

This article was downloaded by: [Advanced Institute of Sanita]
[Advanced Institute of Sanita]

On: 13 February 2007

Access Details: [subscription number 769486267]

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954

Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Grana

Publication details, including instructions for authors and subscription information:

<http://www.informaworld.com/smpp/title-content=t713648917>

Biometeorological characterization of the winter in north-west Spain based on *Alnus* pollen flowering

To link to this article: DOI: 10.1080/00173130600984534

URL: <http://dx.doi.org/10.1080/00173130600984534>

Full terms and conditions of use: <http://www.informaworld.com/terms-and-conditions-of-access.pdf>

This article maybe used for research, teaching and private study purposes. Any substantial or systematic reproduction, re-distribution, re-selling, loan or sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

© Taylor and Francis 2007

Biometeorological characterization of the winter in north-west Spain based on *Alnus* pollen flowering

F. JAVIER RODRÍGUEZ-RAJO¹, M. DELIA FERNÁNDEZ-GONZÁLEZ²,
ANA M. VEGA-MARAY², F. JAVIER SUÁREZ³, ROSA M. VALENCIA-BARRERA² &
VICTORIA JATO¹

¹Department of Plant Biology and Soil Sciences, Sciences Faculty, Vigo University, Ourense, Spain, ²Department of Plant Biology (Botanical Area), Sciences Faculty, León University, León, Spain, and ³Department of Biology of Organisms and Systems, Sciences Faculty, Oviedo University, Oviedo, Spain

Abstract

The timing of pollen appearance in the atmosphere provides a general idea of the flowering onset of plants over a wide area. Woody plants in temperate regions have evolved mechanisms to preserve cells from the risk of frost during adverse weather conditions in the period prior to flowering regulated mainly by temperature. A number of indices have been developed to quantify the rest and heat requirements of temperature, which will enable the plant to adapt to environmental conditions. However, flowering is a dynamic and complex phenomenon and it is difficult to separate individual effects of different meteorological parameters. The use of modified bioclimatic indices could be a major step forward. In this study the *Alnus glutinosa* flowering in four different areas in north-western Spain in the period 1995–2003 is examined, and trends identified by means of information gathered by Hirst pollen traps. Temperature plays an important role in the maturation of reproductive organs and pollen production. Comparison with bioclimatic indices showed that temperature during the 25–55 days preceding pollen release was the main controlling factor, and that relationship between flowering time and bioclimatic indicator values differs according to local conditions. In colder areas, rest and heat temperature requirements are greater because the trees need protection over a longer period; in the Mediterranean region of north-western Spain, the rest temperature requirement and the threshold temperature are both higher than in Eurosiberian areas. Ombrothermic, Continentality and Thermicity indices are thus useful tools for characterizing the various bioclimatic areas of north-western Spain.

Keywords: *Alnus*, pollen, biometeorological indices, chilling hours, growth degree days, north-western Spain

Meteorological parameters, particularly temperature, are recognized as the main variable influencing the timing of budburst and flowering. Weather-related parameters can be used in conjunction with altitude and biogeographical conditions to characterize the bioclimate of a given area. North-western Spain has a high level of bioclimatic variation, since relief and geographical location favour considerable climatic and phytogeographic diversity; the confluence between the Eurosiberian and Mediterranean regions gives the vegetation a transitional character, and species characteristic of both regions are frequently found growing together (Jato et al.,

2004). The study of flowering-season timing in species located at their biogeographical distribution limit, such as *Alnus glutinosa* (L.) Gaertner in north-western Spain, as well as of European-meridional or Mediterranean affiliated species such as *Populus alba* L., *Celtis australis* L. or *Fraxinus angustifolia* Vahl., help us to understand and predict possible ecological changes related to global climate change. On the assumption that atmospheric pollen indicates the time of flowering, aeropalynological data have been used in recent years as phenological data in order to determine the onset of flowering over a wide area (Frenguelli & Bricchi, 1998; García-Mozo et al.,

Correspondence: F. Javier Rodríguez-Rajo, Department of Plant Biology and Soil Sciences, Sciences Faculty, University of Vigo, Campus Universitario As Lagoas, 32004 Ourense, Spain. E-mail: javirajo@uvigo.es

(Received: 18 March 2005; accepted 10 March 2006)

ISSN 0017-3134 print/ISSN 1651-2049 online © 2006 Taylor & Francis
DOI: 10.1080/00173130600984534

2000; Jato et al., 2000; Rodríguez-Rajo et al., 2000; Fornaciari et al., 2000; Galán et al., 2001; Laaidi, 2001). Woody plants in temperate regions have evolved mechanisms to preserve cells from the risk of frost during adverse weather conditions in the period prior to flowering. The developmental process leading to bud dormancy release and thus triggering the onset of growth is mainly regulated by temperature. The strategy involves a period of low temperatures followed by a period of warm temperature. In recent years, a number of indices have been developed to quantify these temperature requirements, which will enable us to predict how the species will respond to changes in climate or to know the plant adaptation to environmental conditions. The “Rest Period” with cold temperatures is generally determined using Chilling Units or Chilling Hours (Aron, 1983; Ashcroft et al., 1977; Faust, 1989; Felker et al., 1983; Richardson et al., 1974; Rickman et al., 1983), while the “Heat Period” required to overcome dormancy is frequently measured in terms of several methods as Day-Degrees, Degree-Hours or Growth Degree-Days (Kramer, 1994; García-Mozo et al., 2000; Jato et al., 2000, 2004; Rodríguez-Rajo et al., 2000; Galán et al., 2001).

