



## Oak pollen seasonality and severity across Europe and modelling the season start using a generalized phenological model

Maria Grundström<sup>a,\*</sup>, Beverley Adams-Groom<sup>a</sup>, Catherine H. Pashley<sup>b</sup>, Åslög Dahl<sup>c</sup>, Karen Rasmussen<sup>d</sup>, Letty A. de Weger<sup>e</sup>, Michel Thibaudon<sup>f</sup>, Santiago Fernández-Rodríguez<sup>g</sup>, Inmaculada Silva-Palacios<sup>g</sup>, Carsten A. Skjøth<sup>a</sup>

<sup>a</sup> National Pollen and Aerobiological Research Unit, School of Science and the Environment, University of Worcester, Henwick Grove, Worcester WR2 6AJ, United Kingdom

<sup>b</sup> Institute for Lung Health, Department of Infection, Immunity & Inflammation, University of Leicester, Leicester, United Kingdom

<sup>c</sup> University of Gothenburg, Department of Biological and Environmental Sciences, P.O. Box 461, 405 30 Gothenburg, Sweden

<sup>d</sup> Astma-Allergi Danmark, Universitetsparken 4, 4000 Roskilde, Denmark

<sup>e</sup> Department of Pulmonology, Leiden University Medical Center, P.O. Box 9600, 2300RC Leiden, the Netherlands

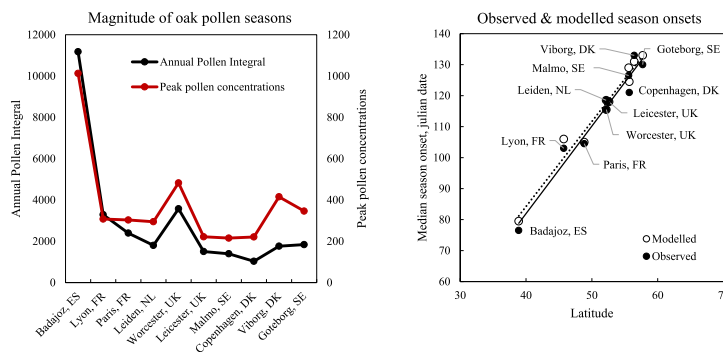
<sup>f</sup> Réseau National de Surveillance Aerobiologique (R.N.S.A.), 11 chemin de la creuzille, Le Plat du Pin – 69690 Brussieu, France

<sup>g</sup> Department of Construction, School of Technology, University of Extremadura, Avda. de la Universidad s/n, Cáceres, Spain

### HIGHLIGHTS

- Atmosphere significantly polluted by oak pollen at several sites across Europe
- Seasons can last up to 2 months due to several oak species dominating the landscape.
- Evaluating several definition methods was important to capture local pollen start.
- 76% of the modelled pollen starts occurred within 4 days or less of observed starts.
- A general model can estimate pollen season onset in areas lacking monitoring.

### GRAPHICAL ABSTRACT



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### ABSTRACT

Oak pollen seasons are relatively unexplored in large parts of Europe despite producing allergens and being a common tree in both continental and northern parts. Many studies are concentrated only on the Iberian Peninsula. In this study, the seasonal pattern of oak pollen in Europe was analysed using 10 observation sites, ranging from Spain to Sweden. The magnitude of peaks and annual pollen integral together with season-length were studied and substantially higher pollen levels and longer seasons were found in Spain. Two northern sites in Denmark and Sweden showed high oak pollen peaks together with two sites in Spain and United Kingdom. The study also tested four common definitions of season start and applied a generalized phenological model for computing the start of the pollen season. The most accurate definition for a European-wide description of the observed oak pollen start was when the cumulative daily average pollen count reached 50 grains per cubic meter. For the modelling of the start a thermal time method based on Growing Degree Day (GDD) was implemented, utilizing daily temperatures and a generalized approach to identify model parameters applicable to all included sites. GDD values varied between sites and generally followed a decreasing gradient from south to north, with some exceptions. Modelled onsets with base temperatures below 7 °C matched well with observed onsets and 76% of the predictions differed  $\leq 4$  days compared to observed onsets when using a base temperature

\* Corresponding author.

E-mail address: [m.grundstrom@worc.ac.uk](mailto:m.grundstrom@worc.ac.uk) (M. Grundström).

of 2 °C. Base temperatures above 7 °C frequently predicted onsets differing >1 week from the observed. This general approach can be extended to a larger area where pollen observations are non-existent. The presented work will increase the understanding of oak pollen variation in Europe and provide knowledge of its phenology, which is a critical aspect both for modelling purposes on large-scale and assessing the human exposure to oak allergens. © 2019 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

## 1. Introduction

Pollen allergy affects up to 40% of the population in Northern Europe (D'Amato et al., 2007). Oak pollen has been highlighted by the European Academy of Allergy and Clinical Immunology as one of eight major tree allergens with Bet v1 related proteins (Ferreira et al., 2014). Oak pollen is considered a moderate cause of pollinosis (e.g. Egger et al., 2008) and the cross reactivity with birch is well established (Hauser et al., 2011), thus also important in relation to diagnostics and treatment of hay fever. Positive skin prick test results from oak pollen have been reported in 29% of tested clients (Farnham, 1990). In the United Kingdom (UK) oak pollen has been reported as one of the main causes for observed increases of cases in hay fever (Ross et al., 1996). Oak trees are found abundantly in Europe contributing to high pollen concentration (Skjøth et al., 2013). In the UK it has also been shown that oak pollen is just as abundant as birch pollen (Skjøth et al., 2015), which is associated with the highest number of sensitized patients to pollen from the Betulaceae family (Heinzerling et al., 2009). Nevertheless, oak is not included in the standard skin prick test panel in Europe (e.g. Heinzerling et al., 2009).

There are a number of common oak species in Europe. In the south, forests are dominated by one group of oaks such as *Q. ilex* and *Q. suber*, while northern European forests are dominated by another group consisting of *Q. petraea* and *Q. robur* (Skjøth et al., 2008). In addition, urban areas have a generally large diversity of oak species, where types such as *Q. ilex* and *Q. palustris* have been imported for ornamental purposes to countries such as the UK, and therefore outside their Southern European native domain. According to Mitchell (1974), the species *Q. ilex* and *Q. rubra* are common ornamentals across the UK. The phenology of species such as *Q. ilex* and *Q. robur* are known to vary substantially (Morin et al., 2010) and thus describing the local oak pollen season in parts of Europe can be complicated. Different areas might be dominated by a variety of species where the overall pollen load is likely to be augmented by a complex mixture of urban trees with a different phenology compared to the native species.

Starting dates for growth and development of reproductive organs vary within and between both genus and species due to different growth requirements (Dahl et al., 2013; García-Mozo et al., 2002). Thus, different tree types will mature and flower at different times throughout the spring period. Temperature is considered one of the most important factors for growth, while threshold temperatures are influenced by both biological and environmental factors (Chuine et al., 1999; García-Mozo et al., 2002; Wielgolaski, 1999). The advancement of phenological phases, such as the flowering and onset of pollen release, can be predicted through the accumulation of temperature during spring and is often utilized in thermal time models such as Growing Degree Day (GDD) (Linkosalo et al., 2008; Rasmussen, 2002). Warming, or more generally, the accumulation of heat, is required to initiate flowering and begins in many tree species after a prolonged period of exposure to cool temperatures (e.g. Newnham et al., 2013). Chilling requirements have been found to vary from 0 to 7.2° for oak (García-Mozo et al., 2002). In an experimental study, Fu et al. (2012) found that the chilling phase did not play a decisive role in the budburst process, budburst dates of a number of genera (beech, birch, oak) were more sensitive to spring warming than winter warming. Model evaluation showed that models either including or excluding chilling were both able to accurately predict budburst. This suggests that chilling

requirements can be discarded from models, with the reservation that climate change and recent observed warmings can make chilling important at some point in the future (Newnham et al., 2013).

