous regions—leads to extended pollen emissions. Pollen originating from higher locations is transported later and over a longer distance to the valley of Garmisch-Partenkirchen but might be deposited earlier. Moreover, it is more difficult to predict the end of the pollen season since the effect of meteorological parameters on pollen emission and dispersion differ throughout the pollen season (Spiexma 1980; Vázquez et al. 2003). Sunshine and temperature are most important for growth and development before flowering occurs; sunshine, rainfall, and relative humidity are the relevant meteorological parameters influencing pollen release, and wind is the major factor responsible for pollen dispersal (Laaidi 2001). The time between the start and the peak of the pollen season is especially reliable for biological phenomena, for example, pollen emission, and less affected by resuspension of pollen that leads to an increase in pollen amounts (Vázquez et al. 2003).

Temporal delay between onset dates in phenology and aerobiology can partly be explained by long- or medium-range pollen transport (Estrella et al. 2006). The easiest way to detect long- or medium-range transport is to operate a pollen station, where no specimen of the considered species is located. This condition is satisfied for the pollen trap at the Schneefernerhaus (UFS), located at 2,650 m a.s.l. We detected intermittently large amounts of birch and grass pollen that definitely do not originate from the near surroundings of the pollen station. At the UFS, birch pollen concentrations in 2008 and 2009 were about 25 % of the amount that was measured in the valley of Garmisch-Partenkirchen. These high

quantities may also be ascribed to the morphology of *Betula* spp. pollen: The almost spherical grains have a small diameter of 22 μm and belong to one of the furthest transported types of pollen grains (Sofiev et al. 2006). Estrella et al. (2006) reported that grass pollen is not as mobile as birch pollen. These grains mostly have a spheroid or ovoid shape and a diameter ranging roughly between 15 and 55 μm (Jäger 2008). We also only detected a smaller fraction of 9 % (2008) and 4 % (2009) of the pollen at the UFS compared to the valley. However, the high amount of pollen in Garmisch-Partenkirchen in 2009 (ca. 9,540 grains m^{-3}) can also be attributed to the location of the pollen trap since it was placed within a meadow in 2009 (2 m above ground level) and not on the roof of a building, as in 2008. First pollen grains at ground level might be up to 2 weeks earlier than at roof level (Rapiejko 1995). Therefore, not only the aerodynamic characteristics of pollen types but also the height of a plant relative to the trap can contribute to differences in pollen amounts.

The time interval between the date when the first birch pollen was emitted in the valley and the date when the first pollen grains were recorded at the UFS was less than 1 week; moreover, the peak of the pollen amount at UFS was only 1 day before the local mean flowering date in Garmisch-Partenkirchen. Hence, pollen counts at the vegetation-free UFS are strongly related to phenological characteristics of the valley. All other local flowering dates at different altitudes were not so well reflected in the pollen data, suggesting that minor birch pollen emissions do not have a major effect on high mountain regions.

The time span between the aerobiological start of the grass pollen season and the mean flowering date of meadow foxtail for three locations in Garmisch-Partenkirchen was only 6 days, suggesting that the selected grass species is one of the earliest flowering ones and hence can be useful for predicting the start of the grass pollen season. Cocksfoot started to flower 2 weeks later, and local pollen emission seems to contribute mainly to the pollen records. However, mean flowering dates for the grass species in higher regions (1,100–1,300 m) were relatively late (16th/30 June) and did not account for an obvious increase in pollen amount in Garmisch-Partenkirchen.

The mean flowering dates of the selected grass species meadow foxtail and cocksfoot in the valley of Garmisch-Partenkirchen also matched an increase in grass pollen at the higher elevated sites of Ehrwald and

UFS (see Fig. 3b). Mean flowering dates of the two species at higher locations corresponded almost exactly with local peaks recorded at higher altitudinal levels, which was especially apparent for Ehrwald.

A minor inconsistency in phenological and aerobiological grass data has to be attributed to the species selected for observation. Whilst pollen of all *Gramineae* species is summarized in the aerobiological data, we only observed phenological behavior of cocksfoot and meadow foxtail. *Gramineae* records include pollen from a larger number of species whose flowering periods overlap from spring to the end of summer (Jato et al. 2006). It is also evident that land use has a great impact on grass pollen concentrations. Therefore, it is obvious that the location of the pollen trap in Garmisch-Partenkirchen, surrounded by large areas occupied by meadows, led to a far higher pollen amount than in Ehrwald or at UFS.