However, the global status of the atmosphere is one of the most important factors in the timing of flowering and meteorological parameters alone do not reflect this effectively. It is difficult to separate out the individual effects of different meteorological parameters, since plants react simultaneously to a combination of factors (Azcón-Bieito & Talón, 2000). Thus, the use of modified bioclimatic indices

integrating several weather-related parameters instead of using simple meteorological measurements could represent a major step toward the understanding the relationship between flowering and environmental conditions (Rivas-Martínez, 1997; Valencia-Barrera et al., 2002). Flowering phenology is better characterized in terms of indices as more closely reflects the needs of the plants (Rivas-Martínez, 1997; Fernández-González et al., 2000; Valencia-Barrera et al., 2002).

In this paper, airborne pollen concentrations of *Alnus glutinosa*, commonly found in the winter fraction of the bioaerosol of north-western Spain, were used in order to attain better knowledge of bioclimatic adaptation in winter-flowering trees. The aim of the study was to determine temperature requirements (chilling hours – CH, and growth degree days – GDD°C) for winter flowering in various bioclimatic areas at different altitudes, and to identify bioclimatic indices, based in the relationship between temperature and water availability, linked to pollen production in winter-flowering trees.

Material and methods

The bioclimatic zones studied are located in the north-west of Spain (Figure 1). Two urban zones located in the Eurosiberian region, one with maritime influence (Vigo) and an inland area with some maritime influence (Oviedo) and two inland urban zones with continental influence (León and Ponferrada) and located in the Mediterranean region were selected (Rivas-Martínez, 1997).

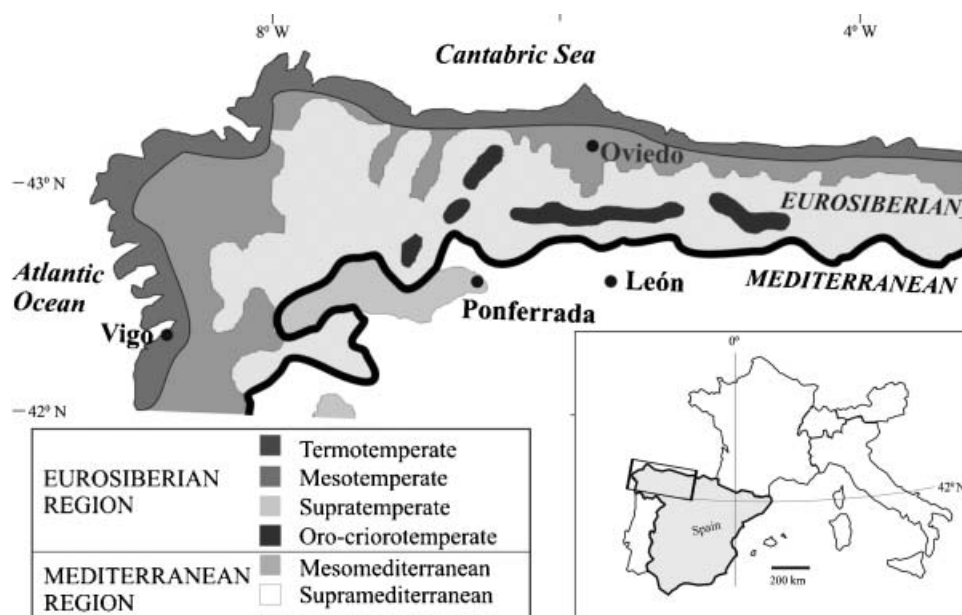


Figure 1. Study area and Bioclimatic regions.

Table I. Sampling site characteristics.

	Vigo	Oviedo	Ponferrada	León
Site coordinates	42°14'N; 8°43'W	43°21'N; 5°52'W	42°33'N; 6°35'W	42°34'N; 5°35'W
Trap environment	Urban	Rural/Urban	Rural/Urban	Rural/Urban
Altitude (m a.s.l.)	50	285	541	830
Annual rainfall (mm)	1412	963	640	550
Annual mean temperature (°C)	14.9	12.5	10.3	10
Bioclimate type	Temperate Hyperoceanic	Temperate Oceanic	Mediterranean Pluviseasonal	Mediterranean Pluviseasonal
	Sub-Mediterranean	Sub-Mediterranean	Oceanic	Oceanic
Phytogeographic region	Eurosiberian	Eurosiberian	Mediterranean	Mediterranean

Biogeographical, climatological and environment details of the four areas are shown in Table I.

Meteorological data were supplied by the Spanish National Meteorological Institute. Mean, minimum and maximum temperatures ($T_{\min}$ and $T_{\max}$), rainfall and relative humidity were recorded continuously from January 1st 1995 (in Vigo, León and Ponferrada) and January 1st 1998 (in Oviedo) to December 31st 2003.

LANZONI VPPS 2000 pollen traps (Hirst, 1952) were used in each locality, placed 15–25 m above ground level in areas close to the meteorological stations. The Lanzoni sampler is calibrated to handle a flow of 10 litres of air per minute, thus matching the human breathing rate. Pollen grains are impacted on a cylindrical drum covered by a melinex film coated with a 2% silicon solution as trapping surface. The drum was changed weekly and the exposed tape was cut into seven pieces, which were mounted on separate glass slides. Pollen identification was performed using microscopes equipped with a 40X/0.95 lens. Pollen counts were made using the model proposed by the R.E.A., consisting in four continuous longitudinal traverses along the 24-hrs slide (Domínguez et al., 1992). We used the 2.5% method (Andersen, 1991) in order to calculate the main flowering period, which includes 95% of the

annual total pollen collected, eliminating the initial period until 2.5% is attained and the final period once 97.5% has been attained.

