

AEROBIOLOGICAL DYNAMICS OF THE CUPRESSACEAE POLLEN IN SPAIN, 1992-98

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SUMMARY: In Spain, the Cupressaceae family comprises two native genera: *Juniperus* (six species) and *Tetraclinis* (one species). It also includes several exotic genera grown as ornamental or forest trees, such as *Cupressus* (numerous species, but *C. sempervirens* and *C. arizonica* are the most abundant), *Chamaecyparis* and *Platycladus* (*Thuja*) as the most common genus. The pollen type Cupressaceae includes the families Taxaceae and Taxodiaceae, and their pollens show cross-reactivity. In recent decades, allergy to these pollens has been clearly recognized. This study analyses the pollen records for the period 1992-98 at 15 sites in the Spanish Aerobiology Network (*Red Española de Aerobiología*, REA). There is no part of Spain free of Cupressaceae pollen and its abundance depends on the number of ornamental plants in the surroundings of the trap and not on geographical parameters. In urban areas, huge variation in the quantities of pollen from year to year is not only due to weather but also to gardening manipulations of the ornamental species. The pollen is present all year round, pollination beginning in September and ending in August, and the maximum concentrations occurring usually in February, but sometimes in March, January, December, or April. In most locations, the pollen concentrations were highest in the periods 1996-97 and 1997-98. In this paper, the use of pollen categories instead of pollen concentrations is recommended. This is to simplify the presentation of the information, specially when defined specifically for the pollen type and taking into consideration the allergy sensitization level. The concept of main pollen season (MPS) does not seem relevant for the characterization of the Cupressaceae aerobiological dynamics. **KEY WORDS:** Aerobiology, allergy, Cupressaceae, *Cupressus*, *Juniperus*, pollen categories, pollen levels, Spain.

RESUMEN: En España la familia Cupressaceae está compuesta por dos géneros nativos, *Juniperus* (con seis especies) y *Tetraclinis* (una especie), y diversos géneros exóticos cultivados como ornamentales o como especies forestales: *Cupressus* (diversas especies, siendo *C. sempervirens* y *C. arizonica* las más abundantes), *Chamaecyparis* y *Platycladus* (*Tiuja*) los más comunes. El tipo polínico Cupressaceae incluye las familias Taxaceae y Taxodiaceae y los pólenes presentan reactividad cruzada. En las últimas décadas, la alergia a estos pólenes ha sido claramente reconocida. En este trabajo se analizan los registros polínicos de Cupressaceae de 15 estaciones de la Red Española de Aerobiología (REA), recogidos durante el período 1992-1998. Prácticamente, no hay ninguna zona de España libre de polen de cupresáceas. Su abundancia depende del número de plantas ornamentales cercanas al captador y no guarda relación con parámetros geográficos. En las áreas urbanas se observan importantes variaciones interanuales en las cantidades de polen, debidas no sólo a la meteorología sino también a los trabajos de jardinería. El polen está presente en la atmósfera durante todo el año; la polinización empieza en Septiembre y acaba en Agosto, y las concentraciones máximas se dan normalmente en Febrero, y algunos años en Marzo, Enero, Diciembre o Abril. Los períodos 1996-97 y 1997-98 han sido los más ricos en polen en casi todas las localidades. En este trabajo se dan argumentos a favor del uso de categorías polínicas en lugar de concentraciones, para simplificar la presentación de la información y especialmente cuando se definen específicamente para el tipo polínico y tomando en consideración el nivel de sensibilización alérgica. El concepto de Período de Polinización Principal no parece necesario para caracterizar la dinámica aerobiológica de Cupressaceae.

PALABRAS CLAVE: Aerobiología, alergia, categorías polínicas, Cupressaceae, *Cupressus*, España, *Juniperus*, niveles polínicos.