Oak is a common tree in woodlands and forested areas in many parts of continental Europe, UK and southern Scandinavia (Skjøth et al., 2008). Despite this, a majority of oak pollen studies are from Spain and the US (Fernández-Rodríguez et al., 2016; García-Mozo et al., 2008, 2006, 2002; Zhang et al., 2015). Few studies cover areas such as northern and western parts of Europe and are often limited to single sites, especially in UK (Corden and Millington, 1999; Norris-Hill, 1998; Skjøth et al., 2015). Additionally, existing studies often present site-specific approaches to modelling oak pollen seasons (e.g. García-Mozo et al., 2002), where base temperatures are distinctive and differ between each site. Thus, site-specific models cannot be extended to other regions or in larger scale modelling where a more general approach is necessary in order to apply the same model parameters. Furthermore, differences between studies in methodology for defining onset (Emberlin et al., 1997; Jäger et al., 1996; Rasmussen, 2002; Spiessma et al., 1995) and calculating the temperature requirement, adds uncertainty when comparing results between sites. Therefore, further studies including sites from large regions adopting a general modelling approach are highly relevant and also important for establishing the characteristics and phenology of oak pollen seasons in other oak abundant regions.

This study aims to describe the oak pollen seasonal variations in a generally unexplored part of western and northern Europe and as part of this establish the most accurate definition of the onset of oak pollen seasons. Additionally, a general approach for predicting the onset of oak pollen seasons over large areas using a thermal-time approach (GDD) has been tested.

## 2. Materials and methods

### 2.1. Data and measurement sites

#### 2.1.1. Pollen and meteorological data

Daily concentrations of oak pollen data were used for the years 2006–2015. The data were obtained by using a seven day volumetric sampler of the Hirst design (Hirst, 1952). Daily slides with collected pollen were analysed under an optical microscope by trained staff using recommended standards in aerobiology (Galán et al., 2014) and pollen from oak trees were identified at the genus level. The pollen data were obtained from 10 sites throughout Europe (Table 1). The coordinates, references to full site descriptions and number of years are given in the table along with the counting method, which is either transverse traverses (Käpyla and Penttinen, 1981) or longitudinal transects (Sikoparija et al., 2011). All counts from the microscope have been converted into daily mean pollen concentrations (grains m<sup>-3</sup>, 24 h) according to international adapted standards (Galán et al., 2017). Furthermore, Table 1 presents common oak species at each respective site, together with the first flowering species and typical pollen season start.

Meteorological data were obtained from nearby climate stations by using the on-line GIS server with data from the Global Summary of the Day (GSOD) meteorological data set. This service is provided by the National Oceanic and Atmospheric Administration (NOAA). Each pollen site was matched with a nearby meteorological station which had acceptable hourly data coverage with respect to daily averaged

**Table 1**

Information of pollen monitoring sites, data cover, location of pollen traps, nearby locations of meteorological stations (global summary of the day), biogeographical classifications of the site regions and common oak species together with first flowering species (where known) and average season start. Where no reference is cited for common oak species, the information is based on phenological observations from local experts.

Site	Pollen data cover	Pollen site location Lat., lon	Counting method	Meteorological site	Biogeographical region	Common oak species	First flowering oak near the site	Oak season start
Badajoz, ES	2008–2015	N38.895972°, W–6.968778°	2 × longitudinal	Telavera La Real	Mediterranean	<i>Q. ilex</i> , <i>Q. suber</i> , <i>Q. canariensis</i> , <i>Q. robur</i> , <i>Q. pyrenaica</i> , <i>Q. fagiens</i> , <i>Q. humilis</i> <sup>b</sup>	<i>Q. ilex</i>	Mid March
Lyon, FR	2006–2014 <sup>a</sup>	N45.727800°, E4.824900°	2 × longitudinal	Saint Exupery airport	Continental	<i>Q. robur</i> , <i>Q. cerris</i> , <i>Q. phellos</i> , <i>Q. rubra</i> , <i>Q. ilex</i> , <i>Q. acutissima</i> , <i>Q. castaneifolia</i>	<i>Q. robur</i> , <i>Q. rubra</i>	Mid April
Paris, FR	2006–2014 <sup>a</sup>	N48.840300°, E2.311100°	2 × longitudinal	Le Bourget airport	Atlantic	<i>Q. pubescens</i> , <i>Q. cerris</i> , <i>Q. rubra</i> , <i>Q. robur</i> , <i>Q. ilex</i> , <i>Q. frainetto</i> <sup>c</sup>	<i>Q. robur</i> , <i>Q. rubra</i>	Mid April
Leiden, NL	2006–2015	N52.165591°, E4.477139°	3 × longitudinal	Schipol airport	Atlantic	<i>Q. robur</i> , <i>Q. petraea</i> , <i>Q. rubra</i> , <i>Q. palustris</i> <sup>d</sup>	<i>Q. robur</i> , <i>Q. rubra</i>	Late April
Worcester, UK	2006–2015	N52.197003°, W–2.242162°	1 × longitudinal	Pershore	Atlantic	<i>Q. robur</i> , <i>Q. petraea</i> , <i>Q. palustris</i> , <i>Q. ilex</i>	<i>Q. palustris</i>	Late April
Leicester, UK	2007–2015	N52.623159°, W–1.122711°	1 × longitudinal	Nottingham East Midland	Atlantic	<i>Q. robur</i> , <i>Q. petraea</i> , <i>Q. rubra</i> , <i>Q. cerris</i> , <i>Q. ilex</i>	<i>Q. rubra</i> , <i>Q. robur</i> , <i>Q. petraea</i>	Late April
Malmö, SE	2006–2015	N55.589798°, E13.002180°	12 × vertical	Malmö Jägersro	Atlantic	<i>Q. robur</i> , <i>Q. petraea</i> <sup>e</sup>	<i>Q. robur</i> , <i>Q. petraea</i>	2nd week in May
Copenhagen, DK	2006–2013	N55.690909°, E12.562000°	12 × vertical	Copenhagen Jaegersborg	Atlantic	<i>Q. robur</i> , <i>Q. petraea</i> <sup>f</sup>	<i>Q. robur</i> , <i>Q. petraea</i>	April–May
Viborg, DK	2006–2013	N56.445257°, E9.405257°	12 × vertical	Karup	Atlantic	<i>Q. robur</i> , <i>Q. petraea</i> <sup>f</sup>	<i>Q. robur</i> , <i>Q. petraea</i>	Mid May
Goteborg, SE	2006–2015	N57.721282°, E12.051044°	12 × vertical	Save	Atlantic/Boreal	<i>Q. robur</i> , <i>Q. petraea</i> <sup>e</sup>	<i>Q. robur</i> , <i>Q. petraea</i>	Mid May

<sup>a</sup> Missing year 2013.

<sup>b</sup> García-Mozo et al. (2002).

<sup>c</sup> Mairie de Paris (2018).

<sup>d</sup> Gemeente Leiden (2018).

<sup>e</sup> Drößler et al. (2012).

<sup>f</sup> Siegmund and Jensen (2001).

temperatures. Station IDs of these sites are given in Table 1. Daily data coverage of 16 h or more were accepted. This level was used for the inclusion of the Spanish meteorological site, as several nearby sites were exhibiting large data gaps. All other sites had very few data gaps and a daily data cover of 21 h was used as a threshold. The number of hourly missing data points varied between 0 and 20 h per year depending on site and was more often below 10, thus presenting sufficient data cover. Data gaps of single days in the time series and up to 7 days long were filled according to Skjøth et al. (2016) by interpolation or by using data from a nearby site requiring both a very high correlation and no significant bias between sites.

