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USE OF PHENOLOGICAL AND POLLEN-PRODUCTION DATA FOR INTERPRETING ATMOSPHERIC BIRCH POLLEN CURVES

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Abstract: Although aerobiological data are frequently used as a flowering sign in phenological research, airborne pollen counts are influenced by a number of factors affecting pollen curves. A study was made about the reproductive biology of birch and environmental factors influencing its pollen release and transport, in order to achieve a reliable interpretation of *Betula* pollen curves. Aerobiological data were recorded in 2002 and 2003 at two sites in NW Spain and phenological observations were carried out on 20 trees from four *Betula* populations (three *Betula alba* L. and one *B. pendula* Roth.). Pollen production was calculated for six *Betula alba* trees. Chilling and heat requirements for triggering development were calculated. Due to differences in the geographical location, budbreak and flowering started first in *Betula pendula*. The flowering period lasted from 8-13 days. Reduced pollen output per anther and catkin in individual trees in 2003 prompted a marked decline in overall pollen production. Major differences observed in birch pollen curves were attributed to the influence both of weather conditions and pollen transport from areas where the flowering occurs at a different time. Heat requirements calculated using phenological and aerobiological data were similar when the peak pollen-count date was used.

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INTRODUCTION

Over the last few years, prompted by the growing importance of global warming, a certain amount of phenological research has been carried out using aerobiological data to determine the timing of flowering [10, 15, 16, 19, 21]. Using long aerobiological data series, it is possible to evaluate delays or advances in the onset of pollination in the major wind-pollinated species. However, in order to achieve a full understanding of the pollen curve and thus ensure the correct application of pollen data, it is essential to take into account the phenology and reproductive biology of the plants, particularly those in the vicinity of the spore trap.

The pattern displayed by pollen curves does not always match that of the flowering phenophase, and a lack of correlation may sometimes be observed between peak flowering date and peak pollen-count date [35]. Knowledge of the flowering phenophase of the major wind-pollinated species thus enables testing of the relationship between reproductive phenology and airborne pollen curves. Moreover, pollen may be transported over long distances before deposition, as is the case with birch pollen [24, 42, 46]; deposition of pollen arising at some distance from the trap may influence the onset of the pollen season as determined by aerobiological sampling.

Aerobiological research must therefore taken into account not only phenological data but also other environmental variables, including meteorological and topographical factors, ability of the pollen grain to be transported over long distances, pollen production, and distance of the

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sampler from the source, and their contribution to airborne pollen counts in space and time.

The genus *Betula* (birch) only grows in the northern hemisphere; it is found across most of Europe and is particularly common in northern and central regions. *Betula alba* L. and *Betula pendula* Roth. [37] are the two birch species found in Spain. Some authors consider both species as members of the same taxonomic section (*Betula alba*) [40]. Birch is represented in Galicia (Northwestern Spain) by *Betula alba* L. [37]. As the dominant tree species, it forms altimontane oro-Cantabrian acidophilic forests, with a clearly Euro-Siberian distribution. It is found at altitudes of over 1,150 m, and is the last tree formation of the altitudinal sequence, with montane thermo-climates and hyper-humid ombro-climates [26]. Its geographical boundary, though fairly controversial, is located in Ancares and Caurel mountains of eastern Galicia [7]. Other birch forests are found in the same area, but on siliceous soils and with a greater Mediterranean influence, in the Galician-Portuguese altimontane layer and the Ourense-Sanabriense and supramediterranean layer. In Galicia's mountains and foothills, non-climatic birches are found in place of montane oak groves, growing on acidic soils at heights of between 600-1,100 m. Birch may also form part of riparian forests, along with *Alnus glutinosa*, *Salix atrocinerea*, *Frangula alnus* and *Fraxinus angustifolia*. *Betula pendula* is grown as an ornamental in some cities in the area.

At flowering, the release of a large number of *Betula* pollen grains into the atmosphere is of considerable allergenic significance. The number of pollen grains per inflorescence was estimated by Erdtman [17] as 6×10^6. *Betula* pollen is therefore a major aeroallergen, common in the air of many European cities; a great deal of research has sought to ascertain airborne pollen seasons for this pollen type [5, 6, 15, 23, 27, 28, 33, 34, 40, 41, 44]. The highest *Betula* pollen counts in Spain are recorded in the northwest of the country, where daily mean pollen concentrations often exceed 100 pollen grains/m^3 and annual values are greater than 1,000 grains [1, 28].

Surveys of *Betula* phenology have been carried out in various areas in order to determine the heat and chilling requirements needed to trigger bud development, and to assess how global climate change might influence phenology in this species. This is particularly important for birch, often found at the altitudinal or latitudinal tree line, where the effect of climate warming on phenophases may be more severe [16, 32, 38, 43].

Previous research on *Betula* phenology in Galicia (northwestern Spain) has addressed differences in phenological behaviour due to a number of environmental factors [29]. Considerable difference have been reported in the onset of flowering populations located at different altitudes and in different geographical areas, and the synchronisation of *Betula* phenology and airborne pollen counts has been evaluated. This follow-up study of *Betula* populations located near two monitoring stations in Ourense province sought to compare aerobiological and phenological data and determine the influence of reproductive biology on pollen curves.