INTRODUCTION

The Cupressaceae family consists of 17 genera, with about 113 species distributed in both the northern and southern hemispheres. They are evergreen resiniferous trees and shrubs, usually highly and regularly branched with relatively slow growth rates. Their leaves are opposite or in whorls of three, and are small, scale-like, imbricate, and closely pressed to the shoot in most species. However, they can be acicular in juvenile plants and in several *Juniperus* species. Information on the Cupressaceae family can be found in BOLÒS & VIGO (1984), CHAMBERLAIN (1965), HEYWOOD (1964), LÓPEZ GONZÁLEZ (1986), MABBERLEY (1987), and WEBERLING (1989).

Plants are commonly monoecious, but there are some dioecious species (*Juniperus*). Flowers are always unisexual, small, without a perianth, and spirally arranged in cones or

strobili. Usually, female strobili are positioned in the upper part of the crown while staminate strobili are mainly found in the lower part. Each stamen bears three to seven pollen sacs on the lower surface. Pollen is usually released in tremendous quantities from each individual and may be seen as yellow clouds when branches are moved (the plants are wind-pollinated). Most genera produce small, dry, and woody cones whereas others, such as *Juniperus*, produce small, fleshy, and berry-like cones.

Only two genera are native to the Iberian peninsula, but another four genera are often planted and occasionally become naturalized. The genera *Juniperus* (juniper) is the most common, with at least six spontaneous species native to Spain. Most of these constitute the brushwood of the evergreen oak forests or several scrub communities in the Mediterranean region. *Tetraclinis articulata* is a monoecious tree endemic to the NW of Africa and the SE

of Spain (in the mountains near Cartagena). It is also used for ornamental purposes.

Among cultivated species, the most important genus is *Cupressus*, with 13 species in the northern hemisphere. The most common cypress species in the area is *C. sempervirens*; it is native to the Aegean region and has been long planted and naturalized in many places. *C. arizonica* is also frequently planted. Other genera often cultivated as forest trees or as ornamental plants are *Chamaecyparis* and *Platycladus* (*Thuja*).

Table I summarizes the floral phenology and the main distribution characteristics for Cupressaceae on the Iberian peninsula.

The pollen grains from Cupressaceae cannot be differentiated under light microscopes, even at the genus level, nor can the pollen grains of Taxaceae (*Taxus baccata*, native to the Iberian peninsula) or Taxodiaceae (*Cryptomeria japonica*, frequently planted as an ornamental). In the aerobiological studies, all these taxa appear under the name Cupressaceae.

Species	Flowering period	Habitat	Altitude (m)	Geographical distribution
<i>Juniperus communis</i> L.	April-May (July)	Mainly on dry mountains	450-1400 (2700)	C, N and SE of Iberian peninsula Europe, Asia and North America
<i>Juniperus oxycedrus</i> L.	March-April	Dry hills mainly near the coast	0-1200	Throughout Iberian peninsula except in NW Mediterranean region
<i>Juniperus nardularis</i> Gand (= <i>J. oxycedrus</i> subsp. <i>arabizyana</i> Franco)	March	Maritime sands	500-1000	South of Iberian peninsula Endemic
<i>Juniperus phoenicea</i> L.	February-March	Dry hills	0-1400	NE and S of Iberian peninsula Mediterranean region and Macronesia
<i>Juniperus thurifera</i> L.	January-May	Dry continental mountains	800-1600	C, E and S of Iberian peninsula French Alps, Corsica, Spain and N of Africa
<i>Juniperus sabbia</i> L.	April	Mountains	1400-2750	E of Iberian peninsula and Cantabrian mountains C and S of Europe, N of Africa and W of Asia
<i>Tetraclinis articulata</i> (Vahl) Masters	February	Dry hills and cultivated	-	Near Cartagena Malta, Cyprus, SE of Spain and N of Africa
<i>Cupressus sempervirens</i> L.	February-April	For long planted and sometimes naturalized	-	Throughout Spain Native of Aegean region
<i>Cupressus arizonica</i> E.L. Greene	January-March	Planted for timber and as ornamental	-	Throughout Spain N of Mexico and SW of United States
<i>Cupressus macrocarpa</i> Hartweg	October-November	Planted for shelter and as ornamental	-	Throughout Spain Native of S of California
<i>Cupressus lusitana</i> Miller	February-April	Planted for timber and as ornamental	-	Throughout Spain Native of Mexico and Guatemala
<i>Chamaecyparis lawsoniana</i> (A. Murray) Parl. (= <i>Cupressus lawsoniana</i> A. Murray)	March-April	Planted for shelter and as ornamental	-	Throughout Spain Native of W of United States
<i>Platycladus orientalis</i> (L.) Franco (= <i>Thuja orientalis</i> L.)	March-April	Mainly planted as ornamental	-	Throughout Spain Native of China