## 2.2. Calculations

### 2.2.1. Definitions of season onset

For an accurate estimate of the local pollen seasonality it is important to eliminate the tails found in the beginning and end of the seasonal pollen curve related to low pollen concentrations (Emberlin et al., 1994). Determination of the onset can be particularly challenging for tree pollen, which has been observed systematically to appear earlier in the atmosphere compared to the local flowering (Estrella et al., 2006). Two aspects need to be considered when determining the onset of the local season. Firstly, pollen transported long range from other regions, which is typically observed prior to the local season (Hjelmroos, 1991; Skjøth et al., 2007) and secondly, the first local peak in pollen concentrations. The onset definition of the local season based on pollen count data needs to be formulated so that it does not start too early, ensuring that non-local pollen is widely excluded, or too late, ensuring that the first local pollen peak is not cut off or missed. Several methods have been used in literature to estimate the pollen season start, such as the cumulative sum technique (Adams-Groom et al., 2002; Driessen et al., 1990), or the fraction of the total annual catch, which was recently defined as the annual pollen integral (API) (Galán et al., 2017). These different methodologies generally provide similar results, potentially with a small systematic bias (Emberlin et al., 1994) but can in some years provide substantial differences (Khwarahm et al.,

2014). Four techniques were therefore tested (Table 2) to define the start of the season in a similar way as previous studies did (Emberlin et al., 1994; Khwarahm et al., 2014) in order to evaluate which definition most accurately represented the start of the local season.

Overall differences were numerically evaluated and the years were investigated individually with respect to the shape of the pollen curve. Years were removed from the analysis if there were indications of substantial long distance transport (LDT) of pollen grains outside the main season. Only one year (2014) from Copenhagen was removed from the analysis due to such indications.

### 2.2.2. Modelling GDD and start of the pollen season

Modelling the onset of the pollen season can be done using both regression type modelling (Adams-Groom et al., 2002) or phenological models (García-Mozo et al., 2008). Phenological models are commonly used within aerobiology to capture phenological events such as bud development in trees and have been carried out with different degrees of complexity in several other studies (e.g. García-Mozo et al., 2008; Linkosalo et al., 2008; McMaster and Wilhelm, 1997). Here we use the phenological modelling approach where the daily GDD has been calculated by using daily average temperature ( $T_{\text{daily}}$ ) calculated from hourly temperatures provided in the GSOD dataset, publically available from

**Table 2**

Different methods to define the start (onset) of the oak pollen season.

Onset definition method	Description
2.5% API	Onset date was obtained when the accumulated daily pollen concentrations had reached 2.5% of the annual pollen integral (API).
3d-5pl	Onset date was obtained when three consecutive days of daily pollen concentrations were above 5.
cumulative $\sum 50$	Onset date was obtained when the cumulative sum of daily pollen concentrations reached 50.
cumulative $\sum 75$	Onset date was obtained when the cumulative sum of daily pollen concentrations reached 75.

**Table 3**  
(a) Median onset dates (Julian day) of different onset definition methods for each site and their respective studied periods. The standard deviation (sd) describes the variation between the onset definition methods for each site. (b) The largest deviations (number of days) for a specific onset definition method of a specific year. Other years showed small variations (7 days or less) between earliest and latest onset definition method.

Site	a) Median onsets for studied period				sd	b) Years with large differences between earliest and latest onset		
	2.5% API	3d-5pl	Cumulative $\sum$ 50	Cumulative $\sum$ 75		Deviating year	Onset definition method	n days
Badajoz, ES	88	83	77	81	4.0	<sup>a</sup>	All	+14–20
Lyon, FR	104	103	103	104	0.5	–	–	–
Paris, FR	101	106	105	107	2.3	2008	2.5% API	–17
Leiden, NL	116	118	119	120	1.5	–	–	–
Worcester, UK	117	115	116	117	0.8	2012	3d-5pl	+12
Leicester, UK	113	120	118	121	3.1	2012, 2014	<sup>b</sup>	$\pm$ 23, –14
Malmö, SE	125	125	127	127	1.0	–	–	–
Copenhagen, DK	119	119	121	124	2.0	2007, 2010, 2012	<sup>c</sup>	–10, –18, +8
Viborg, DK	130	133	133	134	1.5	2006	2.5% API	–12
Goteborg, SE	130	131	130	131	0.5	2015	2.5% API	–11

<sup>a</sup> All years except 2009, 2011 and 2014 differed considerably between onset definitions of the studied period.

<sup>b</sup> In 2012 2.5% API (early onset, –23) and 3d-5pl (late onset, +23). In 2014 2.5% API (early onset, –14).

<sup>c</sup> 2.5% API and Cumulative $\sum$ 75 (2012).

NOAA. The GDD calculation is given by the following equation.

$$GDD = T_{daily} - T_{base}$$

where  $T_{daily} < T_{base}$  then  $T_{daily} = 0$ , thus  $GDD = 0$ .

$T_{base}$  is a chosen cut off temperature, defined as a base temperature under which no growth is assumed to occur. The accumulated sum of daily GDDs was then calculated (cumulative  $\sum$  GDD) with a fixed initial date starting on 1st March for all sites except Badajoz, with initial date set to 1st February, and ending on the date of the observed onset. Every year a threshold GDD was calculated, i.e. the cumulative  $\sum$  GDD on the onset date. The overall GDD threshold for modelling onsets was defined as the median of all yearly cumulative  $\sum$  GDD within the studied period. This GDD is referred to as  $GDD_{s,period}$ . Modelled onsets every year were then defined as the date when the median GDD threshold had been reached.

A sensitivity analysis (re-analysis) was also carried out for individual years by calculating an explicit median GDD threshold representing each specific year being modelled. This GDD threshold was obtained by excluding the cumulative  $\sum$  GDD of that specific year, thus computing the GDD threshold as the median based on the rest of the years within the studied period. This procedure is called cross correlation (the 'leave one out' procedure), which is a common procedure in statistics and has recently been applied in aerobiological studies. This GDD threshold is from here on referred to as  $GDD_{crossval}$ .

### 2.2.3. Evaluation of methods for modelling onset dates

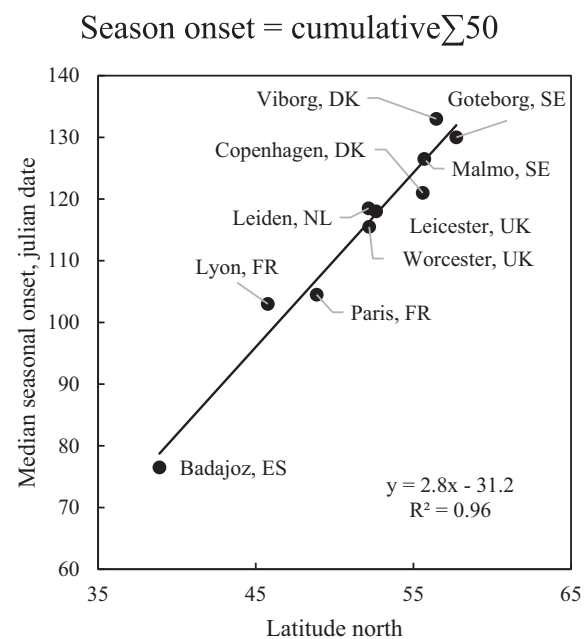
To evaluate the accuracy of the GDD modelled onsets, two methods were used which tested both GDD thresholds ( $GDD_{s,period}$  and  $GDD_{crossval}$ ) and eleven base temperatures ( $T_{base} = 0, 1, \dots$  and  $10$  °C). Thus the accuracy was evaluated both in terms of GDD threshold and  $T_{base}$ . The first evaluation method was based on scoring which was carried out by counting the number of occurrences where the model was able to predict onset dates falling within a 0–7 day difference of the observed onset date. A good prediction of onset dates was determined to fall within a 0–4 day difference of observed onset dates. The GDD threshold combined with a certain  $T_{base}$  which resulted in the highest score was determined to provide the best estimate of GDD and  $T_{base}$ . The second evaluation method was based on regression analysis between observed and modelled onsets, again for both methods of defining the GDD threshold ( $GDD_{s,period}$  and  $GDD_{crossval}$ ) and for the optimal  $T_{base}$  value. This is a sensitivity analysis that will test the difference between using the best GDD value for a specific year compared to the whole study period. The  $GDD_{crossval}$  value can technically only be calculated retrospectively, for instance a reanalysis of pollen data and the overall GDD value can be used when observations are not available, such as periods with data gaps or in forecasting.