4.4 Wind as an explanatory variable

Pollen concentrations at higher elevation sites are still detectable and often fluctuate in magnitude. This can be attributed to local weather conditions that are connected with specific wind directions. Jato et al. (2006) showed that pollen grains were predominantly abundant when turbulences keep wind-dispersed pollen in the air or when weather conditions provided low wind speeds where airborne pollen was transported at a very low velocity.

We only found diurnal variation in pollen amounts for *Gramineae* pollen in Garmisch-Partenkirchen in 2009 (Table 7). However, aerobiological data were only available twice a day for the time spans 0:00–12:00 and 12:00–24:00. Since birch shows its daily peak around midday and grass between 6:00 and 9:00 (Scheid and Bergmann 2004), it is evident that this separation is impractical for birch, but not for grass. Attributing wind directions to aerobiological data at this given temporal resolution does not fully allow an interpretation of medium-range transport. Phenological data at different altitudinal levels (see Sect. 3.4) are therefore more suitable to describe these characteristics.

5 Conclusions

Analyses of the flowering behavior of major allergenic species along an altitudinal gradient in the Zugspitze

area revealed a great dependence on altitude and on exposition. Grass species were found to be most responsive to altitude and therefore to temperature, suggesting that climate change might have considerable effects on the start of the grass pollen season. Moreover, we found a good agreement in the start of phenological and aerobiological season dates, particularly at lower altitude, where local pollen emissions accounted most for the start of the season. In contrast, pollen amounts at the highest and vegetation-free site were predominantly affected by medium-range transport, contributing to high and medically relevant pollen concentrations.

Besides the visual interpretation of temporal pollen curves in relation to phenological onset dates, there is a need for air mass back-trajectories that account for the daily atmospheric circulation pattern. However, the confirmation of these models is the weakest point, and that is why we need more direct observations of nature. This is especially true when considering mountainous and complex areas that are as small as in our study (Fig. 1, total area $\sim 325 \text{ km}^2$, max. distance between pollen traps $\sim 12 \text{ km}$). Back-trajectories also require a spatial grid of meteorological data which we do not have at the necessary resolution. Moreover, a finer temporal resolution of the aerobiological data would further allow for correlating meteorological data, especially wind data, with pollen and would enable a better interpretation and understanding of aerobiological processes.

Acknowledgments The research conducted in this study was supported by grant U 119 (Impacts of climate on pollen season and distribution in the Alpine region) of the Bavarian State Ministry of the Environment and Public Health (StMUG). S.J. and C.Z. gratefully acknowledge the support of the TUM Graduate School's Faculty Graduate Center Weihenstephan at the Technische Universität München.