TABLE 1. Floral phenology and distribution of the Cupressaceae species on the Iberian peninsula

Despite the diversity of species included in the pollen type Cupressaceae, most of the pollen collected in the aerobiological traps corresponds to *Cupressus*. Other ornamental species are less abundant and periodical pruning eliminates most of their flowers. Wild species (*Juniperus*, *Taxus*, and *Tetraclinis*) pollinate with less intensity, and usually grow far away from sampling sites.

According to LEWIS *et al.* (1983), the *Cupressus* species (California endemic species, *C. arizonica*, and *C. sempervirens*) are more likely to cause inhalant allergic reactions than other Cupressaceae species (*Chanacyparis*, *Juniperus*, *Libocedrus*, and *Thuja*). In Europe, allergy to Cupressaceae pollen was considered a rarity until 1975, but it is now a clearly defined clinical entity (PANZANI *et al.*, 1991).

PANZANI *et al.* (1991) noted in a clinical study that in 80% of cases skin tests to *Juniperus communis* correlated with skin tests to *Cupressus sempervirens*, while with *Thuja* the correlation was lower (60%). These

authors also found cross-reactivity with *Cryptomeria japonica* in 65% of cases, and with *Taxus baccata* in 4% of cases.

The definition of critical thresholds for allergy symptoms in patients has not yet been undertaken.

Cupressaceae pollen appears in the atmospheric pollen spectra of all Spanish localities (as reported by several authors in REA (*Red Española de Aerobiología*) bulletins 1 and 3-5). For instance, GALÁN *et al.* (1998) analysed daily variations in Cupressaceae pollen counts from Córdoba, together with climatic variables; and BELMONTE & ROURE (1991) included the comparison of the Cupressaceae pollen dynamics at several Spanish localities.

MATERIAL AND METHODS

In the present paper, Cupressaceae pollen aerobiological data from 15 Spanish localities during the period 1992-98 were

Geographical Region	Aerobiological Station	Geographical characteristics		Climatic characteristics		
		Altitud (m)	Geographical Coordinates	Mean Annual Temperature (°C)	Annual rainfall (mm)	Climate type (Capel, 1981)
North-East	Girona	125	41° 54' N, 02° 46' E	15.0	740	Mediterranean
	Manresa	291	41° 44' N, 01° 30' E	13.5	605	Mediterranean
	LLeida	202	41° 37' N, 00° 38' E	14.8	414	Mediterranean
	Bellaterra	245	41° 34' N, 02° 06' E	15.2	611	Mediterranean
	Barcelona	90	41° 24' N, 02° 09' E	16.5	595	Mediterranean
North-West	Terragona	48	41° 07' N, 01° 15' E	16.7	482	Mediterranean
	Santiago	270	42° 53' N, 08° 32' W	12.9	1288	Temperate cold oceanic
North	Vigo	50	42° 14' N, 08° 43' W	14.9	1412	Temperate cold oceanic
	León	830	42° 34' N, 05° 35' W	10.0	550	Temperate cold continental
Center	Madrid	600	40° 27' N, 03° 45' W	14.0	446	Temperate cold continental
South	Córdoba	123	37° 50' N, 04° 45' W	18.0	600	Mediterranean continental
	Jen	560	37° 46' N, 03° 47' W	17.0	592	Mediterranean continental
	Granada	685	37° 11' N, 03° 35' W	15.1	400	Continental mediterranean
	Málaga	5	36° 47' N, 04° 19' W	18.0	575	Mediterranean subtropical
	Estepona	0	36° 25' N, 05° 09' W	16.8	556	Mediterranean subtropical

TABLE 2. Aerobiological sampling stations and main geographical and climatic characteristics

analysed. All of the stations are integrated in REA, the Spanish Aerobiology Network. Table 2 contains the names of the aerobiological sampling stations and their main geographical and climatic characteristics. The duration of the sampling periods at each station is shown in Table 3.

