How will climate change alter the dynamics of airborne pollen and pollen load of allergenic plants?

The “exceptionally warm year” 2018 in Linz (Upper Austria)—a potential model for the future based on long-term trends

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Summary

Background Globally, climate change is being observed. Pollen allergies have been increasing since the middle of the last century. Outdoors, sensitization against pollen allergens is responsible for the highest prevalence of allergies of eyes and airways. Hence, the following two questions arose: (1) How does climate change become manifest locally–regionally, and do temperatures and precipitation have to be considered exceptional in 2018? (2) How do changing meteorological conditions impact on pollination and pollen load?

Methods Pollen data of the main allergenic plants—collected at the pollen monitoring station Linz, Upper Austria—were analysed; 2018 was compared to the years 1993–2017. By means of statistical methods, the impact of meteorological parameters on pollen seasons and pollen load were examined.

Results Climate change was confirmed for the region. The regional climate has shifted from moderate to warmer and drier (semi-arid) conditions. Preseasonal cumulated meteorological parameters determined flowering and pollen seasons (PS). Start and duration of the pollination of hazel, alder, birch, and grass followed other rules than the seasonal pollen production, termed seasonal pollen integral (SPIn). By its hybrid character, the model-year 2018 offered the unique chance to generate and explain different scenarios of pollen emission and transmission. For the start of flowering of hazel (Corylus), alder (Alnus) and birch (Betula), the coincidence of cumulated mean daily warmth (MDWcumul) and a distinct threshold for the highest temperature of a day (HTD) is necessary and species-specific. In 2018, the earliest begin of the pollen season (PSB) was observed. Frost delayed the PSB. Preseasonal frost as well as cool temperatures caused SPIn of alder and birch to rise, whereas SPIn of hazel were increased by warmer temperatures. Warm weather prolonged pollen seasons of early flowering plants. Heat combined with drought shortened PS of birch in 2018. Cumulated relative humidity (RHcumul) correlated highly significant with the PSB of grasses. Warm and dry conditions in 2018 caused the earliest PSB of grass since 1993. Over the years, SPI and major pollen peaks of grasses have decreased, primarily due to dryness.

Conclusion The assumption that climate warming in Linz over 26 years should have increased pollen concentrations of allergenic plants was not confirmed. On the contrary, trend analyses showed that the pollen load has decreased. Hence, the increase in sensitization to pollen allergens and of the prevalence of pollen allergies ask for other explanations.

Keywords Climate change · Allergenic plants · Pollination/pollen season · Meteorological scenarios · Linz (Upper Austria)

Abbreviations

HTD Highest temperature of a day
LTD Lowest temperature of a day
How will climate change alter the dynamics of airborne pollen and pollen load of allergenic plants?  

**Background**

Pollen are among the most important allergen carriers outdoors. In Austria at least in children, sensitization and aero-allergies depend on the pollen load [1]. In polluted urban areas allergen-specific IgEs were found to be higher (37.8%) as compared to rural areas (25.6%) [2]. Recently in Salzburg, 53.5% out of 501 un-selected teens at an age between 12 and 21 were found to be sensitized against pollen allergens, 26% against Bet v 1 (main allergen of birch). The prevalence of sensitization was as high as 41.7% and dominated by Bet v 1 (grass allergen group 1) and 16.3% against Phl p 1 (grass allergen group 1) [25]. Because of global warming, accelerated at least since 1980, and an increase in CO$_2$ in the air from about 300 to 400 ppm (parts per million) over the past century, an increased pollen load is expected by some scientists [4]. However, comparisons of pollen counts of allergenic plants between different pollen monitoring stations around Europe did not reveal an accordan increase [5]. Diverging pollen trends between allergenic early flowering trees/shrubs and herbal summer plants contributed to a heterogenic pattern of the impact of climate change [6]. The warm and dry “model year 2018” was compared to the regional weather conditions over the past 25 years. Studying their meteorological impact on pollen counts of alder, hazel, birch and grasses should have enabled us to evaluate recent hypotheses on pollination.