References

- Badeck, F.-W., Bondeau, A., Böttcher, K., Doktor, D., Lucht, W., Schaber, J., et al. (2004). Responses of spring phenology to climate change. *New Phytologist*, *162*, 295–309.
- Barry, R. G. (1981). *Mountain weather and climate*. London and New York: Methuen.
- Beniston, M. (2006). Mountain weather and climate: A general overview and a focus on climatic change in the Alps. *Hydrobiologia*, *562*, 3–16.
- Bortenschlager, S., & Bortenschlager, I. (2005). Altering airborne pollen concentrations due to the global warming. A comparative analysis of airborne pollen records from Innsbruck and Obergurgl (Austria) for the period 1980–2001. *Grana*, *44*(3), 172–180.
- Bruns, E. (2009). *Das erste Halbjahr 2009 klimatologisch-phenologisch betrachtet*. Phänologische Betrachtungen vom Deutschen Wetterdienst. Offenbach am Main: Deutscher Wetterdienst, pp. 1–2.
- Cambon, G., Ritchie, J. C., & Guinet, P. (1992). Long-distance transport of airborne pollen in Southern Ontario (Canada). *Canadian Journal of Botany*, *70*, 2284–2293.
- Campbell, I. D., McDonald, K., Flannigan, M. D., & Kringayark, J. (1999). Long-distance transport of pollen into the Arctic. *Nature*, *399*, 29–30.
- Cecchi, L., Torrigiani Malaspina, T., Albertini, R., Zanca, M., Ridolo, E., Usberti, I., et al. (2007). The contribution of long-distance transport to the presence of Ambrosia pollen in central northern Italy. *Aerobiologia*, *23*, 145–151.
- Chen, X. (1994). *Untersuchung zur zeitlich-räumlichen Ähnlichkeit von phänologischen und klimatologischen Parametern in Westdeutschland und zum Einfluss geökologischer Faktoren auf die phänologische Entwicklung im Gebiet des Taunus* (pp. 74–77). Offenbach am Main: Deutscher Wetterdienst.
- Clot, B., Peeters, A. G., Fankhauser, A., & Frei, T. (1995). *Airborne pollen in Switzerland 1994*. Zürich: Schweizerische Meteorologische Anstalt.
- Cornelius, C., Petermeier, H., Estrella, N., & Menzel, A. (2011). A comparison of methods to estimate seasonal phenological development from BBCH scale recording. *International Journal of Biometeorology*, *55*, 867–877.
- D'Amato, G., Cecchi, L., Bonini, S., Nunes, C., Annesi-Maesano, I., Behrendt, H., et al. (2007). Allergenic pollen and pollen allergy in Europe. *Allergy*, *62*, 976–990.
- Defila, C. (2007). Alpine Pflanzenphänologie in der Schweiz. *Promet*, *33*, 36–39.
- Defila, C., & Clot, B. (2005). Phytophenological trends in the Swiss Alps, 1951–2002. *Meteorologische Zeitschrift*, *14*, 191–196.
- DWD (Deutscher Wetterdienst). (1991). *Anleitung für die phänologischen Beobachter des Deutschen Wetterdienstes*. Offenbach am Main: Deutscher Wetterdienst.
- Ellenberg, H. (1996). *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht* (5th ed.). Stuttgart: Ulmer.
- Estrella, N., Menzel, A., Krämer, U., & Behrendt, H. (2006). Integration of flowering dates in phenology and pollen counts in aerobiology: Analysis of their spatial and temporal coherence in Germany (1992–1999). *International Journal of Biometeorology*, *51*, 49–59.
- Frei, T. (1997). Pollen distribution at high elevation in Switzerland: Evidence for medium range transport. *Grana*, *36*, 34–38.
- Galán, C., Cariñanos, P., Garcia-Mozo, H., Alcázar, P., & Domínguez-Vilches, E. (2001). Model for forecasting *Olea europaea* L. Airborne pollen in South-West Andalusia, Spain. *International Journal of Biometeorology*, *45*, 59–63.
- Galán, C., Emberlin, J., Domínguez, E., Bryant, R. H., & Vilamandos, F. (1995). A comparative analysis of daily variations in the Gramineae pollen counts at Cordoba, Spain and London, UK. *Grana*, *34*, 189–198.