MATERIAL AND METHODS

The study was carried in the city of Ourense, situated in a depression 139 m above sea level in northwestern Spain (42º20'N; 7º52'W) and in Pobra de Trives, situated 746 m above sea level (42º20'N; 7º15'W) in the northeast of Ourense province. Ourense city has an oceanic climate with strong Mediterranean influence. Records for the last 30 years show a mean annual temperature of 14.2ºC, maximum average temperature of 20.2ºC and minimum average temperature of 8.2ºC. Annual rainfall is 794 mm, with very irregular distribution over the year; average summer rainfall is only 21.6 mm. The mean annual temperature in Pobra de Trives is 8.9ºC, the maximum average temperature 14.8ºC and the minimum average temperature 3.0ºC. Annual rainfall is 874 mm, also irregularly distributed over the year.

Aerobiologycal survey. Pollen monitoring was carried out in 2002 and 2003 by means of a 7-day LANZONI VPPS 2000 continuous volumetric pollen trap, located on the roof of the Sciences Faculty in Ourense city and in the Culture House in Pobra de Trives (approximately 20 m above ground level). The methodology recommended by Spanish Aerobiological Network – REA – was used [14]. The onset of pollen season was defined according to three different criterion: When 2.5% [2] or 5% [39] of the annual total pollen was reached, and when the prime pollen grains were registered on a continual basis and no more than two days without pollen were detected [30]. Finally, the day on which maximum daily mean pollen concentration was recorded (peak day) was considered to be the population's mean flowering date.

Phenological survey. To characterise floral phenophase, a sampling method was applied from the 1 March to end of flowering (at least once a week) in 2002 and 2003. Four *Betula* populations located at different altitudes were chosen. The population located nearest of the spore trap in Ourense (112 m above sea level) belongs to *Betula pendula* and Xestosa (978 m a.s.l.), Domecelle (860 m a.s.l.) and Mogainza (1,045 m a.s.l.) populations belong to *B. alba* and are located near of the pollen sampling in Pobra de Trives. In every population, a sample of 20 individual trees chosen randomly was used, and in each tree the date of bud break, leaf unfolding and start and end of flowering were noted. The same trees were observed every year.

Bud break date was considered as the 1st day the first leaf-stalk of the plant or of the specific branch observed was detected [47]. The leaf unfolding date was noted when at two or three places in the tree a normal, unwrinkled, leaf surface was visible, but full size had not yet been attained

[4]. The onset of flowering was considered as the 1st day a male catkin distributed its pollen [47]. End of flowering was considered when all the catkins were dried.

Pollen production. Pollen production was determined for six birch trees from the Xestosa population (*Betula alba*), using methods developed by Cruden [8] and Hidalgo [25] to calculate pollen production by anther, flower, catkin, tree and by square meter. *Betula* catkins are formed in the summer, prior to ripening. After dormancy, many catkins fail to start the development process; others, having commenced growth, fail to reach full maturity, and thus to spread pollen. For that reason, both real and potential pollen production were calculated. For potential pollen production, all catkins grown during the previous summer were taken into account, whereas only unaltered catkins (i.e. those unaltered over at least half their length) were counted for calculating real production.

Determining chill and heat requirement. We used the model proposed by Aron [3] in order to obtain the chill accumulation expressed as chilling hours:

$CH = 801 + 0.2523B + 7.574 \times 10^{-4} B^2 - 6.51 \times 10^{-10} B^4 - 11.44\, t_{min} - 3.32\, t_{max}$.

Where $B = 24D\,[(7.2\text{-}t_{min})/(t_{max}\text{-}t_{min})]$, D is the number of days in the period, t_{max} and t_{min} are the mean of the maximum and minimum temperatures of the period respectively.

We used this model selecting the period from the day when the mean temperature decreased below the threshold temperature to the day (at the end of December or in the first half of January) when the minimum was recorded and a change in the temperature trend was detected. Only the days on which meteorological conditions did not enable any physiological activity in the tree were taken into account [30]. This happens when the daily maximum temperature is equal to or less than the threshold temperature [36]. Only temperatures below 7ºC were considered because previous studies showed this to be the most effective temperature for chilling [12].

Two methods for determining the heat requirement were tested, taking into account the period from the day after the chill period to the start of the pollen season (by using aerobiological data), or the start of every phenophase (by using phenological data observed).

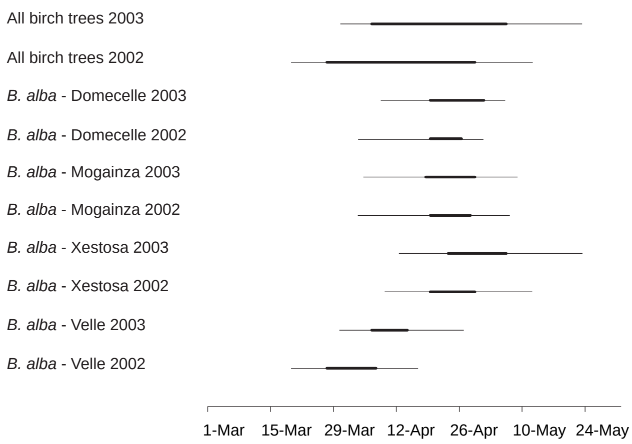

Figure 1. Total (——) and average (**——**) length of *Betula* flowering in studied populations.

1) The heat requirement (HR) was calculated as a function of the sum of the daily maximum temperatures [18]: $HR = \sum t_{max}$.