Flowering start requirements, altitudinal parameters and some bioclimatic indices (Table II) proposed in agrometeorological studies (Rivas Martínez, 1997; Valencia-Barrera et al., 2002) based on temperature and precipitation have been used: Continentality (CI), Thermicity (TI) and Ombrothermic (OI) modified indices (Table II). CI expresses the range between the maximum temperature ($T_{\max}$) and the minimum temperature ($T_{\min}$) for the period considered, TI sums all the relevant temperature measurements for the period considered and OI takes into account both temperature and precipitation considering a threshold value (Valencia-Barrera et al., 2002).

To determine rest period (RP) requirements we have chosen a thermal time model proposed by Aron (1983). In this method the accumulation of chilling hours (CH) between 0°C and 7.2°C is calculated considering the maximum and minimum temperatures and the length of the RP (Table II). Generally, the mean temperature falls below 10°C in the area studied at the beginning of November (Figure 2) and the day when that was happened was considered as the start of the accumulation of chilling hours.

Table II. Equations of continentality (CI) thermicity (CT) and ombrothermic (OI) indices and rest period (RP) and heat period (HP) requirements.

Indices	Equations	
Continentality CI	$C.I. = T_{\max} - T_{\min}$	$T_{\max}$ and $T_{\min}$ expresses the maximum and minimum temperatures of the period considered
Thermicity TI	$T.I. = T + T_{\max} + T_{\min}$	T , $T_{\max}$ and $T_{\min}$ expresses the mean, maximum and minimum temperatures of the period considered respectively
Ombrothermic OI	$O.I. = 10 P_p T_p^{-1}$	P_p is the sum of the precipitation on days where the mean temperature is above 0°C and T_p is the sum of mean temperatures above 0°C for the period considered
Rest Requirements CH	$CH = 801 + 0.2523B + 7.57B^2 \cdot 10^{-4} - 6.51B^4 \cdot 10^{-10} - 11.44T_{i\min} - 3.32T_{i\max}$ $B = 24 D((7.2 - T_{\min}) / (T_{\max} - T_{\min}))$	$T_{i\min}$ and $T_{i\max}$ are respectively the average of minimum and maximum temperatures during the period considered and D is the number of the days of the same period.
Heat Requirements GDD°C	$G.D.D. = \sum[(T_{i\max} + T_{i\min}) \times 0.5] - T_b$	T_n is the sum of °C for n days. $T_{i\max}$ and $T_{i\min}$ are daily maximum and minimum temperature °C of day "i". T_b is the base temperature.

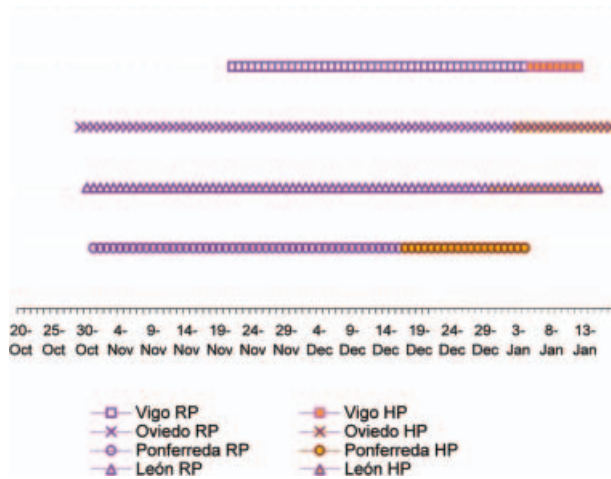


Figure 2. Comparison between the average length of the rest period (RP) and heat period (HP) in the different zones studied from the November 20 to the end of January.

The heat accumulation during the heat period (HP) in order to trigger flowering was expressed as growth degree-days ($GDD^{\circ}C$) and it was obtained by different methods. Firstly, by the summation of daily mean (T), minimum (T_{min}) and maximum (T_{max}) temperatures, then by the sum of the daily temperature amplitude, and also calculated according to the equation proposed by Rickman et al. (1983) (Table II). Heat sums with different base temperatures (4, 4.5, 5, 5.5, 6 and $6.5^{\circ}C$) were used to estimate the most accurate base temperature. The beginning of the period considered was the first day when the mean temperature reached the minimum

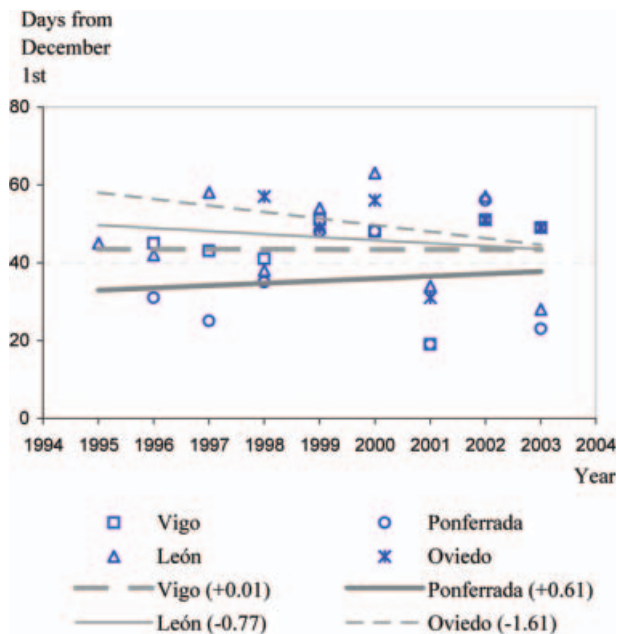


Figure 3. Dates of the start pollen season expressed as the number of days from December first and trend.