- Hirst, J. M. (1952). An automatic volumetric spore trap. *Annals of Applied Biology*, 39, 257–265.
- Jäger, S. (2008). Exposure to grass pollen in Europe. *Clinical and Experimental Allergy Reviews*, 8, 2–6.
- Jarvis, A., Reuter, H. I., Nelson, A., & Guevara, E. (2006). Hole-filled seamless SRTM data V3, International Centre for Tropical Agriculture (CIAT). <http://srtm.csi.cgiar.org>.
- Jato, V., Rodriguez-Rajo, F. J., Alcazar, P., De Nuntiis, P., Galán, C., & Mandrioli, P. (2006). May the definition of pollen season influence aerobiological results? *Aerobiologia*, 22, 13–25.
- Jochner, S., Beck, I., Behrendt, H., Traidl-Hoffmann, C., & Menzel, A. (2011a). Effects of extreme spring temperatures on urban phenology and pollen production: A case study in Munich and Ingolstadt. *Climate Research*, 49, 101–112.
- Jochner, S., Heckmann, T., Becht, M., & Menzel, A. (2011b). The integration of plant phenology and land use data to create a GIS-assisted bioclimatic characterisation of Bavaria, Germany. *Plant Ecology and Diversity*, 4, 91–101.
- Laaidi, M. (2001). Forecasting the start of the pollen season of *Poaceae*: Evaluation of some methods based on meteorological factors. *International Journal of Biometeorology*, 45, 1–7.
- Laaidi, M., Thibaudon, M., & Besancenot, J.-P. (2003). Two statistical approaches to forecasting the start and duration of the pollen season of *Ambrosia* in the area of Lyon (France). *International Journal of Biometeorology*, 48, 65–73.
- Meier, U. (2001). *Entwicklungsstadien mono- und dikotyler Pflanzen*. *BCH-Monographie* (2nd ed.). Berlin: Blackwell Wissenschaftsverlag.
- Menzel, A., & Fabian, P. (1999). Growing season extended in Europe. *Nature*, 397, 659.
- Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aasa, A., Ahas, R., et al. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology*, 12, 1969–1976.
- Rantio-Lehtimäki, A. (1994). Short, medium and long range transported airborne particles in viability and antigenicity analyses. *Aerobiologia*, 10, 175–181.
- Rapiejko, P. (1995). Pollen monitoring in Poland. In R. Spiewak (Ed.), *Pollen and pollinosis: Current problems*. Lublin: Institute of Agricultural Medicine.
- Rötzer, T., & Chmielewski, F. M. (2001). Phenological maps of Europe. *Climate Research*, 18, 249–257.
- Rousseau, D. D., Duzer, D., Cambon, G. V., Jolly, D., Poulsen, U., Ferrier, J., et al. (2003). Long distance transport of pollen to Greenland. *Geophysical Research Letters*, 30. doi:10.1029/2003GL017539.
- Sánchez Mesa, J. A., Smith, M., Emberlin, J., Allitt, U., Caulton, E., & Galán, C. (2003). Characteristics of grass pollen seasons in areas of southern Spain and the United Kingdom. *Aerobiologia*, 19, 243–250.
- Scheid, G., & Bergmann, K.-Ch. (2004). 20 Jahre Stiftung Deutscher Polleninformationsdienst (1983–2003). *Allergo Journal*, 13, 261–268.
- Scherrer, D., Schmid, S., & Körner, C. (2011). Elevational species shift in a warmer climate are observed when based on weather station data. *International Journal of Biometeorology*, 55, 645–654.
- Smith, M., & Emberlin, J. (2005). Constructing a 7-day ahead forecast model for grass pollen at north London, United Kingdom. *Clinical and Experimental Allergy*, 35, 1400–1406.
- Sofiev, M., Siljamo, P., Ranta, H., & Rantio-Lehtimäki, A. (2006). Towards numerical forecasting of long-range air transport of birch pollen: Theoretical considerations and a feasibility study. *International Journal of Biometeorology*, 50, 392–402.
- Spiekma, F. T. M. (1980). Daily hay fever forecast in the Netherlands. Radio broadcasting of the expected influence of the weather on subjective complaints of hay fever sufferers. *Allergy*, 35, 593–603.
- Van de Water, P. K., Keever, T., Main, C. E., & Levetin, E. (2003). An assessment of predictive forecasting of *Juniperus ashei* pollen movement in the Southern Great Plains, USA. *International Journal of Biometeorology*, 48, 74–82.
- Vázquez, L. M., Galán, C., & Domínguez-Vilches, E. (2003). Influence of meteorological parameters on olea pollen concentrations in Córdoba (South-western Spain). *International Journal of Biometeorology*, 48, 83–90.
- Zacharias, F. (1972). *Blühphaseneintritte an Straßenbäumen (insbesondere Tilia x euchlora KOCH) und Temperaturverteilung in Westberlin*, PhD thesis. Berlin: Freie Universität Berlin.
- Zauli, D., Tiberio, D., Grassi, A., & Ballardini, G. (2006). Ragweed pollen travels long distance. *Annals of Allergy, Asthma & Immunology*, 97, 122–123.
- Ziello, C., Estrella, N., Kostova, M., Koch, E., & Menzel, A. (2009). Influence of altitude on phenology of selected plant species in the Alpine region (1971–2000). *Climate Research*, 39, 227–234.