All data were obtained using seven-day volumetric Hirst-type spore traps (HIRST, 1952), following the method adopted by REA (DOMÍNGUEZ *et al.*, 1991). Due to the flowering phenology and pollination dynamics of the Cupressaceae species, the year periods have been taken from September to August.

Only complete annual series have been included in this study. Gaps in the data series have been filled by linear interpolation. When this was not realistic because of the amount of missing data, the whole annual series was excluded from the study. The basic data are, as usual, the mean daily pollen concentrations expressed in the number of pollen grains per cubic meter of air (μm^3).

In the analysis of the variation of this pollen in the localities studied (Table 3), four aspects have been considered. In the annual summary, we give, for each station and year, the sum of the 365 mean daily concentrations (annual sum), the highest mean daily concentration of the year (maximum), and the corresponding date. We have established the main pollen season (MPS) following NILSSON & PERSSON (1981) and have included in the summary the total pollen during the MPS, the beginning and ending dates, and the duration.

In the third aspect of the analysis, daily pollen concentrations have been transformed into an ordinal, 0-4 scale. The categories for

the ordinal scale were defined in a previous study (BELMONTE *et al.*, in press) and are based on the author's experience. The ordinal scale defined for trees (Cupressaceae in this paper) is presented in Table 3, where "n" denotes the mean daily pollen concentrations.

Finally, looking for a graphical synthesis of the annual pollen dynamics at each site, a week has been used as the time unit. Following the convention that the first week of the year is the one that contains the first Thursday, we have converted each daily data series into the corresponding mean weekly pollen concentrations. Then we have calculated, for each station and week of the year, the mean value and the highest value of the period studied. Two series for each site, one for the mean, and the other for the maximum, are plotted in each of the line charts of Figures 1, 2, 3 and 4.

RESULTS AND DISCUSSION

Table 3 can be analysed from several points of view. Looking at the annual sum column, the stations can be decreasingly ordered as follows: Manresa, Madrid, Granada, Tarragona, Barcelona, Málaga, Lleida, Estepona, Girona, Bellaterra, Jaén, Córdoba, Santiago de Compostela, Vigo, and León. This ordering is approximately the same as that obtained on the basis of the maximum daily concentration in the September-August period.

As could be expected for a pollen type mainly composed of plants used as ornamental, no geographical explanation was found for the above-mentioned ordering.

If we compare the different annual sums and maximum concentrations in each station,