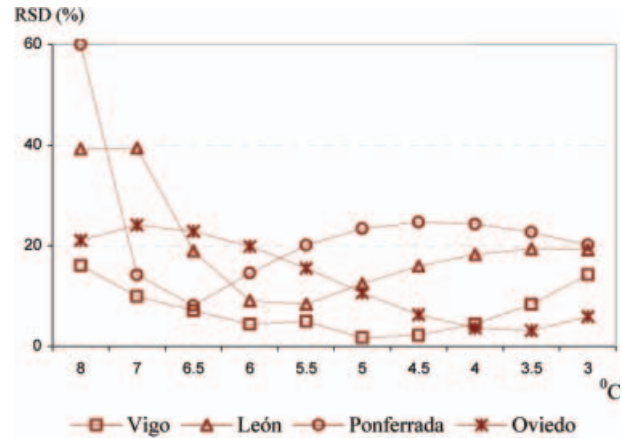


Figure 4. Relative standard deviation coefficients (RSD) considering different threshold temperatures in each locality.

values of the year and temperature curve started to follow a positive trend (Figure 2).

In the statistical approach, standard deviation coefficient (SD) and relative standard deviation (RSD) are calculated both in order to select the most accurate results (lower coefficients) of the amount of the requirement's variation and base temperatures used. Finally Spearman's correlation test was used to find a possible degree of association between all parameters studied.

Results

In north-western Spain, the alder flowers at the start of winter. *Alnus* pollen is one of the first to appear in the annual spectrum, and is recorded in the atmosphere mainly in January and February. During the years under study, there was some variation in pollen-season start dates (Figure 3). The positive slope of the line in Western areas indicate a gradual

Table III. Rest requirements calculated by using the most accurate base temperature as result to select the lower relative standard deviation coefficient.

Period	Location			
	Vigo ($5^{\circ}C$)	Oviedo ($3.5^{\circ}C$)	León ($5.5^{\circ}C$)	Ponferrada ($6.5^{\circ}C$)
1995–96	663	—	977	830
1996–97	661	—	1128	904
1997–98	688	—	1161	823
1998–99	687	720	1072	959
1999–00	668	690	1134	989
2000–01	666	682	1103	814
2001–02	666	726	1201	835
2002–03	682	699	934	814
Mean	673	704	1089	871
S.D.	11.13	19.11	91.26	70.31
RSD coef. %	1.66	2.72	8.38	8.07

Table IV. Heat period (HP) requirements calculated by using base temperatures of 0°C, the most accurate in all locations as result to select the lower relative standard deviation (RSD) coefficient.

Period	Location			
	Vigo	Oviedo	León	Ponferrada
1995–96	55	–	223	170
1996–97	79	–	142	92
1997–98	104	–	63	189
1998–99	85	67	72	336
1999–00	172	119	85	42
2000–01	60	42	57	323
2001–02	182	321	226	130
2002–03	65	63	129	164
Mean	100	122	125	181
S.D.	49.85	114.71	68.68	103.26
RSD coef. %	49.82	93.88	55.17	57.12

delay in the onset of the pollen season, while the slope for Oviedo and León shows that the pollen season has tended to begin progressively earlier in recent years (Figure 3).

The RP requirements for overcoming the dormancy period differed in terms of both quantity and threshold temperature (Figure 4). The most accurate base temperature oscillated within a range of 3.5°C for Oviedo and 6.5°C for Ponferrada. Coefficients of RSD were similar for all study sites, and ranged from 1.66% to 8.38% (Table III). The lowest chilling hour numbers (CH) were found for Vigo with 673 and the highest for León with an average 1 089 CH (Table III). Once RP were fulfilled, HP began until the onset of flowering. Considerable year-on-year differences in temperature accumulation were recorded over the study. The average ranged from 100 to 181 GDD°C (Table IV) with a very high RSD coefficient (>48%). The duration of both RP and HP were different for every city (Figure 2).

In order to obtain a better knowledge of the onset of flowering in different weather conditions and at different altitudes, modified indices of Continentality (CI), Thermicity (TI) and Ombrothermic (OI) were calculated for all study sites and years (Table V). The lowest CI was found for Vigo and the highest for León; the reverse was true of the TI.

Table V. Values of the continentality (CI), thermicity (TI) and ombrothermic (OI) Indices, calculated during the winter period.

Localities	CI	TI	OI
Vigo	20.5	32.6	6.9
Oviedo	22.2	27.8	3.6
Ponferrada	24.2	19.9	5.6
León	24.3	14.6	5.0

Table VI. Coefficients of Spearman's correlation test (*95% and **99.9% of significance).