According to the Zentralanstalt für Meteorologie und Geodynamik (ZAMG, Central Institute for Meteorology and Geodynamics) in Vienna, 2018 was the warmest among the past 251 years of meteorological recording (since 1768, 14 of the 20 warmest years have occurred during the 2000s). It is characterized by 12.2°C, the highest yearly mean of temperature, 2.3°C above 1980 and the driest year since 1852, reflected by a 42% drop of precipitation [7]. From 1993 to 2017, the yearly mean of the highest temperatures of a day (HTD$_{ym}$), of the lowest daily temperatures (LTD$_{ym}$) as well as of the mean temperatures (MTD$_{ym}$) have risen progressively. In 2018, all three values were above the expected trend. Precipitation has not dropped significantly over 25 years, but was extremely low in 2018 (Fig. 1a). With an increasing frequency of heat waves the danger of droughts has risen, too, especially in a region predisposed to low rainfall [8]. The climate change in Linz is reflected by increasing numbers of days >20°C (R$^2$ = 0.26; p = 0.009) and >25°C (R$^2$ = 0.18; p = 0.035) in the years 1993 to 2017. Simultaneously, frost decreased significantly until 2018 (R$^2$ = 0.16; p = 0.027). January 2018 was rather warm (4.5°C above the monthly average) and, at the same time, with a precipitation of 97 mm, the wettest within the past 26 years. After cold spells in February and March 2018, the air has become warmer, reaching temperatures in April counting to the warmest of the last quarter of the century. This period was accompanied by ongoing dryness (relative humidity RH in April: only 51.8%—see also Fig. 8). In 2018, over 10 months temperatures were above the average of 1993–2017. However in two months they had fallen significantly below the monthly mean (Fig. 1b), characterizing 2018 as a hybrid year.

The most obvious consequence of climate warming is an “early spring” [9, 10]. According to Keenan et al. [11], this forward shift results in an earlier termination of vegetation. In the Northern biosphere, the enhanced CO$_2$ emission could have increased the biomass of plants [12], but this effect might be outweighed by repeated phases of low or even lacking precipitation during summer and fall [13]. In clinico-palynological terms, onset, duration and intensity of pollination define the pollen season [14]. For the forecast of its beginning, the Austrian Pollenwarndienst (pollen information service) used the highest temperatures of a day (HTD) [15–17] and cumulated mean daily temperatures (MTD$_{cumul}$) [18] summed up from December 1, of the previous year, or January 1, of the present year. The reasoning was that (a) in Cen-

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**Table**

| Acronym | Definition | Details |
|---------|------------|---------|
| MDF    | Mean daily frost $=\int_{24}^{}$ hourly temperatures $<0 ^\circ C/24$ h | Frost is defined as temperature $<0 ^\circ C$, with the freezing temperature of water being considered the physiological threshold for plant vegetation. |
| MDF$_{cumul}$ | Mean daily frost cumulated starting from January 1 for each year | |
| MDW    | Mean daily warmth $=\int_{24}^{}$ hourly temperatures $>0 ^\circ C/24$ h | |
| MDW$_{cumul}$ | Mean daily warmth/temperatures $>0 ^\circ C$ cumulated starting from January 1 for each year | |
| MTD    | Mean temperature of a day $=\int_{24}^{}$ hourly temperatures/24 h | |
| PC     | Mean pollen concentration of a day noted as pollen/m$^3$ air | |
| PREC   | Daily precipitation in mm = L/m$^2$ | |
| PREC$_{cumul}$ | Daily precipitation cumulated starting from January 1 | |
| PS     | Pollen season—pollination | |
| PSB    | Begin of pollen season—onset of pollination/flowering: phenologically defined as the first day for hazel, alder and birch, reaching 10 pollen/m$^3$ (PC10) or 5 pollen/m$^3$ (PC5) with grass species | |
| PSE    | End of flowering/pollination—last day with pollen concentration identical to PSB | |
| RH     | Relative humidity in % = effective pressure of water vapour in air/maximal pressure at the saturation point, determined by temperature | |
| RH$_{cumul}$ | RH cumulated starting from January 1 | |
| SPI n | Seasonal Pollen Integral = sum of mean daily pollen counts (PC) of a season |
Fig. 1  

(a) Means of highest, mean and lowest temperatures of a year as well as daily means of precipitation in Linz—2018 vs. 1993 through 2017. While there was no significant reduction with precipitation, temperatures increased significantly between 1.53 and 1.81 °C. 