Site	Years	Annual summary			Main Pollen Season				Number of days per Categories				
		Annual sum	Maximum	Maximum	Pollen sum	Beginning	Endline	Duration	Cat. 0	Cat. 1	Cat. 2	Cat. 3	Cat. 4
		P/m ³	P/m ³	Date	P/m ³	Date	Date	Nr days	(n<1)	(1-n<2)	(2-n<5)	(5-n<10)	(n>10)
Girona	1996-97	5969	231	27.02	5581	27/10	21.04	177	141	143	49	15	17
	1997-98	5679	330	22.02	5145	18/01	4.04	77	187	122	18	18	20
Maresa	1996-97	17125	1920	12.02	15990	19/10	7.04	171	112	145	49	27	32
	1997-98	10236	1037	16.02	9237	6/01	15.03	73	129	184	22	7	23
Lleida	1996-97	10257	1016	26.02	9272	21/10	2.04	164	158	118	43	23	23
	1997-98	4661	432	28.02	4207	24/11	21.03	118	169	163	9	9	15
Bellaterra	1994-95	4300	350	25.02	3878	4/12	13.04	131	176	146	26	7	10
	1995-96	4507	302	24.03	4058	28/10	22.04	178	142	168	32	16	8
	1996-97	7841	803	13.02	7113	19/10	15.04	179	146	133	55	13	17
	1997-98	4591	321	7.03	4137	25/12	9.04	106	169	149	24	9	14
Barcelona	1994-95	6393	496	13.02	5725	27/11	12.04	137	152	146	39	12	16
	1995-96	7606	486	18.02	6879	13/12	11.04	121	156	144	24	23	19
	1996-97	11614	1077	13.02	10474	22/10	8.04	169	135	137	45	22	25
	1997-98	6484	377	8.03	5853	7/01	4.04	88	165	139	31	9	21
Tarragona	1996-97	12047	799	13.02	10962	20/10	8.04	171	127	127	55	32	24
	1997-98	6222	643	5.03	5622	16/12	3.04	109	152	156	28	11	18
Santiago de Compostela	1993-94	478	42	5.03	437	14/12	25.05	163	239	121	5	0	0
	1994-95	1027	69	25.03	928	12/12	7.05	147	180	173	10	2	0
	1995-96	162	7	11.03	146	7/12	13.06	190	258	108	0	0	0
	1996-97	1387	118	12.01	1259	12.01	16.04	95	208	141	10	5	1
1997-98	1260	73	10.02	1145	9.01	15.04	97	212	129	21	3	0	
Vigo	1995-96	500	44	22.03	452	21/11	20.04	152	230	132	4	0	0
	1996-97	1119	87	12.01	1015	11/12	6.04	117	200	150	12	3	0
	1997-98	732	107	10.01	665	18/12	31.03	104	238	122	3	1	1
León	1994-95	407	13	25.01	369	28/11	24.05	209	261	101	0	0	0
	1995-96	555	49	23.03	505	11/10	14.07	278	254	109	3	0	0
	1996-97	514	40	6.02	465	5.01	16.04	102	282	79	4	0	0
	1997-98	783	60	6.03	710	20.01	25.03	65	301	51	10	3	0
Madrid	1993-94	8404	600	12.02	7589	27/12	1.04	96	151	150	36	14	24
	1994-95	9086	1041	14/12	8206	8/12	12.05	95	120	185	21	16	22
	1995-96	5494	593	6.02	4966	23/12	27.03	96	119	197	22	15	13
	1996-97	22815	1257	28.01	20709	22/11	12.05	111	119	138	38	13	57
1997-98	13046	3952	17.02	11830	18/01	13.05	55	150	154	20	20	21	
Córdoba	1992-93	4387	405	14.02	3994	22/01	24.05	62	206	116	17	15	11
	1993-94	1737	133	21.02	1571	27/12	15.03	79	211	132	12	6	4
	1994-95	873	83	16.02	788	30/11	4.04	126	221	132	11	1	0
	1995-96	3766	425	5.03	3413	3.02	23.03	56	199	139	7	9	12
	1996-97	11493	659	17.02	10374	24/10	21.03	149	162	117	56	20	30
	1997-98	5449	770	10.02	4931	11/04	6.03	55	188	134	16	14	13
Jaén	1996-97	7412	667	7.02	6943	20/10	1.03	133	172	138	19	14	22
	1997-98	3008	201	15.02	2784	1/11	5.03	125	202	128	20	9	6
Granada	1992-93	8105	1085	21.02	7373	15.01	20.03	65	169	141	19	19	17
	1993-94	8540	1234	26.02	7797	6/01	16.03	70	180	138	13	13	21
	1994-95	6451	972	21.02	5825	2.01	29.03	87	155	169	15	8	18
	1995-96	6612	646	23.03	6024	9.02	15.04	67	196	121	20	11	18
	1996-97	19103	1088	16.02	17490	29/10	25.03	148	130	140	30	28	37
	1997-98	17615	1837	16.02	15949	13.01	5.03	52	158	146	18	13	30
Málaga	1992-93	4399	414	22.02	3974	22/12	27.03	96	218	101	20	16	10
	1993-94	3754	602	29.01	3384	17.01	23.05	66	205	119	21	10	10
	1994-95	3258	156	4.04	2961	16/11	19.04	155	175	138	36	10	6
	1995-96	11858	1067	29.02	10737	25.02	4.04	36	184	132	19	7	24
	1996-97	17044	803	21.02	15375	21/10	24.03	155	152	119	30	22	42
1997-98	6039	423	23.02	5508	14/10	25.03	163	200	115	19	12	19	
Estepona	1995-96	3407	494	29.03	3089	31/10	16.04	169	217	114	18	11	6
	1996-97	10896	1429	25.02	10166	6/10	25.03	171	166	122	33	17	27