## 3. Results and discussion

### 3.1. Definitions and evaluations of pollen season onset methods

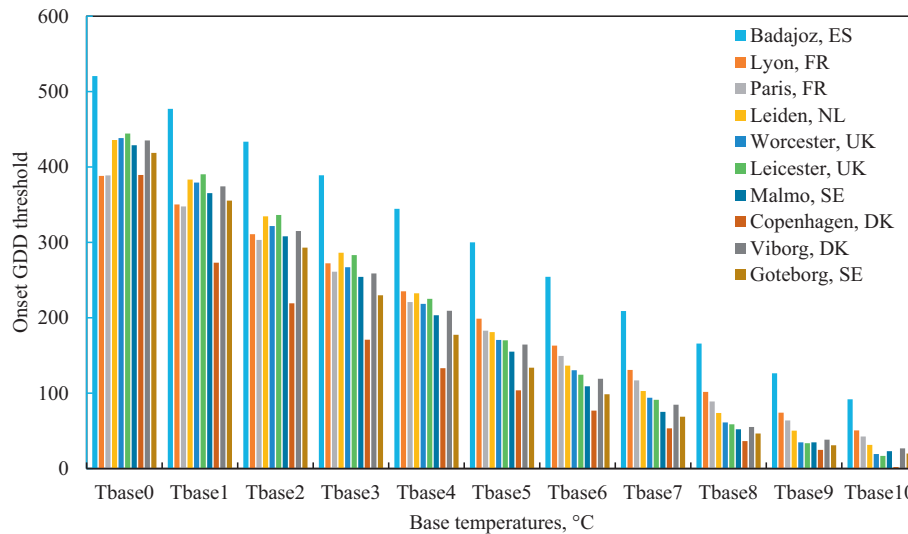
For many sites pollen season onsets differed on an average basis very little between different definition methods, as shown by the low standard deviations in Table 3a. The smallest variations ( $sd < 2$ ) between onset definitions were observed in Lyon, Leiden, Worcester, Malmö, Viborg and Goteborg, often varying from 0 to 4 days between earliest and latest onset definition. Badajoz and Leicester had larger variations ( $sd > 2$ ) with 11 and 8 days difference respectively between earliest and latest onset definition.

For individual years, the difference between the earliest and latest defined onsets usually varied between 0 and 7 days. However, for some years some definition methods differed more, the 2.5% API definition showed several examples of large differences for many sites (Paris, Leicester, Copenhagen, Viborg and Goteborg) as can be seen in Table 3b. The difference could be up to 23 days, which was the case for Leicester 2012. Other high differences included: 20 days in Badajoz 2010, 18 days in Copenhagen 2010, 17 days in Paris 2008, 12 days in Viborg and



**Fig. 1.** Relationship between latitude and the median oak pollen season onset for the studied period. The season onset was defined as the day when the accumulated sum of daily oak pollen concentrations reached above 50 grains  $m^{-3}$  (cumulative $\sum$ 50).



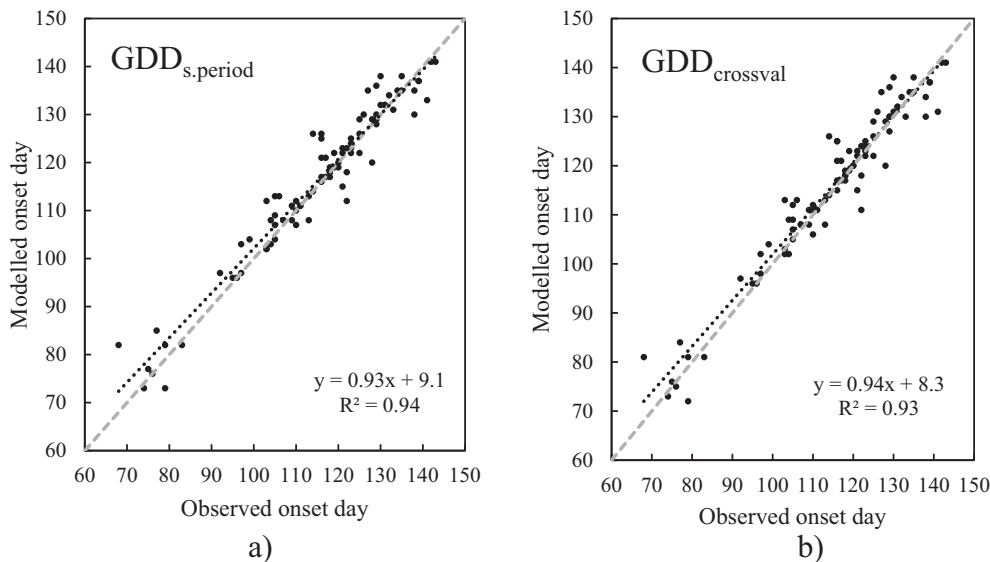


**Fig. 2.** Growing Degree Day (GDD) thresholds corresponding to observed onset dates for oak pollen seasons and different base temperatures ( $T_{base0}$ – $T_{base10}$  °C) for the studied period at each site (sites are arranged according to latitude). Season onsets were defined with the cumulative  $\Sigma_{50}$  method.

### 3.2. Observed oak pollen onsets and characteristics of oak pollen seasons

The onset of the oak pollen seasons in Europe followed a latitude gradient where start date increased on average by circa 2.8 days per latitude north (Fig. 1). In the US, start date increased by 3.6 days per latitude (Zhang et al., 2015), which means onsets occurred on average 28 days earlier in Europe for similar latitudes. This is partly explained by the differing onset definitions used but also due to the relatively milder winter temperatures in Europe produced by the Gulf stream, which also extends temperate broadleaf forests further north in Europe compared to North America. The most southern site (Badajoz) had the earliest onset with the median onset date of day 77 (mid-March) and the two northern-most sites (Viborg and Goteborg) had the latest start on day 133 and 130 (second week in May) as can be seen in Table 4a. Badajoz onset dates (day 77) are comparable to Roseville, California (Zhang et al., 2015) and Cordoba, Spain (Garcia-Mozo et al., 2000), where onset date for oak pollen was found to be day 81

and 72 respectively, and for other sites in Spain the mean start date was day 88 (García-Mozo et al., 2006), differing somewhat from Badajoz. The sites in France usually showed start dates around day 103–105 (second week in April), where Lyon is comparable to Vancouver, USA (Zhang et al., 2015) both located on a similar latitude north. Leiden, Worcester and Leicester showed onsets towards the end of April on around day 116–119 (Table 4a). In a study from Derby, UK, for an earlier time period, the onset of oak pollen showed a linear negative trend for the years 1970–1997 (Corden and Millington, 1999). Onsets in Derby varied from day ~140 in 1970 to day ~120 in 1997, meaning a varying difference of two days to three weeks in onsets compared to the median onset (day 118) found in our study for Leicester, located only ~30 km south-east of Derby. If the trend in Derby has continued over time, onset there is probably at a similar date as that observed today in both Leicester and Worcester. The negative trend itself is most likely due to warmer temperatures as was suggested by Corden and Millington (1999). However, since we are dealing with



**Fig. 3.** Relationship between modelled and observed onsets using the median Growing Degree Day (GDD) thresholds: a)  $GDD_{s.period}$  and b)  $GDD_{crossval}$  and base temperature 4 °C. The grey dashed line signifies a 1:1 line.

different stations, species differences could also be a plausible explanation of potential differences in the timing of onsets between the sites. As can be seen from Table 1, different oak species grow in both Leicester and Worcester. In Leicester the non-native oak, *Q. rubra*, could be the first flowering oak, different to what has been observed in Worcester. Ornamental oak trees are very common in the UK and we cannot be sure which oak species (ornamental or native) grows near the site in Derby and thus may influence its pollen season onset differently. Furthermore, there were large year to year variations in onsets for many sites (Table 4a), notably at Paris, Malmo, Copenhagen and Viborg, which showed the largest variation in the onset dates with relatively large standard deviations (11–14). Conversely, in Lyon and Badajoz for most years, the onset day varied only a few days from the median

throughout the studied period. Copenhagen showed the largest difference between earliest and latest onset with a 35 day (~1 month) difference between years 2007 and 2010 (onsets on day 106 and 141) within the studied period.