(b) Yearly and monthly mean temperatures in Linz—2018 vs 1993 through 2017. In 2018 MMTs were above average in 10 of 12 months (“warm year”). February and March were characterized by MMTs below average caused by frost. Accordingly, 2018 was a heat–frost year, being therefore a hybrid one. That had different impacts on early (hazel, alder, birch) and summer bloomers (grass species). 

Central Europe trees and shrubs need a cold stimulus for further temperature-dependent development of their catkins [19, 20] and (b) from the phenological point of view, cumulated temperature is the primary driving force for hazel, alder and birch [21]. With hazel budding and growth of leaves follow the bloom, whereas with birch both processes occur together. Allergenic summer plants (grass and herbs) differ in this regard. Growth and differentiation occur in the same year before flowering. For them favourable “start-up-con-
Main pollen catchment areas for alder (Alnus glutinosa) around the town for birch (Betula pendula) of the Danube and her tributaries, and the green belt (comprises 47.3% forest and grassland, 34.8% built-up areas, including industry, 6.4% waters, 11.6% traffic areas, and 4.2% waters, 11.6% traffic areas), is open towards the prealpine plain (S-SW). Its area comprises 34.8% built-up areas, including industry, 6.4% waters, 11.6% traffic areas, and 47.3% forest and grassland.

Main pollen catchment areas for alder (Alnus glutinosa and A. incana) are the riverside/riparian forests of the Danube and her tributaries, and the green belt around the town for birch (Betula pendula), hazel (Corylus avellana) and grass (Poaceae).

**Methods**

The pollen monitoring station in Linz (ATLINZ, N48.303179/E14.305636°, start 1985) of the Upper Austrian Pollenwarndienst [23] uses a Burkard pollen trap. It is installed 20 m above ground on the roof of the Kepler University Clinic, Medical Campus III (formerly AKh—General Hospital Linz). Pollen counts have been carried out by the same analyst since 1987 in a standardized manner [24], using a light microscope. The mean pollen concentrations per m³ air (PC = pollen/m³) are transferred to the EAN (European Aeroallergen Network) data bank, run in cooperation with the Austrian Pollenwarndienst in Vienna. Data for this study were retrieved from there. Seasonal sums of mean daily PCs are called seasonal pollen integral (SPIn) [25]. Data of serial pollen counts for alder, hazel, birch and grass, having been continuously recorded since 1993, were analyzed. Seasonal data sets with gaps >6 days were omitted.

Begin and end of pollen seasons—pollination (PSB—PSE)—were defined phenologically as first and last days of a year, reaching 10 pollen/m³ (PC10) by alder, hazel, birch and, and 5 pollen/m³ (PC5) by grass species, respectively. The time in-between was considered the pollen season or its duration. Because 6 leap years fall into the study period, running days were preferred over calendar days.

The Zentralanstalt für Meteorologie und Geodynamik (ZAMG Vienna-Salzburg) provided meteorological data from 1993–2018 in form of hourly and daily temperatures (°C), precipitation (PREC in mm = L/m²) and relative humidity (RH in %). They were collected at the monitoring station in the city of Linz (M1), which is situated at 1 km from the pollen monitoring station. From hourly values, the highest temperature (HTD), the mean temperature (MTD) and the lowest temperature (LTD) of a day were derived. The mean daily warmth (MDW) was defined as integral of 24 hourly temperatures >0°C/24 h and the cumulated one as daily MDW summed up from January 1 (MDWcumul). In contrast, the mean daily frost (MDF) was regarded the integral of 24 hourly temperatures <0°C/24 h. Thus frost and cumulated frost (MDFcumul—summed up beginning at January 1) reflect temperatures <0°C. Thereby, the freezing point of water was considered the physiological threshold for plant life.