2) We also calculated the heat requirement by taking into account the days, after chilling, when the meteorological conditions enable plant physiological activity, either totally ($t_{min}>th$) or partially ($t_{max}>th>t_{min}$) (referred as vegetative activity – VA – by Jato [30]. In this case, we considered HR as a function of the sum of the difference between the daily maximum temperature and the threshold temperatures: $HR = \sum(t_{max}\text{-}th)$.

If t_{max} is less than or equal to the threshold temperature ($t_{max}<th$), the values are set to 0.

Different threshold temperatures from 0.5-8ºC were tested in increments of 0.5ºC, for heat requirement.

RESULTS

Phenological findings. *Betula pendula* was the first to commence each phenophase. Budbreak took place in early April in *B. alba*, and 28 or 18 days earlier (in 2002 and 2003, respectively) in *B. pendula* (Tab. 1).

Flowering commenced on average 12-18 days after budbreak, and was not always preceded by leaf unfolding. Indeed, for both years and all populations with the exception of Mogainza, leaf unfolding took place either at the same

Table 1. Start average dates of observed phenophases and flowering length.

	Betula pendula		*Betula alba*					
	Velle		Xestosa		Mogainza		Domecelle	
	2002	2003	2002	2003	2002	2003	2002	2003
Bud break	10-Mar	21-Mar	7-Apr	8-Apr	1-Apr	5-Apr	3-Apr	6-Apr
Leaf unfolding	23-Mar	29-Mar	17-Apr	18-Apr	14-Apr	14-Apr	15-Apr	13-Apr
Flowering onset	27-Mar	6-Apr	19-Apr	23-Apr	19-Apr	18-Apr	18-Apr	19-Apr
End of flowering	7-Apr	14-Apr	29-Apr	6-May	28-Apr	29-Apr	26-Apr	1-May
Length of flowering	11 days	8 days	10 days	13 days	9 days	11 days	8 days	12 days

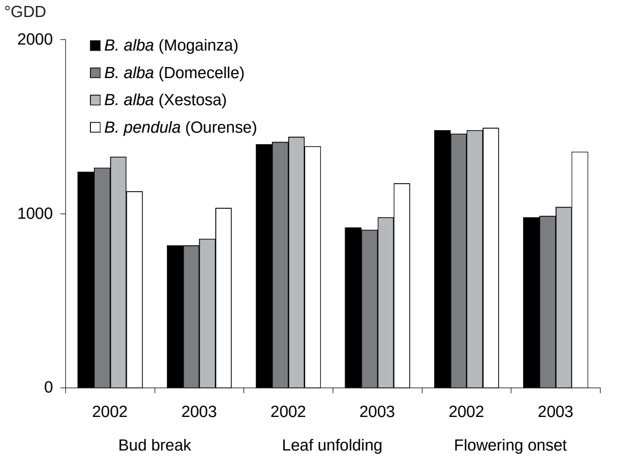

Figure 2. GDDºC accumulated from the end of chilling period to the onset of observed phenophases.

Table 2. Start and ending dates and chilling accumulated in Ourense and Pobra de Trives in 2002 and 2003.

		Start date	End date	Acumulated chilling
Ourense	2001-02	02-Nov	25- Dec	715
	2002-03	05-Dec	15-Jan	656
P. Trives	2001-02	04-Nov	25- Dec	935
	2002-03	13-Nov	11-Jan	933

time as, or even later than, flowering. This was particularly common in 2002.

Given the mean dates for onset and ending, flowering lasted between 8-13 days, depending on the population and the year (Tab. 1 and Fig. 1). The three *B. alba* populations displayed a longer flowering period in 2003, while the *B. pendula* flowering period was shorter in that year.

The minimum and maximum dates for onset and end of flowering mark the total duration of the period when birches were releasing pollen into the atmosphere. For all study populations as a whole, the pollen-release period lasted from mid-March to late May in Ourense (on average from late March–late April in 2002, and from early April–early May in 2003) (Fig. 1).

A slight delay was detected in every phenophase in 2003, the delay being more marked in the *B. pendula* population.

The standard deviation coefficient was less than 10% in each population and year, with the exception of budbreak in 2002 (over 10% in every population), thus showing fairly homogeneous behaviour with regard to the phenological dates observed.

Chilling and heat requirements. Taking 7ºC as the threshold temperature, the chilling requirement was accumulated in Ourense from early November–late December in 2002, and from early December–mid January in 2003. Chilling requirements were met on similar dates in Pobra de Trives in 2002; however, chilling accumulation start was earlier in 2003. Accumulated chilling was greater in Pobra de Trives (935 and 933 chilling hours, respectively, in 2002 and 2003 versus 715 and 656 units, respectively, in Ourense) (Tab. 2).

From the end of chilling, heat requirements were calculated for every phenophase and population; *B. alba* and *B. pendula* displayed similar requirements in 2002 (differences were greater in the first phenophases after dormancy and smaller at flowering). In 2003, however, higher heat accumulation was required by *B. pendula* in every phenophase (Fig. 2), with 1,492 and 1,354 GDDºC (calculated according to Galán *et al.* 2001 method) accumulated prior to the onset of flowering in both years, compared with a value between 978 and 1,479 GDDºC, depending on the year and population, for *B. alba* (Tab. 3). Heat requirements were lower in 2003 for all populations and phenophases, the year-on-year difference being more marked for *B. alba* populations.