Indices	R value
Cont. Index & G.D.D. units	0.289
Cont. Index & Days G.D.D.	0.417*
Cont. Index & C.H. units	0.450*
Cont. Index & Days C.H.	0.354
Cont. Index & Threshold C.H.	0.438*
Cont. Index & Onset Flowering	0.004
Term. Index & G.D.D. units	–0.219
Term. Index & Days G.D.D.	–0.578**
Term. Index & C.H. units	–0.910**
Term. Index & Days C.H.	–0.441*
Term. Index & Threshold C.H.	–0.597**
Term. Index & Onset Flowering	–0.115
Ombrot. Index & G.D.D. units	–0.240
Ombrot. Index & Days G.D.D.	–0.255
Ombrot. Index & C.H. units	–0.137
Ombrot. Index & Days C.H.	–0.321
Ombrot. Index & Threshold C.H.	0.173
Ombrot. Index & Onset Flowering	–0.343
Altitude	R value
Altitude & G.D.D. units	0.175
Altitude & Days G.D.D.	0.524**
Altitude & C.H. units	0.943**
Altitude & Days C.H.	0.345
Altitude & Threshold C.H.	0.592**
Altitude & Onset Flowering	0.138
Temperature requirements	R value
G.D.D. units & Days C.H.	–0.401*
G.D.D. units & Threshold C.H.	0.318
G.D.D. units & Onset Flowering	–0.335
Days G.D.D. & Days C.H.	–0.133
Days G.D.D. & Threshold C.H.	0.457
Days G.D.D. & Onset Flowering	–0.169
C.H. units & Threshold C.H.	0.584**
C.H. units & Onset Flowering	0.177
Days C.H. & Threshold C.H.	–0.170
Days C.H. & Onset Flowering	0.592**

The lowest OI was recorded for Oviedo and the highest for Vigo.

The following parameters characterizing rest period (RP) and heat period (HP) were correlated with these indices and with altitude data: CH, length of rest period, threshold temperatures during the rest period, GDD°C, length of heat period, date of onset of flowering and average mean temperature from November to January. Correlation analyses were performed using the results obtained (Table VI), and some parameters were compared in graph form (Figure 5). For Index and Altitude, a significant positive correlation was found for number of C.H. units and the length of the Heat period, with a p-value of 0.05 for the Continentality index (CI) and $p < 0.01$ for Altitude. A negative correlation was observed between these parameters and the Thermicity index (TI).

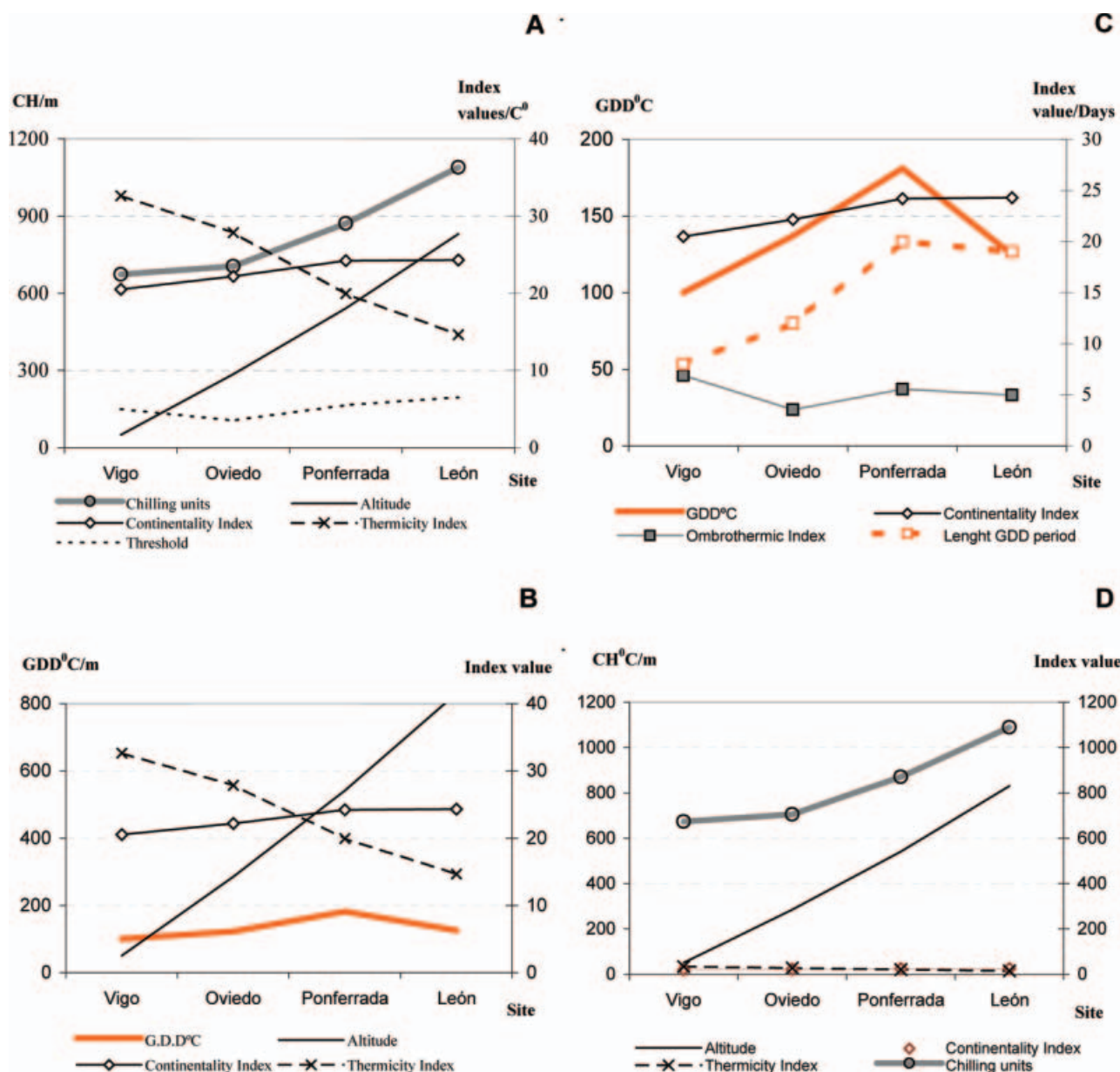


Figure 5. Graphical representation of chilling hours (CH) versus altitude, continentality index (CI), thermicity index (TI) and threshold test period requirements (A & D), and (B, C) Growth Degree-days versus Altitude, CI and TI.