For the meteorologically driven start of the pollen season, especially for early flowering plants, both, the cumulated mean daily warmth (MDWcumul = MDW summed up from January 1) and a distinct threshold of HTD were considered necessary. The influence of frost was studied by using the MDFcumul. Between 1993 and 1999 MDWcumul and MDFcumul were derived from semi-hourly temperatures of the meteorological station M2, about 2.2 km away from the pollen monitoring station. These data originate from the Upper Austrian Air Quality Monitoring Station, Ö LUftmessnetz. From 2000 onward, only hourly temperature data of the ZAMG (M1) were used.

For figures, tables and regression analyses Microsoft Excel (Microsoft Excel 2003 and 2010, Microsoft Corporation, Redmont, WA, USA) and SigmaPlot, Systat Software (SigmaPlot 11, Systat Software, Incorporation, CA, USA) were used with their implemented analytical functions.

**Fig. 2** Beginning of bloom of alder vs. frost [MDFcumul]. The linear regression (R² = 0.5280; p = 0.002) shows that frost (MDFcumul) delayed the start of flowering from 1993 to 2018 (19 seasons). Compared to 2018 the longest delays were found in the years 2005 and 2006. In 2006, a maximum of frost was observed. The 95% limits are depicted. MDFcumul mean daily frost cumulated from day January 1 for each year, PSB beginning of pollination/pollen season.
Table 1  Begin of pollen seasons/pollination (PSB) of hazel, alder, birch and grass according to their PC thresholds (PC10 and PC5) between 1993 and 2018

| Begin of pollination (PSB) | Hazel PC10 day | Alder PC10 day | Birch PC10 day | Grass PC5 day |
|---------------------------|----------------|---------------|---------------|--------------|
| Shift forward             | None           | None          | None          | Tendency     |
| Significance              | p = 0.34       | p = 0.88      | p = 0.59      | p = 0.062    |
| Mean                      | 55.4           | 51.7          | 93.0          | 118.6        |
| Standard error            | 3.43           | 2.90          | 1.79          | 2.40         |
| Median                    | 58.5           | 50.0          | 91.5          | 117.0        |
| Standard deviation        | 15.35          | 12.64         | 7.16          | 8.98         |
| Minimum                   | 31             | 31            | 81            | 107          |
| Maximum                   | 86             | 74            | 109           | 136          |
| Seasons                   | 20             | 19            | 16            | 14           |
| SD%Mean (coefficient of variation) | 27.7          | 24.4          | 7.7           | 7.6          |

Begin of pollination/pollen season (PSB) and its statistical spread (= corridor of PSB)

1. Pollen concentration 5 pollen/m³, PC10 pollen concentration 10 pollen/m³

Results

Alder (Alnus) and hazel (Corylus)

Pollen season (PS)—start, course and duration of pollination

Frost significantly delayed PSB (the begin of the pollen season) of alder. The greatest delays were observed 2006 (maximal frost at day 86), 2005 and 2003 (Fig. 2). The high variance of PSB (Table 1) is explained by varying phases and intensities of frost.

Fig. 3 revealed that frost has postponed flowering and pollination, respectively, of hazel if the necessary levels of MDWcumul and HTD threshold were (are) not reached in time. Due to the warm January 2018, being almost free of frost, the pollen seasons of hazel and alder started as early as January 31. On this day, MDWcumul was found to be 126.4°C and the maximal HTD 1–5 days before PSB 11.2°C (Table 2). On average, MDWcumul, reflecting the preseasonal thermal energy, must have reached a relatively constant 103.8°C (median 99.9°C) and HTDcumul mean 175.1°C, before the bloom could start.