The length of the oak pollen season varied highly between sites (Table 4b). Generally longer seasons (>50 days) were observed at southern and non-coastal sites (Badajoz, Lyon, Worcester, Leicester) and shorter seasons at northern and coastal sites (Leiden, Malmo, Copenhagen, Viborg and Goteborg). Long seasons may indicate that several species with different flowering times are contributing to the overall pollen season. In Spain several oak species dominate the vegetation (García-Mozo et al., 2006) and in Extremadura there are five main oak species; *Q. ilex*, *Q. suber*, *Q. pyrenaica*, *Q. coccifera* and *Q. faginea*

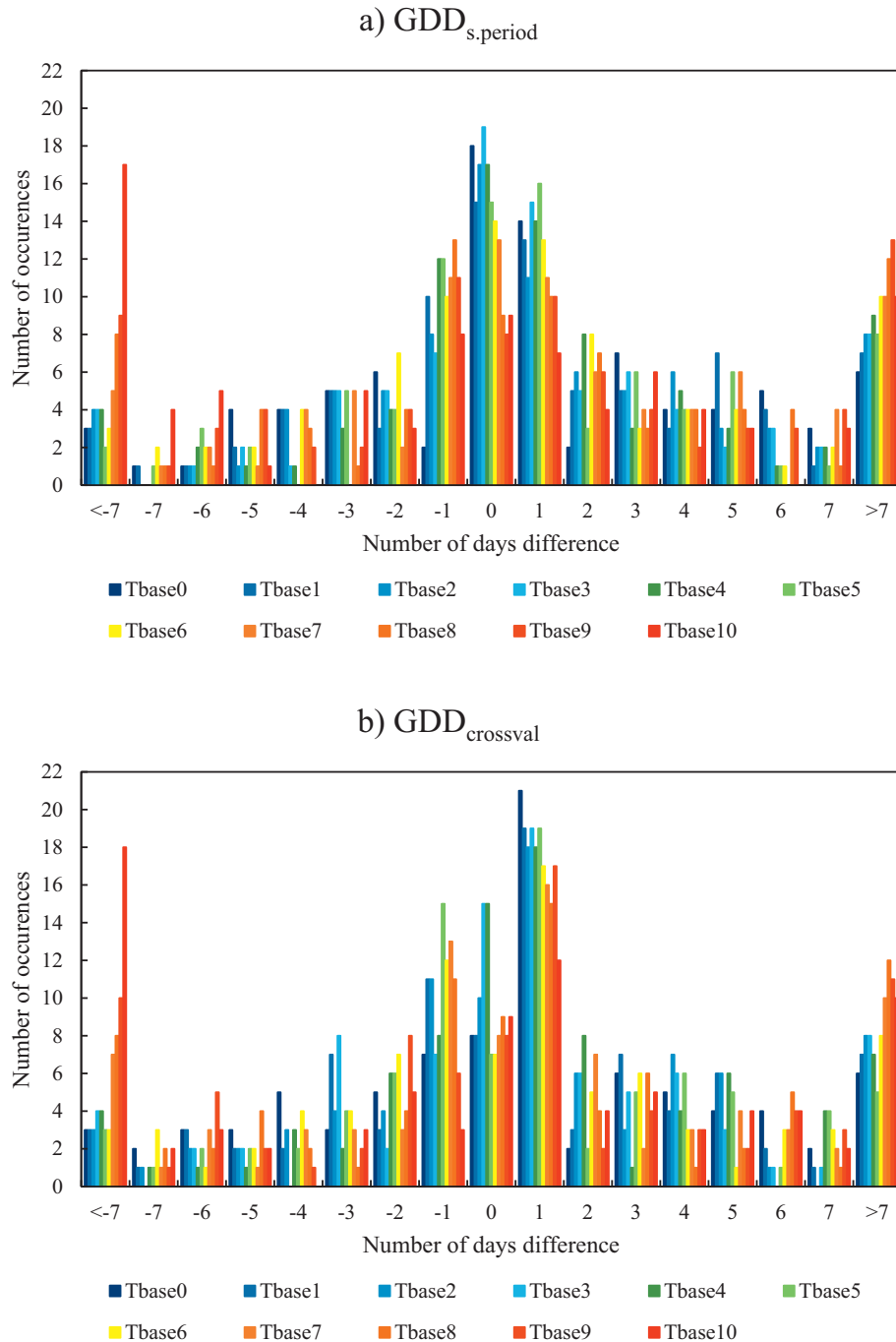


Fig. 4. The number of occurrences (data points) of 0 to >7 days difference between modelled and observed season onsets using different base temperatures ( $T_{base\ 0}$ – $T_{base\ 10}$  °C) and Growing Degree Day (GDD) thresholds (a)  $GDD_{s,period}$  and (b)  $GDD_{crossval}$ . All data points of the studied sites are included and the total number of occurrences is thus 89 for each  $T_{base}$  series.

(Table 1, Fernández-Rodríguez et al., 2016). In parts of Scandinavia only two species dominate, *Q. petraea* and *Q. robur* (Drößler et al., 2012; Siegismund and Jensen, 2001), both with a relatively synchronized temporal flowering phase thus resulting in shorter seasons (Bacilieri and Kremer, 1994). The longest seasons were observed in the southern site Badajoz with a median length of 81 days. The shortest season was observed in Viborg with a median length of 17 days.

Oak pollen levels in terms of API (Table 4c) and peak concentrations (Table 4d) showed very high values in Badajoz as expected. The region has a high abundance of oak trees (Fernández-Rodríguez et al., 2016) with favourable dry and warm climate conditions, both contributing to high atmospheric pollen load. High API was also observed in Worcester and Lyon, and high peak levels were observed in Worcester together with two northern sites (Viborg and Goteborg). Lower APIs were observed in the north, both due to lower density of oak trees in forested areas in these regions (Skjøth et al., 2008) and unfavourable weather conditions, with frequent rainfall, typical for Atlantic regions in western and northern Europe.

### 3.3. GDD thresholds for observed oak pollen onsets

From Fig. 2 it can be observed that thresholds of  $GDD_{s,period}$  values corresponding to observed onsets for different base temperatures ( $T_{base0} - T_{base10}$ ) varied between sites. As expected Badajoz showed the largest thresholds for all base temperatures (e.g. 521 °C with  $T_{base0}$  and 92 °C with  $T_{base10}$ ), a study in Spain found similar GDD thresholds with Badajoz, however, the GDD accumulation was initiated one month earlier than in our study (García-Mozo et al., 2002). Copenhagen showed the lowest  $GDD_{s,period}$  thresholds (e.g. 389 °C with  $T_{base0}$  and 2 °C with  $T_{base10}$ ). Fig. 2 lists the sites in a south to north order and a south-north decreasing gradient of thresholds was noticeable from base temperature 5 ( $T_{base5}$ ) and onwards with some sites deviating from the pattern such as Copenhagen and Viborg, which respectively showed lower and higher values than expected. For lower base temperatures, GDD did not show a clear gradient and GDD thresholds fluctuated noticeably between sites. For some base temperatures and sites, the difference in GDD was quite small, northern sites Malmo and Viborg were at times similar to southern sites Lyon and Paris, sometimes even larger ( $T_{base0}$  and  $T_{base1}$ ). Sites with large distances from each other had similar GDDs for low base temperatures ( $T_{base0}$  and  $T_{base1}$ ), which can be noted for e.g. Lyon and Paris, Leiden and Worcester and Leiden and Leicester, but in between these groups of sites the GDD differences were large. While for  $T_{base3}$  and  $T_{base4}$  the GDD difference between the mentioned sites were very low, illustrating a complex, variable pattern when considering base temperatures.