TABLE 3. Parameters to evaluate the presence and impact of Cupressaceae pollen in several Spanish localities.

we can see that there is a huge variation from year to year. The period 1996-97 was the highest in airborne Cupressaceae pollen, with León being the exception. When the series was long enough, 1997-98 was the second highest in abundance, with the exceptions being Barcelona, León and Málaga.

In most stations, the highest maximum of the study period coincided with the highest annual sum, except for Girona, Vigo, Madrid, Córdoba, and Granada.

The maximum mean daily concentration was obtained in February in 61.8% of the cases, in March in 23.6%, and in January in 10.9%.

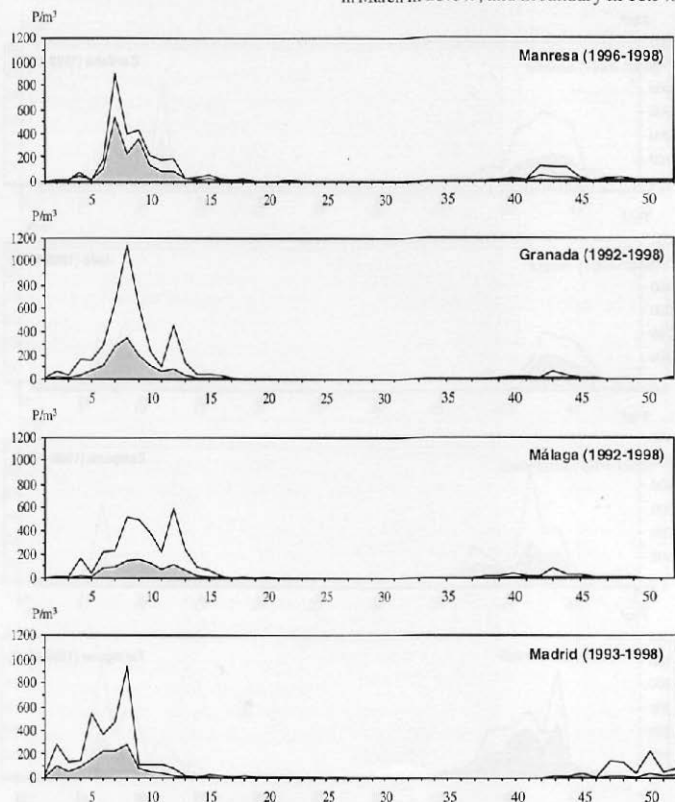


FIGURE 1. Graphical synthesis of the annual dynamics of the Cupressaceae pollen at the REA sites with highest concentrations. For each station and week of the year, the mean concentration and the highest concentration of the period studied are plotted.

The earliest maximum in the table corresponded to Madrid, with 1041 p/m³ on 14/12/94, and the latest at Málaga, with 156 p/m³ on 04/04/95.

Now that it is generally accepted that Cupressaceae pollen causes allergic reactions, thresholds have to be investigated. As

a first step, the authors propose the use of categorical pollen. Frequencies for categorical data are given on the right side of Table 3. After the experience of the Catalan research group, levels 0 and 1 (< 20 p/m³) are not suspected of causing allergic reactions. Problems in highly sensitized patients may