Years with an early PSB were associated with prolonged PS. As PS duration of hazel correlated significantly with raised daily temperatures (R²=0.72; p<0.001), pollination was prolonged in warm years, but not combined with higher SPIn.
Table 2  Relationship between highest temperature of a day and beginning of the pollen seasons (PSB) of hazel (Corylus), alder (Alnus), birch (Betula) and grass (Poaceae)

| Highest temperature of a day at the beginning of pollen season (PSB) | HTD°C @ PSB |
|---------------------------------------------------------------|-------------|
|                                                               | Median      | Mean ± 1 SD | Range     |
| **HAZEL (Corylus) PC5**                                       |             |             |           |
| Day 0                                                         | 11.10       | 9.95 ± 5.02 | 1.5–18.1  |
| Day –1 to –5                                                  | 11.05       | 10.79 ± 3.22| 4.4–16.9  |
| **HAZEL (Corylus) PC10**                                      |             |             |           |
| Day 0                                                         | 11.65       | 11.30 ± 4.16| 2.7–18.1  |
| Day –1 to –5                                                  | 11.70       | 11.55 ± 2.88| 5.1–16.9  |
| **ALDER (Alnus) PC5**                                         |             |             |           |
| Day 0                                                         | 9.50        | 9.64 ± 4.44 | 1.5–16.2  |
| Day –1 to –5                                                  | 10.90       | 10.57 ± 3.47| 4.1–16.9  |
| **ALDER (Alnus) PC10**                                        |             |             |           |
| Day 0                                                         | 10.30       | 10.17 ± 4.15| 1.5–16.6  |
| Day –1 to –5                                                  | 10.30       | 10.63 ± 3.51| 4.5–16.9  |
| **BIRCH (Betula) PC10**                                       |             |             |           |
| Day 0                                                         | 16.65       | 16.91 ± 3.87| 10.5–23.9 |
| Day –1 to –5                                                  | 16.45       | 17.51 ± 3.72| 9.7–23.1  |
| **BIRCH (Betula) PC100**                                      |             |             |           |
| Day 0                                                         | 20.05       | 20.00 ± 4.06| 13.2–29.7 |
| Day –1 to –5                                                  | 21.35       | 21.10 ± 3.16| 15.2–26.0 |
| **GRASS (Poaceae) PC5**                                       |             |             |           |
| Day 0                                                         | 19.95       | 19.76 ± 6.66| 8.7–30.2  |
| Day –1 to –5                                                  | 22.95       | 23.14 ± 3.50| 14.9–29.4 |

Influence of frost on flowering and pollen production of alder and hazel

Weak episodes of frost with MDF cumul just below 0 °C preceded the PSB of hazel and alder in 2018 (Fig. 4). In 2018 from February 24 to March 4, a cold spell interrupted the pollination of hazel. The bloom of alder started together with hazel, but showed a low PC at the beginning. The maximum expansion was delayed. It revealed two major peaks, which were abruptly stopped by a second cold spell between March 18 and March 22. With alder, neither frost before nor after PSB has caused damages. In 2018, the lowest LTDs of –4.6 down to –9.1 °C were observed between day 56 and 61, occurring 5 to 8 days before the first main pollen peak. Looking only at the pollination in 2018, it could be concluded that chills lead to pulsed PCs in a time- and dose-dependent manner. However, taking all years from 1993 to 2018 into account, it can be shown that the SPIn were correlated linearly positive with cumulated frost up to the end of pollination (MDW cumul $R^2 = 0.196$; $p = 0.0575$), and negative with warmth (MDW cumul $R^2 = 0.276$, $p = 0.021$). This revealed that temperatures below and slightly above zero degree positively affected SPIn. No close relationship, regarding the timing, was found. In contrast to alder, SPIn of hazel was not influenced by frost ($R^2 < 0.1$). On the contrary, warm temperatures increased the SPIn of hazel up to MDW cumul of about 500 °C, levelling off there.