Heat requirements were also calculated taking into account the onset of the airborne pollen season, as delineated using various different criteria and also taking into account the dates on which maximum pollen counts were recorded, known as peak dates (Tab. 4). Regardless of the method used, values were lower in 2003, and heat requirements in Pobra de Trives were lower than in Ourense. The results obtained using the method developed by Galán [18], based on the sum of maximum temperatures applied to the peak date, agreed most closely with those obtained using phenological data for the onset of flowering (Tab. 3 and 4).

Pollen production. Pollen production by anther ranged between 11,448 and 16,560 pollen grains in 2002 and between 6,316 and 13,742 pollen grains in 2003. A marked decline in pollen production was observed in 2003 compared to 2002, especially due to the reduction in the number of catkins/tree (average 11,086 and 9,982 well-developed catkins, respectively, in 2002 and 2003) and also in the amount of pollen/anther (average 13,696 and 8,990, respectively, in 2002 and 2003). Pollen production per catkin averaged 8,196,374 in 2002 and 4,791,070 in 2003. Mean pollen production per tree, both much potential and real, and also by square meter, was almost twice as high in 2002 (Fig. 3). The proportion of normally-developed catkins as a percentage of total catkins grown in the previous summer was similar in both years (average 74% in 2002 and 76.4% in 2003), and ranged from 62% and 90%, depending on the tree and the year.

Aerobiological results. *Betula* pollen was recorded in the atmosphere of Ourense and Pobra de Trives from mid-March–late May. In both places, total annual *Betula* pollen counts were higher in 2002 (2,848 vs. 1,107 pollen grains, respectively, in 2002 and 2003 in Ourense, and 3,952 vs. 1,034 pollen grains in Pobra de Trives). April recorded the highest pollen counts at both sites and in both years (58.2%

Table 3. Heat requirements calculated by means Galán *et al.* [18] and Jato *et al.* [30] methods for every phenophase and population.

Heat accumulation method	Galán	Jato															
		0.5	1	1.5	2	2.5	3	3.5	4	4.5	5	5.5	6	6.5	7	7.5	8
2002																	
B. pendula																	
Bud break	1128	1090	1052	1014	976	938	900	862	824	786	748	710	672	634	596	558	520
Leaf unfolding	1387	1343	1298	1254	1209	1165	1120	1076	1031	987	942	898	853	809	764	720	675
Flowering onset	**1492**	1446	1399	1353	1306	1260	1213	1167	1120	1074	1027	981	934	888	841	795	748
End of flowering	1700	1648	1596	1544	1492	1440	1388	1336	1284	1232	1180	1128	1076	1024	972	920	868
B. alba (Mogainza)																	
Bud break	1239	1190	1141	1092	1043	994	945	896	847	798	749	700	651	602	553	504	455
Leaf unfolding	1398	1343	1287	1232	1176	1121	1065	1010	954	899	843	788	732	677	621	566	510
Flowering onset	**1479**	1421	1363	1305	1247	1189	1131	1073	1015	957	899	841	783	725	667	609	551
End of flowering	1703	1641	1578	1516	1453	1391	1328	1266	1203	1141	1078	1016	953	891	828	766	703
B. alba (Domecelle)																	
Bud break	1264	1214	1164	1114	1064	1014	964	914	864	814	764	714	664	614	564	514	464
Leaf unfolding	1412	1356	1300	1244	1188	1132	1076	1020	964	908	852	796	740	684	628	572	516
Flowering onset	**1459**	1402	1344	1287	1229	1172	1114	1057	999	942	884	827	769	712	654	597	539
End of flowering	1663	1602	1540	1479	1417	1356	1294	1233	1171	1110	1048	987	925	864	802	741	679
B. alba (Xestosa)																	
Bud break	1327	1275	1222	1170	1117	1065	1012	960	907	855	802	750	697	645	592	540	487
Leaf unfolding	1441	1384	1327	1270	1213	1156	1099	1042	985	928	871	814	757	700	643	586	529
Flowering onset	**1479**	1421	1363	1305	1247	1189	1131	1073	1015	957	899	841	783	725	667	609	551
End of flowering	1722	1659	1596	1533	1470	1407	1344	1281	1218	1155	1092	1029	966	903	840	777	714
2003																	
B. pendula																	
Bud break	1033	1000	967	934	901	868	835	802	769	736	703	670	637	604	571	538	505
Leaf unfolding	1174	1137	1100	1063	1026	989	952	915	878	841	804	767	730	693	656	619	582
Flowering onset	**1354**	1313	1272	1231	1190	1149	1108	1067	1026	985	944	903	862	821	780	739	698
End of flowering	1515	1470	1425	1380	1335	1290	1245	1200	1155	1110	1065	1020	975	930	885	840	795
B. alba (Mogainza)																	
Bud break	817	774	731	688	645	602	559	516	473	430	387	344	301	258	215	172	129
Leaf unfolding	919	872	825	778	731	684	637	590	543	496	449	402	355	308	261	214	167
Flowering onset	**978**	929	880	831	782	733	684	635	586	537	488	439	390	341	292	243	194
End of flowering	1117	1063	1008	954	899	845	790	736	681	627	572	518	463	409	354	300	245
B. alba (Domecelle)																	
Bud break	817	774	731	688	645	602	559	516	473	430	387	344	301	258	215	172	129
Leaf unfolding	908	862	815	769	722	676	629	583	536	490	443	397	350	304	257	211	164
Flowering onset	**987**	938	888	839	789	740	690	641	591	542	492	443	393	344	294	245	195
End of flowering	1145	1090	1034	979	923	868	812	757	701	646	590	535	479	424	368	313	257
B. alba (Xestosa)																	
Bud break	855	811	767	723	679	635	591	547	503	459	415	371	327	283	239	195	151
Leaf unfolding	978	929	880	831	782	733	684	635	586	537	488	439	390	341	292	243	194
Flowering onset	**1038**	987	935	884	832	781	729	678	626	575	523	472	420	369	317	266	214
End of flowering	1214	1156	1098	1040	982	924	866	808	750	692	634	576	518	460	402	344	286