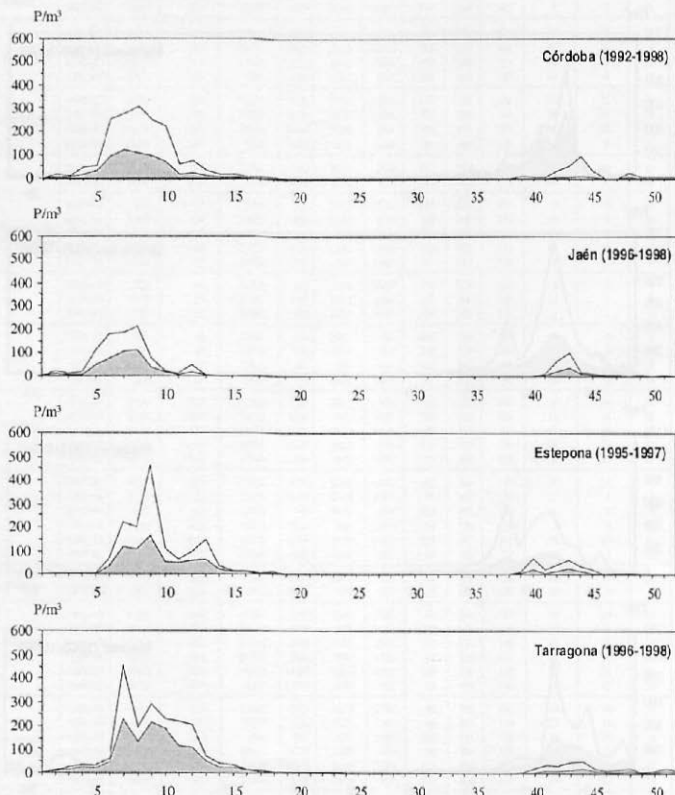


FIGURE 2. Graphical synthesis of the annual dynamics of the Cupressaceae pollen at some of the REA sites with median concentrations. For each station and week of the year, the mean concentration and the highest concentration of the period studied are plotted.

begin when level 2 (20-50 p/m³) and level 3 (50-100 p/m³) are reached, and the pollen clearly causes allergic responses in people when concentrations reach level 4 (> 100 p/m³).

In Córdoba, a positive skin test reaction to Cupressaceae pollen was observed in 3.5%

of allergic patients (GALÁN *et al.*, 1998). In Vigo, the prevalence of Cupressaceae skin positives in pollinotics was 1% (BELMONTE *et al.*, 1998). In Zaragoza, *Cupressus* pollen affected less than 1% of the pollinotics (BELMONTE *et al.*, in press). These results suggest that our proposal of categorization of

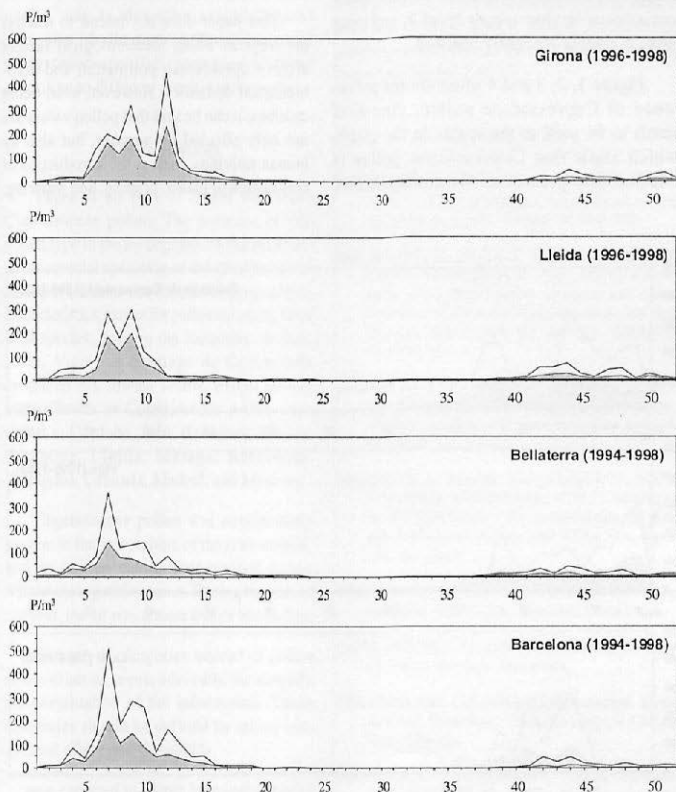


FIGURE 3. Graphical synthesis of the annual dynamics of the Cupressaceae pollen at some of the REA sites with median concentrations. For each station and week of the year, the mean concentration and the highest concentration of the period studied are plotted.

aerobiological data for Cupressaceae needs revision. However, more data on sensitization are needed.