Finally, when parameters characterizing temperature requirements were correlated (Table VI), a significant negative correlation ($p < 0.01$) was found between number of GDD°C units and length of the RP. Positive correlations were observed between number of CH units and threshold temperatures, and between length of the RP and onset of flowering.

Discussion

The *Alnus glutinosa* pollination period started earlier at western sites. Despite a certain amount of variation, the overall trend displayed a positive slope

for western cities and a negative slope for eastern cities, suggesting a gradual trend towards homogeneity in the study area as a whole over recent years. These trends may in part be caused by temperature and rainfall on the days on which mean temperature was above 0°C, since the onset of the pollen season displayed a significant correlation ($p > 0.1$) with the Ombrothermic index (OI). The cities with a high OI (Vigo and Ponferrada) tended to show delayed onset, whilst sites with low OI (León and Oviedo) displayed an increasingly earlier start. A number of studies addressing the effect of possible climate change on the beginning of flowering report that, in recent years, winter pollinated species have tended to delay the onset of the flowering period

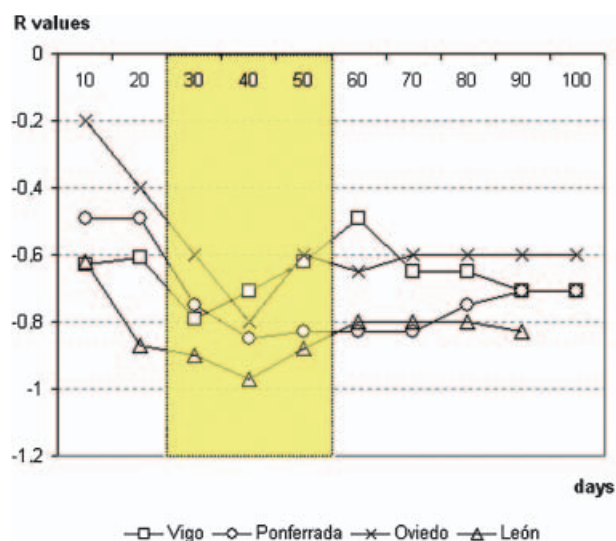


Figure 6. Spearman coefficient correlation between the *Alnus* pollen season start date and mean temperatures over 10 to 100 previous days (in 10-day steps). R value with $p < 0.05$ is indicate by grey shading.

(Frenguelli, 2002) as seen at the western sites studied. Similarly, spring-pollination species (Corden & Millington, 1999; Emberlin et al., 2002) have tended to begin the pollen season progressively earlier (as occurred here at eastern sites).

Most authors agree that temperature is the factor exerting the clearest influence on the onset of winter-flowering, since the timing of pollination is due to major and successive temperature requirements (Spieksma et al., 1989; Frenguelli et al., 1991; Jato et al., 2000). Some researchers report a statistically-significant association between the day on which the pollen season starts and the temperature over the previous days. In order to determine the length of the period prior to flowering during which temperatures most influenced the flowering start date, a study was made of the correlation between the date of the pollen season start and mean temperatures over 10 to 100 days (in 10-day steps) prior to that date (Figure 6). According to Spieksma et al. (1989), 40–50 days with temperatures below 9.1°C are required for *Alnus* to start flowering. Similar results were found here; the most important effect was exerted by temperatures over the previous 40 days in Ponferrada, León and Oviedo. In Vigo, the most important effect was exerted over a shorter period of only 30 days prior to flowering. Trees require physiological protection for shorter periods, since annual mean temperatures are higher due to the proximity of the sea. This period of time has been used in an attempt to predict the onset of flowering by quantifying RP and HP requirements, on the grounds that awareness of pollen start dates is

of great importance to allergy sufferers (Richardson et al., 1974; Faust, 1989; Frenguelli & Bricchi, 1998; Jato et al., 2000).

As reported in previous studies performed at the same sites (Jato et al., 2000; Rodríguez-Rajo et al., 2000, 2004), the low-temperature or RP, defined as the period in which buds remain dormant due to growth-arresting physiological conditions in the bud itself, started on the day when mean temperature fell below the threshold value, generally in the first week of November (with the exception of Vigo where it started in the second half of November) (Figure 2). The forcing-temperature period (HP) started in the first week of January (with the exception of Ponferrada, where it began in mid-December), when minimum values and a change in temperature trend were recorded. To a certain extent, year-on-year differences in flowering start dates within a given study area may be attributed both to higher temperatures during the RP and to lower temperatures during HP (Jato et al., 2000). Consequently, flowering may start at the end of December when the temperature is high, but may then be delayed until the end of January when minimum temperatures below zero are recorded in December and/or early January (Jato et al., 2004).