and 78.8% of total annual counts in Ourense in 2002 and 2003, respectively, and 80% and 92% in P. Trives). *Betula* pollen accounted for 9.4% and 6.5% of total annual pollen in 2002 and 2003, respectively, in Ourense, and for 12.1% and 5% in Pobra de Trives. Counts of over 100 pollen grains/m^3 were recorded over 13 and 3 days in Ourense, and over 12 and 2 days in Pobra de Trives, in 2002 and 2003, respectively.

Table 4. Heat requirement calculated by means Galán *et al.* [18] and Jato *et al.* [30] methods in Ourense and Pobra de Trives with aerobiological data.

Heat accumulation method		Galán	Jato															
Threshold			0,5	1	1,5	2	2,5	3	3,5	4	4,5	5	5,5	6	6,5	7	7,5	8
Atmospheric Pollen Season according Jato *et al.* [30]																		
Ourense	2001-02	1327	1284	1240	1197	1153	1110	1066	1023	979	936	892	849	805	762	718	675	631
	2002-03	858	829	800	771	742	713	684	655	626	597	568	539	510	481	452	423	394
P. Trives	2001-02	947	905	863	821	779	737	695	653	611	569	527	485	443	401	359	317	275
	2002-03	643	607	570	534	497	461	424	388	351	315	278	242	205	168	132	96	59
Atmospheric Pollen Season according Torben [45]																		
Ourense	2001-02	1416	1371	1326	1281	1236	1191	1146	1101	1056	1011	966	921	876	831	786	741	696
	2002-03	1010	978	945	913	880	848	815	783	750	718	685	653	620	588	555	523	490
P. Trives	2001-02	1108	1063	1017	972	926	881	835	790	744	699	653	608	562	517	471	426	380
	2002-03	722	682	642	602	562	522	482	442	402	362	322	282	242	202	162	122	82
Atmospheric Pollen Season according Nilsson & Pearson [39]																		
Ourense	2001-02	1441	1396	1350	1305	1259	1214	1168	1123	1077	1032	986	941	895	850	804	759	713
	2002-03	1072	1038	1004	970	936	902	868	834	800	766	732	698	664	630	596	562	528
P. Trives	2001-02	1130	1084	1038	992	946	900	854	808	762	716	670	624	578	532	486	440	394
	2002-03	739	699	658	618	577	537	496	456	415	375	334	294	253	212	172	131	91
Peak date																		
Ourense	2001-02	1441	1396	1350	1305	1259	1214	1168	1123	1077	1032	986	941	895	850	804	759	713
	2002-03	1382	1341	1299	1258	1216	1175	1133	1092	1050	1009	967	926	884	843	801	760	718
P. Trives	2001-02	1557	1498	1438	1379	1319	1260	1200	1141	1081	1022	962	903	843	784	724	665	605
	2002-03	855	811	767	723	679	635	591	547	503	459	415	371	327	283	239	195	151

The pollen curve for 2002 shows two periods with high counts at both sites, separated in each case by an interval of around 15 days. The first period took place from the end of March–early April. A second period was observed in mid-April at both sites. The intensity of the two peaks registered was similar in Ourense (265 and 251 pollen grains/m^3), but in Trives there was a considerable difference between them (178 vs. 501 pollen grains/m^3). By contrast, a single period with high counts was observed in 2003 (first fortnight in April) in both places (Fig. 4). Maximum values (220 and 243 pollen grains/m^3) were recorded on similar dates (7 and 8 April in Ourense and Pobra de Trives, respectively), followed thereafter by a drop in pollen counts.

The airborne pollen season, calculated using criteria suggested by Jato [30] and Nilsson & Persson [39], was shorter in 2003 in both places, and showed a slightly earlier onset in 2003 in Ourense; by contrast, onset was delayed in 2003 in P. Trives (Tab. 5).

DISCUSSION

Despite altitudinal and meteorological differences between Ourense and P. Trives, the airborne pollen season started at almost the same time (especially in 2002). There were year-on-year differences in weather conditions, with higher rainfall and more rainy days in 2003 in March and

Table 5. Atmospheric pollen season calculated according different criteria and years.