Birch (Betula)

PS—start and duration

Between 1993 and 2018, PSB has not varied much around day 91.5 (median) and days 93.0 ± 7.2 (arithmetic mean ± 1 SD; Table 1). At PSB on April 2 in 2018, the cumulated temperature for the final development of catkins (MDW cumul) reached 314.2 °C and HTD 13.7 to 14.5 °C, respectively. Fig. 5 shows for birch how the time-corridor of PSB is determined by three interacting variables: (1) the species specific PSB, (2) the cumulated warmth (MDW cumul) as driving force, and (3) the HTD threshold as the final trigger for the opening of the male catkins. Over all seasons, frost delayed the PSB only marginally ($R^2 = 0.22$; $p = 0.066$). The thermal energy demanded for PSB (bloom) remained relatively constant at MDW cumul 336.1 ± 55.8 (mean ± 1 SD; median 335.4 °C). In 16 seasons, the threshold of HTD 1 to 5 days prior to PSB amounted to 17.5 ± 3.7 °C (Table 2). Similar corridors for the PSB of alder and hazel can be constructed.

The length of PS of birch increased significantly with intraseasonal temperatures >0 °C (MDW cumul $R^2 = 0.7953$; $p < 0.001$), but the influence of precipitation was negligible (DP cumul $R^2 = 0.014$; $p = 0.15$). A unique situation occurred in 2018, when heat waves caused drought, which together shortened PS duration (Fig. 6a).

Impact of low preseasonal temperatures on pollen productivity of birch

In 2003, birch showed the highest SPIn. The years 2004, 2005 and 2006 ranged similar to 2018 above the
Influence of warm temperatures and frost on the pollen concentrations of alder (*Alnus*) and hazel (*Corylus*) in 2018. Minimal frost (*MDF* cumul −0.9°C) in January before bloom started on day 31 where *MDW* cumul of 126.4°C (dashed line) coincided with the HTD threshold of 11.2°C. Hazel revealed the same PSB criteria. Frost in February and March interrupted the bloom of hazel and delayed the main phase of alder. Even the lowest temperatures did not harm the flowering of alder. On the contrary, they stimulated the production of pollen. *PC* pollen count/concentration (per cubic meter), *MDF* cumul mean daily frost, *MDW* cumul mean daily warmth/temperature >0°C, HTD highest temperature of a day. Pollen counts of alder from January 31 to April 30

Grasses (*Poaceae*)

PS—start and duration

Over the years, a tendency towards an earlier start of PS was observed. In 2018, the earliest occurred on day 107. The PS duration has remained rather constant over the years (R² < 0.1). The pollen seasons with PCs lasted 106.1 ± 17.2 days (mean ± 1 SD), and 108 days in 2018.

In 2018, the pollen season began earlier than in the years from 1994 to 2017; correspondingly the main pollen peak was shifted forward (Fig. 7a). As the number of pollen peaks was similar in 2018 [26] to the years 1994–2017 [30], it is assumed that they were caused by pulsed or successive flowering of different grass species. The higher amplitude of pollen peaks in the first half of PS might be caused by species with a higher pollen production [27]. Haying may lower PCs in the second half of the PS.

Influence of changing wet and dry conditions on the pollen production of grass

There was a close correlation between cumulated preseasonal relative humidity (*RH* cumul) and PSB (R² = 0.8826; p < 0.001; Fig. 8a). It exceeded that of temperature (*MDW* cumul R² = 0.3173; p = 0.005) and precipitation (*PREC* cumul R² = 0.3377; p = 0.004), which are both needed for growth of plants and development of their blossoms. RH represents precipitation, soil moisture and evaporation in relation to temperature. RH decreases substantially during hot days. Low RH indicates dryness (=deficit in water supply, diminished evaporation). Dryness, respectively drought,
leads to an earlier onset of PS, whilst wet and warm weather conditions delay the bloom of grass. Because of the highly significant correlation between RH, and PSB, RH offers a powerful tool in forecasting the PSB of grass. The highest SPI were recorded in the years 1994, 2001, 2002 and 2004. Over 25 years, the yearly means of RH have decreased continuously from 79 to 71% (R² = 0.699; p < 0.001). Finally in 2018, RH reached a minimum of about 67%, indicating a continuous development towards drier and warmer semi-arid conditions. SPI (R² = 0.36; p = 0.024) and the PCs of the main pollen peaks (R² = 0.32; p = 0.035) decreased synchronously from 1994 to 2018. Because of data gaps (11 out of 25 years were missing), some uncertainty remained regarding the interpretation of the linear decline over 25 years. The polynomial regression of SPI revealed a biphasic curve with an R² = 0.39. SPI could have stabilized at a lower level between 2005 and 2018 (Fig. 7b).