Some sites located on similar latitudes showed very similar GDD values (Leiden, Worcester and Leicester), while some northern sites on similar latitudes showed quite large differences (e.g. Copenhagen and Malmo). The temperature pattern for Malmo and Copenhagen

were as expected very similar (Table S1). It rained more in Malmo during January–March, while for April and May the precipitation pattern was very similar (Fig. S1). Thus, dryer conditions during the first 3 months of the year could have had an influence on the lower GDD in Copenhagen compared to Malmo. Furthermore, it is currently unknown whether any ornamental oak trees grow near the pollen traps in either Copenhagen or Malmo, thus differing oak species with separate flowering periods may also be a plausible explanation why such different GDD thresholds were observed at these closely located sites.

Differences in GDD between sites are partly explained by climate adaptations of the trees, different base temperature requirements has been shown to occur within the same species growing in different climates (Dahl et al., 2013). Thus, sites with distinctly different climate regimes, such as the sites located far apart in our study, are subject to influence from climatic adaptations on the GDD threshold. Furthermore, as mentioned, GDD differences can also be due to ornamental oak trees in urban parks and gardens exhibiting different temperature requirements compared to the native oak species associated with each site. Current analytical methods in pollen monitoring programs rely on optical recognition, which makes it very difficult to separate tree pollen at the species level (e.g. Wrońska-Pilarek et al., 2016). Pollen types are therefore given at the genus level only. When comparing oak pollen from different sites over a large geographical area with several climate zones such as Europe we inevitably compare pollen from different species. Even on a smaller region such as Spain, species differences can give rise to variances in GDD values, as has been shown and discussed by García-Mozo et al. (2002) and for the US by Zhang et al. (2015). When comparing Badajoz and Worcester for example, the comparison reflects two different species; *Q. ilex* (García-Mozo et al., 2008) and *Q. palustris*. These two species are the first flowering oak trees in each respective region of the pollen monitoring stations and likely have separate temperature requirements for the initiation of flowering. In Worcester, *Q. ilex* is one of the latest flowering species, normally occurring in the end of May/beginning of June, 1–1.5 months after the local oak season onset. Until pollen monitoring can be done at the species level, GDD thresholds will be subject to species bias. It is therefore important to point out that GDD comparisons between regions can currently only reflect oak on the genus level. In addition, tree species with normally separate flowering periods can, in some years be relatively synchronized and show similar GDDs. Near the pollen trap in Worcester a local stand of ornamental trees belonging to *Q. palustris*, normally flowers 2 weeks before the native oak *Q. robur*. In 2018 phenological observations of the local oak trees (not shown) revealed a relatively synchronized flowering period between these species and are thought to be coupled to the cold spring delaying the flowering of several species. This synchronicity further complicates the determination of species-specific GDD thresholds and is another reason for finding identification methods for pollen on the species level.

### 3.4. Modelled versus observed onsets – two evaluation methods

Two methods (regression and scoring) were used to evaluate the accuracy and precision of the two GDD onset models ( $GDD_{s,period}$  and  $GDD_{crossval}$ ). The regression method produced the strongest relationship ( $R^2 = 0.94$ ) between modelled and observed onset dates using  $T_{base4}$  for  $GDD_{s,period}$  (Fig. 3a). For the same base temperature, a difference of 4 days or less between modelled and observed onsets was very common, the scoring method covered 75% (67/89 data points) of all analysed stations and years (Fig. 4a). For the higher model precision of 2 days difference or less, base temperature 4 covered 62% (55/89 data points) of all studied years. Base temperatures 3 and 5 were also associated with very strong relationships ( $R^2 = 0.93$ , Table 5a). In fact, base temperatures below 7 °C produced almost equivalent relationship strengths, suggesting very little indication of a superior base temperature to use for modelling onset dates. Similar conclusions can be drawn for the sensitivity analysis ( $GDD_{crossval}$ ) which produced strong

**Table 5**

Relationships between modelled and observed onsets for different base temperatures (0–10 °C) using the Growing Degree Day (GDD) threshold for the studied period: a)  $GDD_{s,period}$  and b)  $GDD_{crossval}$ . Statistical significance (\*\*\*) indicates a p-value < 0.001.

$T_{base}$	a) $GDD_{s,period}$		b) $GDD_{crossval}$	
	$R^2$	p-Value	$R^2$	p-Value
0	0.92	***	0.91	***
1	0.92	***	0.92	***
2	0.92	***	0.92	***
3	0.93	***	0.93	***
4	0.94	***	0.93	***
5	0.93	***	0.93	***
6	0.92	***	0.92	***
7	0.90	***	0.90	***
8	0.87	***	0.87	***
9	0.84	***	0.85	***
10	0.76	***	0.78	***



relationships between modelled and observed onsets for base temperatures below 7 °C (Fig. 3b). The strongest relationship ( $R^2 = 0.93$ ) was found for  $T_{base3}$  and from Fig. 4b it can be determined that 76% (68/89 data points) of the occurrences showed a 4 day difference or less between observed and modelled onset for this base temperature. The number of occurrences with 2 days difference or more reduced significantly for both  $GDD_{s,period}$  and  $GDD_{crossval}$ . For a week or longer difference ( $n \text{ days} > 7$ ) the higher base temperatures ( $\geq 7$  °C) were on average twice as common in occurrence for both  $GDD_{crossval}$  and  $GDD_{s,period}$  (Fig. 4a and b). The strong relationships found for both GDD approaches show they are both robust.

As mentioned in Section 3.3 some sites located on different latitudes showed similar GDD thresholds for observed onsets, this however did not result in similar modelled onsets (Fig. 3a). A certain accumulated temperature will be reached at different times and depends greatly on latitude. Southerly sites will reach a given GDD sooner in comparison with northern sites, thus resulting in an earlier onset. A GDD threshold similar for two different locations is thus expected to result in different onset dates, as has been shown with observed onsets for e.g. Paris and Leiden ( $T_{base3}$ ,  $-T_{base5}$ ). The modelled onsets of the two sites often differed by more than a week, as was also the case for the observed onsets seen in Table 4a.

Zhang et al. (2015), found a somewhat lower correlation for modelled oak pollen onsets in the US using a base temperature of 5 °C, with the same initial start date for heat accumulation (1st March) but a different method for both the GDD calculation and modelling. In a study from Spain, base temperatures varied between 4 and 11 °C for different sites thus differing from our results, partly due to the site-specific approach used but also due to a different calculation method for GDD together with a different initial date for heat accumulation (García-Mozo et al., 2002). In other site-specific studies on other tree genera, variable base temperatures have also been seen, such as in Denmark (Rasmussen, 2002). It should also be mentioned that a base temperature at a certain site is likely to be an adaptation to the prevailing climate and thus it is to be expected that site-specific studies give different results. In a general model approach such adaptations cannot however be explicitly expressed. This study identified a base temperature which has been uniformly evaluated with consideration to all sites, which allows for a general modelling approach and applicability to areas where no pollen observations exist.

#### 4. Concluding summary

This study has shown that oak pollen seasons are a relatively unexplored field within aerobiology despite the fact that oak pollen is considered to be among the eight most important trees causing respiratory allergic reactions on a global scale and among the 12 most important aeroallergens in Europe (Ferreira et al., 2014). This study is the first to show the oak pollen seasonal characteristics and its variation over a large area in Europe and thus provides cross-boundary information of the timing and magnitude of the oak pollen load relevant to, for example, health professionals and citizens. Oak pollen onsets, GDD thresholds for onsets, season length, pollen peaks and API have been established and a generalized phenological model implemented for predicting the oak pollen start on a genus level across Europe. This generalized approach is applicable despite the known fact that different oak species grow throughout Europe and can be extended to a larger area where oak pollen measurements are non-existent.

Some of the most important conclusions from this study:

- Long oak seasons were observed in Badajoz (ES), Lyon (FR), Worcester (UK) and Leicester (UK), these regions have several oak species likely flowering at different times.
- High Annual Pollen Integrals were common in Badajoz (ES) and Worcester (UK), these two sites together with northern sites Viborg (DK) and Goteborg (SE), also showed relatively high peak

concentrations.