In order to overcome the RP, the most accurate threshold temperature in the Eurosiberian zone is lower than that found in Mediterranean areas ($3.5\text{--}5^{\circ}\text{C}$ versus $5.5\text{--}6.5^{\circ}\text{C}$, respectively). Correlation analysis showed that in areas with a greater continental character, greater altitude and a lower Thermicity index (TI), higher threshold temperatures were required. This trend is shown in graph form in Figure 5A. In areas closer to the Mesomediterranean level, such as Ourense, a base temperature of 5.5°C was required to overcome dormancy (Rodríguez-Rajo et al., 2004); a similar temperature has been reported for other Eurosiberian regions belonging to the Supratemperate bioclimatic type. Other studies also report a very low coefficient of RSD for this threshold temperature (Frenguelli et al., 1991; Jato et al., 2000); some suggest that temperatures in the range 2.5 to 9.1°C are effective as chilling hours, temperatures around 5°C being the most effective for ending dormancy in many plants (Nooden & Webber, 1978; Jato et al., 2000). The number of chilling hours (CH) required to overcome dormancy was higher at Mediterranean sites (see graph, Figure 5A); this finding was confirmed by the correlation analysis (Table VI) which showed that in areas with greater Continentality and altitude a larger number of CH were required; by contrast, in areas with lower TI a larger number of CH. RP requirements differ according to the climate of the plant habitat: in

colder areas, requirements are greater because the trees need to be protected over a longer period.

Finally the number of GDD°C required to overcome the dormancy period were accumulated over a short period, thus the GDD°C number is low. Temperature accumulation during HP displayed greater variation than temperature accumulation during RP, and correlation between the slope of the temperature during the HP and the length of the HP yielded a Spearman R value of -0.443 ($p < 0.01$), suggesting that the faster the increase in temperatures, the fewer the heat days required. As several authors have reported, the coefficients of standard variation are higher than for the RP (Jato et al., 2000; Rodríguez-Rajo et al., 2004); this may mean that chill requirements are most important for *Alnus* to start flowering. A simple behaviour change, in which temperatures start rising, may prompt *Alnus* to flower faster as temperatures increase. The lowest RSD coefficient was obtained with maximum temperature, as occurred in Santiago (Jato et al., 2000). Studies based on *Alnus* flowering in north-western Spain showed that the RSD coefficient decreased with falling threshold temperatures (Jato et al., 2000), the most accurate threshold temperature always being 0°C (Rodríguez-Rajo et al., 2004). Correlation analysis showed that in areas with more continental character, higher altitude and lower Thermicity index, a longer HP was required.

The relationship between flowering onset and both RP and HP requirements has been reported by a number of authors, who have found that Rest temperatures accelerate the renewal of growth once dormancy is broken; the more Chilling Hours are accumulated, the fewer forcing units are subsequently needed for budburst (Myking & Heide, 1995; Chuine & Cour, 1999; Jato et al., 2000; Rodríguez-Rajo et al., 2004). Similar results were obtained here; the longer the RP, the fewer Heat units required for flowering (Table VI). Several researchers suggest that, for the same taxon, the shorter the period in which Rest is accumulated, the longer the required period of high temperatures (Landsberg, 1974; Richardson et al., 1974; Aron, 1983; Myking, 1997). Correlation between the length of the RP and the date of the onset of flowering shows that, in areas where the tree needs to be protected from adverse meteorological conditions in order to preserve cells from risk of frost during a long period of time, a delay in the phenological state of anthesis has been induced.

Conclusions

The physiological behaviour of winter-spring flowering woody plants is subject to constant variation due

to the action of various bioclimatic parameters. Before flowering, temperature plays a particularly important role in the maturation of reproductive organs and is the primary factor influencing the growth and development of plants and pollen production. The most important effect is exerted by temperatures over the previous 25–55 days, and particularly during the preceding 40 days.

RP and HP requirements differ according to the climate of the plant habitat. In colder areas, these requirements are greater because the trees need protection over a longer period. In the Mediterranean region of north-western Spain, the RP requirement and the threshold temperature are both higher than in Eurosiberian areas, confirming the altitude effect of this character.

The use of bioclimatic indices enables a better understanding of flowering processes, since plants react to a combination of weather parameters, rather than to any individual parameter alone. Ombrothermic, Continentality and Thermicity indices are thus useful tools for characterizing the various bioclimatic areas of north-western Spain.

Acknowledgements

This study was funded by the Xunta de Galicia's Environment Department. The authors would like to thank the University of Vigo for the grant awarded.

References

- Andersen, T. B. (1991). A model to predict the beginning of the pollen season. *Grana*, 30, 269–275.
- Aron, R. (1983). Availability of chilling temperatures in California. *Agric. Meteorol.*, 28, 351–363.
- Ashcroft, G. L., Richardson, E. A. & Schuyler, D. S. (1977). A statistical method of determining Chill Unit and Growing Degree Hour requirements for deciduous fruit trees. *Hortoscience*, 12, 347–348.
- Azcón-Bieito, J. & Talón, M. (2000). *Fundamentos de fisiología vegetal*. Madrid: McGraw-Hill.
- Chuine, I. & Cour, P. (1999). Climatic determinants of budburst seasonality in four temperate-zone tree species. *New Phytol.*, 143, 339–349.
- Corden, J. & Millington, W. (1999). A study of *Quercus* pollen in the Derby area, UK. *Aerobiologia*, 15, 29–37.
- Dominguez, E., Galán, C., Villamandos, F. E. & Infante, F. (1992). Handling and evaluation of the data from the aerobiological sampling. *Monogr. Rea*, 1, 1–18.
- Emberlin, J., Dentandt, M., Gehrig, R., Jaeger, S., Nolard, N. & Rantio-Lehtimäki, A. (2002). Responses in the start of *Betula* (birch) pollen seasons to recent changes in spring temperatures across Europe. *Int. J. Biometeorol.*, 46, 159–170.
- Faust, M. (1989). *Physiology of temperate zone fruit trees*. Chichester, New York, Brisbane, Toronto, Singapore: J. Wiley & Sons.
- Felker, F. C., Robitaille, H. A. & Hess, F. D. (1983). Morphological and ultrastructural development and starch