Discussion

In Linz, temperatures have risen during the summer more than during the winter half-year over a period of 26 years. While temperatures below zero have hardly decreased over the years, MDW has increased by 0.056°C a year (R² = 0.4151; p < 0.001). The correlation between warming and decline of frost was highly significant (R² = 0.519; p = 0.00002), indicating both a reduction in intensity as well shortening of the frost periods in winter [28]. In contrast to temperature, precipitation has shown only a minor decrease. Overall, the climate became warmer and drier, which is reflected in a significant and progressive decline of relative humidity (RH). Because Linz is located in a region with low precipitation, borderline situations such as drought and urban overheating might occur earlier. When the observed weather trends continue, the exceptional year 2018 might anticipate what in about 20 years will be considered “normal”.

The year 2018 was an exceptionally warm and dry year in Linz, with temperatures significantly above and precipitation below average in 10 of 12 months. Cold spells during February and March characterised the year as a hybrid one. Cool weather conditions during this time stimulated the production of pollen of alder and birch.

Climate warming over the past 26 years did not show a statistically significant increase in seasonal pollen production (SPI). Instead, fluctuations in pre-
seasonal weather conditions were identified as primary drivers of the annual variance of PF of hazel, alder, birch and grass. Over the past 26 years, temperatures >0°C cumulated over the first 90 days of the year (MDW_{cumul}) did not reveal a significant change (R² = 0.023; n.s.), which was quite in contrast to the rise of temperature over the whole year (R² = 0.339; p = 0.0018). The phenological reasons and biological laws underlying the observed high variance are discussed. In the future, a forward shift of the pollen seasons of birch and grass is expected first. It appears that this has already begun with grass.

The vegetative and generative development of catkins of the early flowering trees and shrubs already starts in the previous summer. During the following spring the species-specific coincidence of cumulated forcing temperatures (MDW_{cumul}) and a distinct minimal temperature threshold (HTD) as the final signal for catkin opening is necessary for the start of bloom. These interrelationships are illustrated in the “pollination-onset-corridor model” exemplified for birch—analogously, corridor-models can be constructed for hazel and alder. They provide the base for the annual forecast of the PSB. Frost was the third meteorological parameter determining PSB. Frost delayed the start of PS of hazel and alder and explained its high variance. Frost was maximal in 2006. There the pollen season started 55 days later than in 2018. Warm winters with little frost shifted forward the PSB of hazel and alder. Despite the variability over the past 26 years, the preseasonal MDW_{cumul} as well as the HTD threshold have remained relatively constant.
indicating that they are the main drivers for the start of PS.

It is important to outline that different mechanisms drive PSB and pollen production (SPIn) of hazel, alder and birch. In 2018, frost interrupted the flowering of hazel and alder. On the other hand, preseasonal frost and cool temperatures stimulated SPIn of alder, while hazel required warmer conditions. The birch showed the paradox that it needed higher temperatures for flowering compared to hazel and alder, but cooler temperatures to stimulate SPIn [18]. The underlying mechanisms are unknown. With respect to the nordic/alpine and mountainous distribution of Silver birch (Betula pendula) and Gray alder (Alnus incana), this appears to be a reasonable strategy, since spring frost mainly determines the borders of vegetation in these areas [29]. The stimulation of hazel by warmer temperatures could be related to its origin from Southeastern Europe and Asia Minor. The warmth–frost hypothesis could explain variations in SPIn of hazel, alder and birch with stimulation of flowering in colder years and an earlier PSB in warmer years lacking frost. The year 2003 revealed the highest SPIn of alder and birch. Such years rich in pollen (“mast years”) could be explained by the synergy of preseasonal stimulation of pollen production by cold/frost together with enhanced budding during the previous year [30]. Higher temperatures during the pollen season prolonged the PS of birch, hazel and alder. However, heat waves combined with drought, like in 2018, shortened the pollen season of birch. This circumstance is pertinent for the intensity of the birch pollen load in overheated urban areas. In contrast to the impact of preseasonal temperatures on SPIn of early bloomers, warm temperatures during the pollen seasons only played a minor, modifying role.