Criteria	Jato *et al.* (2002) [30]				Nilsson & Pearson (1981) [39]				Torben (1991) [45]			
	Ourense		Pobra de Trives		Ourense		Pobra de Trives		Ourense		Pobra de Trives	
Year	2002	2003	2002	2003	2002	2003	2002	2003	2002	2003	2002	2003
Start date	21-Mar	13-Mar	18-Mar	25-Mar	25-Mar	23-Mar	26-Mar	01-Apr	24-Mar	20-Mar	25-Mar	31-Mar
End date	21-May	24-Apr	25-May	18- May	26-Apr	17-Apr	27-Apr	27-Apr	28-Apr	23-Apr	30-Apr	09- May
Length (days)	62	42	69	55	33	26	33	27	36	35	37	40
Max (grains/m^3)	265	220	501	243	265	220	501	243	265	220	501	243
Date of max	25-Mar	07-Apr	22-Apr	08-Apr	25-Mar	07-Apr	22-Apr	08-Apr	25-Mar	07-Apr	22-Apr	08-Apr
Total pollen (%)	2842 (99.8%)	1083 (97.8%)	3936 (99.6%)	1016 (98.3%)	2597 (91.2%)	1053 (95.1%)	3662 (93%)	942 (91.1%)	2724 (95.6%)	1080 (97.6%)	3829 (96.9%)	994 (96.1%)

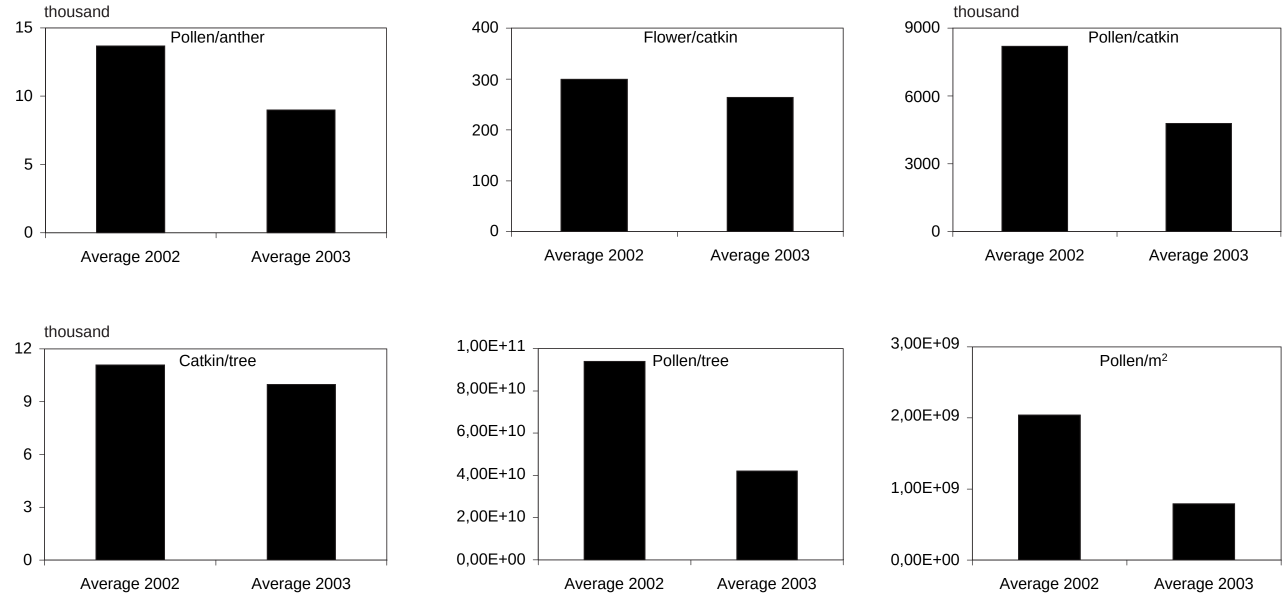

Figure 3. Pollen production average in 2002 and 2003.

April in both cities (Tab. 6); this may have exerted the washing-out effect on airborne pollen frequently noted in aerobiological studies. Rainy days were particularly frequent at the start of the pollen season (second fortnight in March) and after 10 April. Weather conditions during the flowering period in 2002 were more favourable for the release and dispersal of pollen grains. Warm, sunny days with no rain favour high pollen counts; rainfall therefore presumably had less effect on 2002 pollen curves, which thus better reflect the phenological behaviour of the birch populations. The two pollen peaks observed in 2002 coincided with the flowering period of birches located near the spore trap and at a greater distance. In Ourense, the first peak included the maximum peak value, and coincided with the flowering of the birches around the city (Fig. 4), while the second was recorded at a time when the *Betula* population in the vicinity of the monitoring station had finished its flowering period. The reverse was true in P. Trives, where the second peak – which included the maximum peak value – coincided with the flowering of most birches around the spore trap. A first peak was noted, slightly later than that observed in Ourense; the start of the airborne pollen season was detected prior to the onset of birch flowering on the outskirts of P. Trives.

Table 6. Precipitation and rainy days number in March and April in both localities.

		March		April	
		2002	2003	2002	2003
Ourense	Precipitation (mm)	41	113	25	89
	Rainy days number	11	12	10	19
P. Trives	Precipitation (mm)	55	78	29	108
	Rainy days number	11	12	7	14

The total annual *Betula* pollen count was lower in 2003. Airborne pollen counts are influenced by a number of factors affecting aerobiological processes: pollen production, release from the anthers and transport. Weather conditions are the factors most often analysed in order to chart their correlations with pollen counts. Rainy days and falling temperatures slow down the tissue dehydration required to prompt anther dehiscence; and conditions conducive to anthesis are not met, and the whole process can be delayed or reduced [9]. The marked differences in weather conditions observed in 2003, particularly with regard to the number of rainy days in March and April, might account for the lower pollen counts recorded (Tab. 6, Fig. 4). Moreover, the high wind speeds registered in mid-April might have caused the shedding of a large number of the catkins observed a few days prior to flowering.