- The most accurate onset definition was determined to be the cumulative  $\sum 50$ .
- GDD thresholds at observed onset varied considerably between sites, the highest GDD was observed in Badajoz (SP) and the lowest in Copenhagen (DK).
- The general approach model produced the best result using the GDD threshold for base temperature of 4 °C where 75% of the modelled onsets fell within four days difference from observed onsets.
- Base temperatures below 7 °C all produced very strong results for modelled onset dates, covering between 71 and 75% of all modelled onsets falling within four days difference from observed onsets.
- The sensitivity analysis ( $GDD_{crossval}$ ) also produced very strong relationships between observed and modelled onsets with base temperatures below 7 °C where 70–76% of all observations fell within 4 days difference from observed onset, indicating robustness of the methods used.
- The study has revealed that there are several and variable oak species in different parts of Europe, which adds complexity when comparing the phenology of oaks on genus level in different regions.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2019.01.212>.

#### References

- Adams-Groom, B., Emberlin, J., Corden, J., Millington, W., Mullins, J., 2002. Predicting the start of the birch pollen season at London, Derby and Cardiff, United Kingdom, using a multiple regression model, based on data from 1987 to 1997. *Aerobiologia (Bologna)* 117–123.
- Bacilieri, R., Kremer, A., 1994. Genetic, morphological, ecological and phenological differentiation between *Quercus petraea* (MATT.) LIEBL. and *Quercus robur* L. in a mixed stand of northwest of France. *Silvae Genet.* 44, 1–10.
- Chuine, I., Cour, P., Rousseau, D.D., 1999. Selecting models to predict the timing of flowering of temperate trees: implications for tree phenology modelling. *Plant Cell Environ.* 1–13.
- Corden, J., Millington, W., 1999. A study of *Quercus* pollen in the Derby area, UK. *Aerobiologia (Bologna)* <https://doi.org/10.1023/A:1007580312019>.
- Dahl, Å., Galán, C., Hajkova, L., Pauling, A., Sikoparija, B., Smith, M., Vokou, D., 2013. The onset, course and intensity of the pollen season. *Allergenic Pollen*. Springer Netherlands, Dordrecht, pp. 29–70 [https://doi.org/10.1007/978-94-007-4881-1\\_3](https://doi.org/10.1007/978-94-007-4881-1_3).
- D'Amato, G., Cecchi, L., Bonini, S., Nunes, C., Annesi-Maesano, I., Behrendt, H., Liccardi, G., Popov, T., Van Cauwenberge, P., 2007. Allergenic pollen and pollen allergy in Europe. *Allergy Eur. J. Allergy Clin. Immunol.* 62, 976–990. <https://doi.org/10.1111/j.1398-9995.2007.01393.x>.
- Drriessen, M.N.B.M., van Herpen, R.M.A., Smithuis, L.O.M.J., 1990. Prediction of the start of the grass pollen season for the southern part of the Netherlands. *Grana* 29, 79–86. <https://doi.org/10.1080/00173139009429978>.
- Drößler, L., Attocchi, G., Jensen, M., 2012. Occurrence and management of oak in southern Swedish forests. Introduction to southern Swedish conditions and forest types. *Forstarchiv* 169, 163–169. <https://doi.org/10.4432/0300-4112-83-163>.
- Egger, C., Focke, M., Bircher, A.J., Scherer, K., Mothes-Luksch, N., Horak, F., Valenta, R., 2008. The allergen profile of beech and oak pollen. *Clin. Exp. Allergy* 38, 1688–1696. <https://doi.org/10.1111/j.1365-2222.2008.03092.x>.
- Emberlin, J., Jones, S., Bailey, J., Caulton, E., Corden, J., Dubbels, S., Evans, J., McDonagh, N., Millington, W., Mullins, J., Russel, R., Spencer, T., 1994. Variation in the start of the grass pollen season at selected sites in the United Kingdom 1987–1992. *Grana* <https://doi.org/10.1080/00173139409427839>.
- Emberlin, J., Mullins, J., Corden, J., Millington, W., Brooke, M., Jones, S., 1997. The trend to earlier Birch pollen seasons in the U.K.: a biotic response to changes in weather conditions? *Grana* 36, 29–33.