With grass, the earliest start of PF was seen in 2018. It was caused by dryness and rather warm tempera-
Fig. 8 a Grass species (Poaceae)—relative humidity and onset of pollination. Applying multivariate analysis, RH\text{cumul} dominates the forecast of PSB ($R^2 = 0.8787; \ p = 4.37 \times 10^{-11}$) so much that both underlying factors MDW\text{cumul} ($R^2 = 0.317; \ p = 0.0051$) and PREC\text{cumul} ($R^2 = 0.338; \ p = 0.0036$) become unimportant. Because of the significant relation between RH and PSB, RH\text{cumul} could be preferentially used predicting the PSB of grass. b Yearly means of relative humidity from 1993 to 2018. There is a continuous drop of relative humidity over 26 years, which points to the development towards a semi-arid climate. RH relative humidity, PSB beginning of pollination/pollen season, MDW\text{cumul} cumulated mean warmth/temperatures $>0^\circ \text{C}$, PREC\text{cumul} daily precipitation cumulated from January 1 on dryness (RH-deficit) shifts PSB of grass forward.

The lowest relative humidity (RH) ever found reflected the ratio of dryness to temperature. Over 26 years not only the cumulated RH has fallen progressively (Fig. 8a), but by itself RH\text{cumul} has turned out to be the best predictor for PSB of grass (Fig. 8b). Applying multivariate analysis, RH\text{cumul} dominated the prediction of PSB so much that MDW and DP\text{cumul} became minuscule/unimportant. Wet weather combined with warm temperatures shifted the PSB backwards in contrast to a forward shift by dry and warm conditions. From 1994 to 2018 the SPIn of grass has dropped in a similar linear manner as the main peaks have.

Using a polynomial regression, a biphasic course was found, with SPIn stabilizing at a lower level from 2006 to 2018. In general, longer rainy periods lower PC. In 2018 they were replaced by episodic spells of rain. The latter pattern is predicted to occur more frequently with climate warming [31]. Rainy episodes could stimulate growth and pollen production over the following days [32, 33] and compensate at least in part for the reduced pollen release caused by dryness or even drought. Such compensating mechanisms could explain the mentioned stabilized SPIn of grass in recent years of climate warming. Over time the duration of PS of grass has remained relatively constant. Accordingly, the early start of grass bloom in 2018 was associated with an earlier end of the flowering season. This supports the hypothesis that an early spring might lead to an earlier end of vegetation in autumn [11].

Despite progressive climate warming over the last quarter of the century and elevated CO$_2$ concentrations, the pollen concentrations of hazel, alder, birch and grass by trend analysis have not risen, on the contrary they have declined over time. The increase of pollen allergy and of the prevalence of sensitization especially in young people [34] cannot be explained directly by climate warming, but must have other reasons. Among them several other causative factors or complex interactions might be responsible: aerogenic ones like air pollution, alteration of allergens, toxic
or combined toxic–allergic effects on humans as well as on plants; NOx, O3, VOC (nitrogen oxides, ozone, volatile organic compounds, respectively) which by themselves can be related to climate change [35–37], or in general an urban environment. Apart from the mentioned factors there is a number of other non-aerogenic enhancers of sensitization and allergic reactions likely.

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Conflict of Interest B. Schmidt has been working as a pollen analyst for the Austrian Pollenwarndienst over the past 32 years, but there is no conflict of interests with the present publication. H.A.E. Schinko and B. Lamprecht have no conflict of interests.

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