- accumulation during chilling of sour cherry flower buds. *Am. J. Bot.*, 70, 376–386.
- Fernández-González, D., Comtois, P. & Valencia-Barrera, R. M. (2000). On the use of bioclimatic indices in airborne pollen forecasting. In Am. Meteor. Soc. (Eds), *10th Int. Palynol. Congr. Nanjing 2000*. Abstracts (p. 42). Boston, MA: AMS.
- Fornaciari, M., Orlandi, F. & Romano, B. (2000). Phenological and aeropalynological survey in an olive orchard in Umbria (Central Italy). *Grana*, 39, 246–251.
- Frenguelli, G. (2002). Interactions between climatic changes and allergenic plants. *Monaldi Arch. Chest. Dis.*, 57, 141–143.
- Frenguelli, G. & Bricchi, E. (1998). The use of the pheno-climatic model for forecasting the pollination of some arboreal taxa. *Aerobiologia*, 14, 39–44.
- Frenguelli, G., Spieksma, F. Th. M., Bricchi, E., Romano, B., Mincigrucci, G., Nikkels, A. H., Dankart, W. & Ferranti, F. (1991). The influence of air temperature on the starting dates of the pollen season of *Alnus* and *Populus*. *Grana*, 30, 196–200.
- Galán, C., García-Mozo, H., Cariñanos, P., Alcázar, P. & Domínguez-Vilches, E. (2001). The role of temperature in the onset of the *Olea europaea* L. pollen season in southwestern Spain. *Int. J. Meteorol.*, 45, 8–12.
- García-Mozo, H., Galán, C., Gómez-Casero, M. T. & Domínguez-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*, 39, 194–199.
- Hirst, J. M. (1952). An automatic volumetric spore-trap. *Ann. Appl. Biol.*, 36, 257–265.
- Jato, V., Frenguelli, G., Rodríguez-Rajo, F. J. & Aira, M. J. (2000). Temperature requirements of *Alnus* pollen in Spain and Italy (1994–1998). *Grana*, 39, 240–245.
- Jato, V., Rodríguez-Rajo, F. J., Dacosta, N. & Aira, M. J. (2004). Heat and chill requirements of *Fraxinus* flowering in Galicia (NW Spain). *Grana*, 43, 1–7.
- Kramer, K. (1994). Selecting a model to predict the onset of growth of *Fagus sylvatica*. *J. Appl. Ecol.*, 31, 172–181.
- Laaidi, M. (2001). Forecasting the start of the pollen season of Poaceae: evaluation of some methods based on meteorological factors. *Int. J. Biometeorol.*, 45, 1–7.
- Landsberg, J. J. (1974). Apple fruit bud development and growth; analysis and an empirical model. *Ann. Bot.*, 38, 1013–1023.
- Myking, T. (1997). Dormancy, budburst and impacts of climatic warming in coastal-inland and altitudinal *Betula pendula* and *B. pubescens* ecotypes. In H. Lieth & M. D. Schwartz (Eds), *Phenology in seasonal climates. I* (pp. 51–66). Leiden: Backhuys Publ.
- Myking, T. & Heide, O. M. (1995). Dormancy release and chilling requirements of buds of latitudinal ecotypes of *Betula pendula* and *B. pubescens*. *Tree Physiol.*, 15, 697–704.
- Nooden, L. & Weber, J. (1978). Environmental and hormonal control of dormancy in terminal buds of plants. In M. E. Clutter (Ed.), *Dormancy and development arrest* (pp. 220–260). New York: Acad. Press.
- Richardson, E. A., Schuyler, D. S. & Walker, D. W. (1974). A model for estimating the completion of rest of “Redhaven” and “Elberta” peach trees. *Hortoscience*, 9, 331–332.
- Rickman, R. W., Klepper, B. L. & Peterson, C. M. (1983). Time distributions for describing appearance of specific culms of winter wheat. *Agron. J.*, 75, 551–556.
- Rivas-Martínez, S. (1997). Syntaxonomical synopsis of the potencial natural plants communities of North America I. *Itinera Geobot.*, 12, 5–148.
- Rodríguez-Rajo, F. J., Dopazo, A. & Jato, V. (2004). Environmental factors affecting the start of the pollen season and concentrations of airborne *Alnus* pollen in two localities of Galicia (NW Spain). *Ann. Agric. Environ. Med.*, 11, 35–44.
- Rodríguez-Rajo, F. J., Méndez, J. & Jato, V. (2000). Influencia de la temperatura en la floración de *Quercus* en el sur de Galicia (Ourense y Vigo, 1994–98). *Acta Bot. Malac.*, 25, 153–163.
- Spieksma, F. Th. M., Frenguelli, G., Nikkels, A. H., Mincigrucci, G., Smithuis, L., Bricchi, E., Dankart, W. & Romano, B. (1989). Comparative study of airborne pollen concentrations in central Italy and The Netherlands (1982–1985). *Grana*, 28, 25–36.
- Valencia-Barrera, R., Comtois, P. & Fernández-González, D. (2002). Bioclimatic indices as a tool in pollen forecasting. *Int. J. Biometeorol.*, 46, 171–175.