Potential pollen production per anther, number of anthers and flowers, and plant size determine the amount of pollen dispersed during the flowering period. Knowledge of a species' pollen production is essential in order to determine the maximum amount of pollen that a population can spread, thus improving pollen forecasting. However, the flowering intensity of many tree species may vary considerably from year to year; in birch species this variation is attributed to weather-related factors and to the system of resource allocation among years [40]. Fluctuations in pollen production may account for the biannual or triannual cycles widely reported for airborne *Betula* pollen [13, 23, 34]. Here, there was a sharp fall in catkins/tree and pollen/anther in 2003, which might help to account for the marked decline in pollen counts for that year; however, this is unlikely to be the sole factor influencing airborne pollen counts.

In P. Trives, the airborne pollen season started prior to the onset of flowering. *Betula* pollen morphology favours

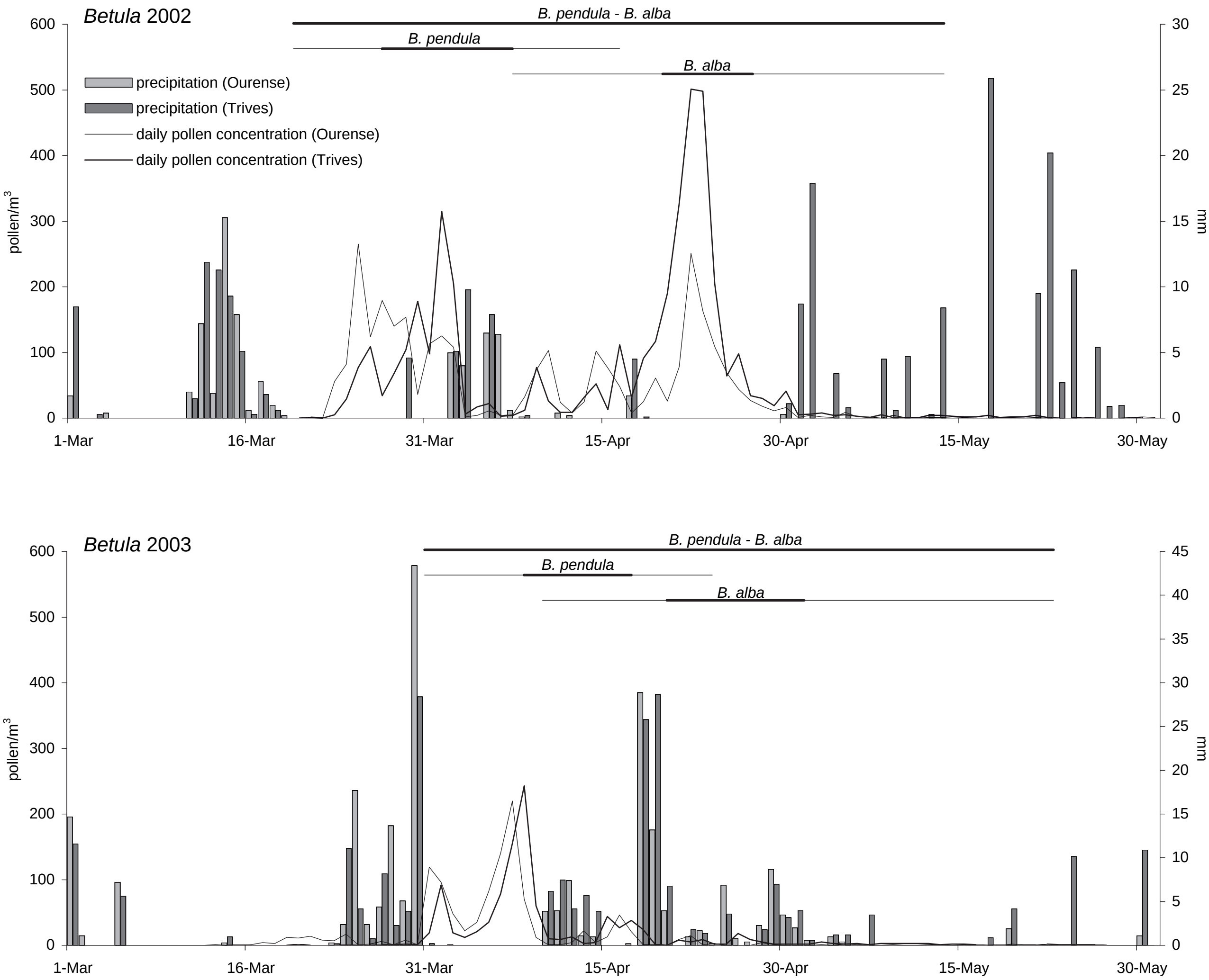

Figure 4. Daily pollen concentrations and precipitation in Ourense and P. Trives. Line: flowering periods of *Betula* in 2002 and 2003 (—— average duration and —— maximum length).

its transport over medium or long distances, and it was detected in the air several weeks before the onset of the flowering period [24, 46]. Topographical characteristics must also be taken into account when considering pollen transport; a sampling station located at a high altitude can detect pollen transported from lower areas [22]. The topography of the area around P. Trives is characterised by high mountains (up to 1,800 m a.s.l.) with a steep slope down to the Sil River (100 m a.s.l.). The marked variations in altitude give rise to considerable climatic diversity over relatively short distances. Thus, *Betula* pollen from populations located at lower altitudes, even at some distance from the spore trap, may be transported into the sampling area, prompting the start of the airborne pollen season prior to the onset of flowering. Moreover, the longer airborne pollen season as measured using the delimitation criterion suggested by Jato [30] might be attributable to pollen coming from birch trees located at higher altitudes.