- 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). *Int. J. Biometeorol.* 51, 49–59.
- Farnham, J.E., 1990. New England tree pollen and skin test reactivity. A three year study. *Aerobiologia (Bologna)* 6, 212–213.
- Fernández-Rodríguez, S., Durán-Barroso, P., Silva-Palacios, I., Tormo-Molina, R., Maya-Manzano, J.M., Gonzalo-Garijo, Á., 2016. Quercus long-term pollen seasons trends in the southwest of the Iberian Peninsula. *Process. Saf. Environ. Prot.* <https://doi.org/10.1016/j.psep.2015.11.008>.
- Ferreira, F., Gadermaier, G., Wallner, M., 2014. Tree pollen allergens. *Global Atlas of Allergy*, pp. 18–21.
- Fu, Y.H., Campioli, M., Deckmyn, G., Janssens, I.A., 2012. The impact of winter and spring temperatures on temperate tree budburst dates: results from an experimental climate manipulation. *PLoS One* <https://doi.org/10.1371/journal.pone.0047324>.
- Galán, C., Smith, M., Thibaudon, M., Frenguelli, G., Oteros, J., Gehrig, R., Berger, U., Clot, B., Brandao, R., E.Q.W. Group, 2014. Pollen monitoring: minimum requirements and reproducibility of analysis. *Aerobiologia (Bologna)* 30, 385–395. <https://doi.org/10.1007/s10453-014-9335-5>.
- Galán, C., Ariatti, A., Bonini, M., Clot, B., Crouzy, B., Dahl, A., Frenguelli, G., Gehrig, R., Isard, S., Levetin, E., Rogers, C.A., Thibaudon, M., Sauliene, I., Smith, M., Sofiev, M., 2017. Recommended terminology for aerobiological studies. *Aerobiologia (Bologna)*, 293–295 <https://doi.org/10.1007/s10453-017-9496-0>.
- García-Mozo, H., Galán, C., Gomez-Casero, M.T., Dominguez-Vilches, E., 2000. A comparative study of different temperature accumulation methods for predicting the start of the Quercus pollen season in Córdoba (South West Spain). *Grana* <https://doi.org/10.1080/00173130051084322>.
- García-Mozo, H., Galán, C., Aira, M.J., Belmonte, J., Díaz De La Guardia, C., Fernández, D., Gutiérrez, A.M., Rodríguez, F.J., Trigo, M.M., Dominguez-Vilches, E., 2002. Modelling start of oak pollen season in different climatic zones in Spain. *Agric. For. Meteorol.* [https://doi.org/10.1016/S0168-1923\(02\)00003-5](https://doi.org/10.1016/S0168-1923(02)00003-5).
- García-Mozo, H., Galán, C., Jato, V., Belmonte, J., Díaz De La Guardia, C., Fernández, D., Gutiérrez, M., Aira, M.J., Roure, J.M., Ruiz, L., Trigo, M.M., Domínguez-Vilches, E., 2006. Quercus pollen season dynamics in the Iberian Peninsula: response to meteorological parameters and possible consequences of climate change. *Ann. Agric. Environ. Med.* 13, 209–224.
- García-Mozo, H., Chuine, I., Aira, M.J., Belmonte, J., Bermejo, D., Díaz de la Guardia, C., Elvira, B., Gutiérrez, M., Rodríguez-Rajo, J., Ruiz, L., Trigo, M.M., Tormo, R., Valencia, R., Galán, C., 2008. Regional phenological models for forecasting the start and peak of the Quercus pollen season in Spain. *Agric. For. Meteorol.* 148, 372–380. <https://doi.org/10.1016/j.agrformet.2007.09.013>.
- Gemeente Leiden, 2018. Groene Kaart Leiden. Digit. Green Map Munic. Leiden. URL <https://groenekaart.leiden.nl/#/>, Accessed date: 20 December 2018.
- Hauser, M., Asam, C., Himly, M., Palazzo, P., Voltolini, S., Montanari, C., Briza, P., Bernardi, M.L., Mari, A., Ferreira, F., 2011. Bet v 1-like pollen allergens of multiple Fagales species can sensitize atopic individuals. *Clin. Exp. Allergy* 41, 1804–1814. <https://doi.org/10.1111/j.1365-2222.2011.03866.x>.
- Heinzerling, L.M., Burbach, G.J., Edenharter, G., Bachert, C., Bindslev-Jensen, C., Bonini, S., Bousquet, J., Bousquet-Rouanet, L., Bousquet, P.J., Bresciani, M., Bruno, A., Burney, P., Canonica, G.W., Darsow, U., Demoly, P., Durham, S., Fokkens, W.J., Giavi, S., Gjomarkaj, M., Gramiccioni, C., Haahtela, T., Kowalski, M.L., Magyar, P., Muraközi, G., Orosz, M., Papadopoulos, N.G., Röhnelt, C., Stingl, G., Todo-Bom, A., Von Mutius, E., Wiesner, A., Wöhrl, S., Zuberbier, T., 2009. GA2LEN skin test study I: GALEN harmonization of skin prick testing: novel sensitization patterns for inhalant allergens in Europe. *Allergy* <https://doi.org/10.1111/j.1398-9995.2009.02093.x>.
- Hirst, J.M., 1952. An automatic volumetric spore trap. *Ann. Appl. Biol.* 39, 257–265.
- Hjelmroos, M., 1991. Evidence of long-distance transport of Betula pollen. *Grana* 30, 215–228.
- Jäger, S., Pessi, A.M., Helander, M., Nilsson, S., Berggren, B., Ramfjord, H., 1996. Trends of some airborne tree pollen in the Nordic countries and Austria, 1980–1993: a comparison between Stockholm, Trondheim, Turku and Vienna. *Grana* <https://doi.org/10.1080/00173139609429078>.
- Käpylä, M., Penttinen, A., 1981. An evaluation of the microscopical counting methods of the tape in Hirst-Burkard pollen and spore trap. *Grana* 20, 131–141.
- Khwarahm, N., Dash, J., Atkinson, P., Newnham, R.M., Skjøth, C.A., Adams-Groom, B., Caulton, E., Head, K., 2014. Exploring the spatio-temporal relationship between two key aeroallergens and meteorological variables in the United Kingdom. *Int. J. Biometeorol.*, 529–545 <https://doi.org/10.1007/s00484-013-0739-7>.
- Linkosalo, T., Lappalainen, H.K., Pertti, H., 2008. A comparison of phenological models of leaf bud burst and flowering of boreal trees using independent observations. *Tree Physiol.* 28, 1873–1882.
- Mairie de Paris, 2018. PARISDATA. Les arbres. URL <https://opendata.paris.fr/explore/dataset/les-arbres/table/?refine.genre=Quercus>, Accessed date: 20 December 2018.
- McMaster, G.S., Wilhelm, W.W., 1997. Growing degree-days: one equation, two interpretations. *Agric. For. Meteorol.* 87, 291–300.
- Mitchell, A., 1974. A Field Guide to Trees of Britain and Northern Europe. William Collins Sons & Co Ltd, Glasgow.
- Morin, X., Roy, J., Sonié, L., Chuine, I., 2010. Changes in leaf phenology of three European oak species in response to experimental climate change. *New Phytol.* <https://doi.org/10.1111/j.1469-8137.2010.03252.x>.
- Newnham, R.M., Sparks, T.H., Skjøth, C.A., Head, K., Adams-Groom, B., Smith, M., 2013. Pollen season and climate: is the timing of birch pollen release in the UK approaching its limit? *Int. J. Biometeorol.*, 391–400 <https://doi.org/10.1007/s00484-012-0563-5>.
- Norris-Hill, J., 1998. A method to forecast the start of the Betula, Platanus and Quercus pollen seasons in North London. *Aerobiologia (Bologna)* 14, 165–170. [https://doi.org/10.1016/S0393-5965\(98\)00040-7](https://doi.org/10.1016/S0393-5965(98)00040-7).
- Rasmussen, A., 2002. The effects of climate change on the birch pollen season in Denmark. *Aerobiologia (Bologna)* 18, 253–265.
- Ross, A.M., Corden, J.M., Fleming, D.M., 1996. The role of oak pollen in hay fever consultations in general practice and the factors influencing patients' decisions to consult. *Br. J. Gen. Pract.* 46, 451–455.
- Siegmund, H.R., Jensen, J.S., 2001. Intrapopulation and interpopulation genetic variation of Quercus in Denmark. *Scand. J. For. Res.* 16, 103–116. <https://doi.org/10.1080/028275801300088143>.
- Sikoparija, B., Pejak-Sikoparija, T., Radisic, P., Smith, M., Soldevilla, C.G., 2011. The effect of changes to the method of estimating the pollen count from aerobiological samples. *J. Environ. Monit.* 13, 384–390.
- Skjøth, C.A., Sommer, J., Stach, A., Smith, M., Brandt, J., 2007. The long range transport of birch (Betula) pollen from Poland and Germany causes significant pre-season concentrations in Denmark. *Clin. Exp. Allergy* 1204–1212.
- Skjøth, C.A., Geels, C., Hvidberg, M., Hertel, O., Brandt, J., Frohn, L.M., Hansen, K.M., Hedegaard, G.B., Christensen, J.H., Moseholm, L., 2008. An inventory of tree species in Europe—an essential data input for air pollution modelling. *Ecol. Model.*, 292–304 <https://doi.org/10.1016/j.ecolmodel.2008.06.023>.
- Skjøth, C.A., Sikoparija, B., Jäger, S., EAN-Network, 2013. Pollen sources. *Allergenic Pollen. Springer Netherlands, Dordrecht*, pp. 9–27 [https://doi.org/10.1007/978-94-007-4881-1\\_2](https://doi.org/10.1007/978-94-007-4881-1_2).
- Skjøth, C.A., Baker, P., Sadyś, M., Adams-Groom, B., 2015. Pollen from alder (Alnus sp.), birch (Betula sp.) and oak (Quercus sp.) in the UK originate from small woodlands. *Urban Clim.* <https://doi.org/10.1016/j.uclim.2014.09.007>.
- Skjøth, C.A., Damialis, A., Belmonte, J., De Linares, C., Fernández-Rodríguez, S., Grinn-Gofroń, A., Jędrzycka, M., Kasprzyk, I., Magyar, D., Myszkowska, D., Oliver, G., Páldy, A., Pashley, C.H., Rasmussen, K., Satchwell, J., Thibaudon, M., Tormo-Molina, R., Vokou, D., Ziemianin, M., Werner, M., 2016. Alternaria spores in the air across Europe: abundance, seasonality and relationships with climate, meteorology and local environment. *Aerobiologia (Bologna)* 32, 3–22. <https://doi.org/10.1007/s10453-016-9426-6>.
- Spieksma, F.Th.M., Emberlin, J.C., Hjelmroos, M., Jäger, S., Leuschner, R.M., 1995. Atmospheric birch (Betula) pollen in Europe: trends and fluctuations in annual quantities and the starting dates of the. *Grana* 3, 51–57.
- Wielgolaski, F., 1999. Starting dates and basic temperatures in phenological observations of plants. *Int. J. Biometeorol.* 42, 158–168.
- Wrońska-Pilarek, D., Danielewicz, W., Bocianowski, J., Maliński, T., Janyszek, M., 2016. Comparative pollen morphological analysis and its systematic implications on three European oak (Quercus L., Fagaceae) species and their spontaneous hybrids. *PLoS One* <https://doi.org/10.1371/journal.pone.0161762>.
- Zhang, Y., Bielory, L., Cai, T., Mi, Z., Georgopoulos, P., 2015. Predicting onset and duration of airborne allergenic pollen season in the United States. *Atmos. Environ.* <https://doi.org/10.1016/j.atmosenv.2014.12.019>.