As could be expected, there is a correlation between high annual sums of Cupressaceae pollen and the number of days when pollen levels reach 3 and 4, while low annual pollen sums occur in sites where level 4, and even level 3, counts are rarely reached.

Figure 1, 2, 3 and 4 illustrate the prevalence of Cupressaceae pollen. Attention needs to be paid to the scales in the graph, which show that Cupressaceae pollen is continuously present in the atmosphere of

the sites studied. Annual curves present similar forms at all sites, with high concentrations during winter-early spring and autumn. These results coincide with those obtained by BELMONTE & ROURE (1991), who report that for *Juniperus* species pollination takes place in summer.

This paper does not intend to discuss the ways in which meteorological factors affect Cupressaceae pollination and aerobiological dynamics. However, even being cautious, it can be said that pollen values are not only affected by weather, but also by human activities, such as the introduction or elimination of plants, pruning, and watering.

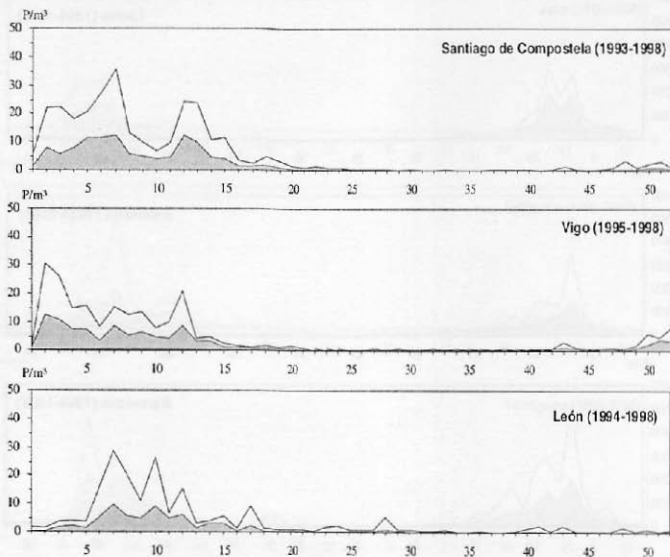


FIGURE 4. Graphical synthesis of the annual dynamics of the Cupressaceae pollen at the REA sites with lower concentrations. For each station and week of the year, the mean concentration and the highest concentration of the period studied are plotted.

The use of the MPS to characterize Cupressaceae pollen curves is questionable. Even if it is more useful for Cupressaceae than in other cases, MPS-related parameters are so influenced by the amounts of pollen in the annual season that they do not produce any new information.

It is the author's opinion that a more useful way to describe aerobiological dynamics of allergenic pollen types is by using taxon-specific categories, defined according to different sensitization levels.

CONCLUSIONS

There is no part of Spain free from Cupressaceae pollen. The presence of this pollen type in the air depends on the presence of ornamental species near the aerobiological station. No relation was found with geographical characteristics, except for pollen coming from wild species. Among the localities studied, León, Vigo and Santiago de Compostela produced the lowest levels. Progressively higher levels of Cupressaceae pollen were found in Córdoba, Jaén, Bellaterra, Girona, Estepona, Lleida, Málaga, Barcelona, Tarragona, Granada, Madrid, and Manresa.

Cupressaceae pollen was continuously present in the atmosphere of the sites studied, and the highest values were reached during winter-spring and autumn. During the rest of the year, the air was almost free of this pollen.

The use of categories instead of pollen concentrations seems advisable for simplify the presentation of the information. These categories should be defined by taking into account allergenic thresholds.

As expected in plants frequently planted as ornamental, humans will be a cause of variation in the pollen levels together with meteorological parameters.

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