Like other temperate-zone tree species, *Betula* requires a period of chilling temperatures to break dormancy, followed by a period of forcing temperatures to trigger the onset of growth. In previous studies, a threshold temperature of 7ºC for chilling yielded the best results for birch [12]. Here, accumulation of chilling was greater in P. Trives (860 m a.s.l.) than in Ourense (139 m a.s.l.). Differences in chilling accumulation were observed between years in Ourense (lower in 2003), but not in P. Trives (Tab. 2). The average GDDs required to induce budbreak was similar for both *Betula* species studied and for the various *B. alba* populations (1,081 for *B. pendula* and 1,028, 1,040 and 1,091 respectively for Mogainza, Domecelle and Xestosa *B. alba* populations). However, the main difference in behaviour between the two species was the lower value for accumulated GDD during the period from budbreak to leaf unfolding and, especially, from leaf unfolding to the onset of flowering. The number of days between budbreak and onset of flowering was lower in *B. alba* (12-15 days, vs. 16-18 days in *B. pendula*). A marked decline in accumulated heat was observed in 2003 in *B. alba* populations, but not in *B. pendula*; this might be linked to lower

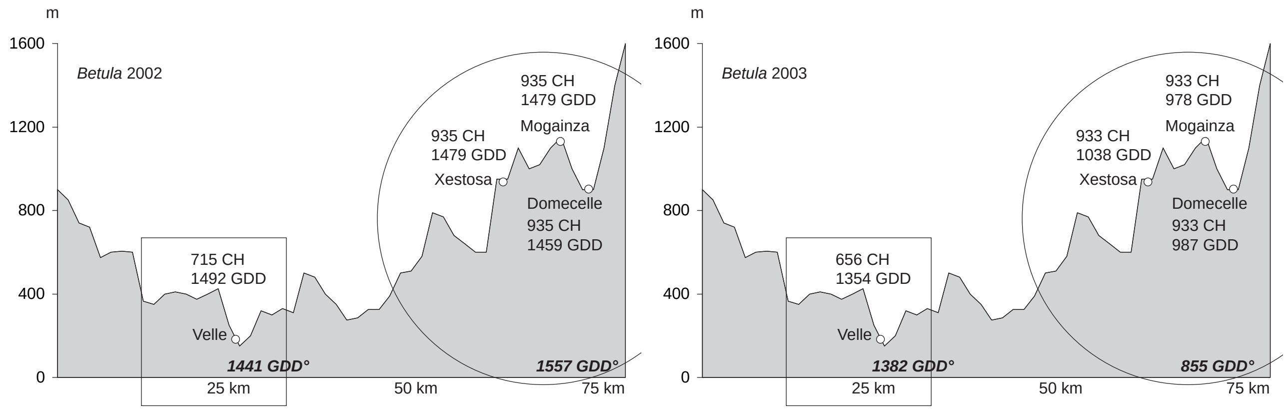

Figure 5. CH and GDDºC acumulated by *Betula* in Ourense and Pobra de Trives surroundings. CH calculated according Jato *et al.* [30] method and 7ºC as threshold temperature; GDDº by Galán *et al.* [18] method. In bold letters – results obtained taking into account aerobiological data.

chilling accumulation in Ourense. Long chilling treatment in P. Trives enhanced growth and lowered the heat requirement, a finding previously reported by various authors [2, 11, 20, 31, 38].

In both years, the heat requirement calculated on the basis of the mean date of flowering onset in the *Betula pendula* population agreed very closely with that calculated on the base of the date on which the maximum daily mean pollen count was recorded in Ourense (Fig. 5). As indicated earlier, the first peak detected in the *Betula* pollen curve in Ourense coincided with the flowering period of populations around the spore trap. Measurements of airborne *Betula* pollen counts indicated the timing of flowering of populations around the city, and the peak date could be assumed to be the mean date of anthesis for the population around the sampling station, as suggested by Chuine [10]. However, in P. Trives the GDDs obtained in 2002 using the mean start-date for flowering in populations around the city were slightly lower than those obtained using the peak date; the reverse was true in 2003. The peak date in 2003 did not coincide with the date of onset of flowering of birch trees around the spore trap. Adverse weather conditions (rain and wind) at the start of flowering in *B. alba* populations prompted a major decline in pollen release and consequently a substantial drop in pollen counts in P. Trives. Pollen captured here at the start of the pollen season should thus be assumed to come from further away, or lower down, from the spore trap, and aerobiological data recorded in P. Trives should not be used to calculate heat requirements for birch trees.

CONCLUSIONS

Airborne pollen counts do not always match flowering periods. Airborne *Betula* pollen may be detected prior to and after flowering. Potential pollen production is dependent on weather conditions over the previous summer; but weather conditions both prior to and during flowering also exert a marked influence on pollen dispersal and on the amount of pollen captured. Pollen transported over medium or long distances into the sampling range can greatly influence the pollen season start-date, and should therefore be taken into account when using airborne pollen data in phenological surveys. Phenological studies should be made of major wind-pollinated tree species in order to improve the interpretation of airborne pollen data.

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