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The effect of meteorological parameters on diurnal patterns of airborne olive pollen concentration

FRANCISCA ALBA, CONSUELO DÍAZ DE LA GUARDIA, PAUL COMTOIS

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Aerobiological studies carried out in the atmosphere of Granada using a Hirst-type volumetric spore trap during the period 1993–1996 show that there is not a single diurnal pattern for olive pollen (*Olea europaea* L.) over the course of the main pollen season. Examination of the behaviour of airborne olive pollen concentration allows the establishment of either regular (54.4% of the studied days) or irregular (45.6% of the time) patterns of diurnal variation. On a given day, the pattern found will depend on a combination of different factors: the origin of the captured pollen (either local or regional), source distribution in relation to the pollen sampler, topography, and different meteorological variables (mean air temperature, sunshine hours, total rainfall, relative humidity, wind speed and direction, and periods of calm). Regional sources were significant contributors to city centre pollen concentrations when moderate (<10 km/h) winds from the 4th quadrant and warm temperatures (19–26°C) allow swift transport from the W-NW of the province.

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Olive trees (*Olea europaea* L.) are widely cultivated in the south of the Iberian Peninsula. In the Province of Granada, olive groves account for 49.5% of the total area dedicated to agriculture (127 208 Ha). This single-species crop is located at 650–1400 m above sea level, mainly in the north-west, west, south-west and south regions of the Province (Fig. 1). However, as a result of the high pollen production of this species (approximately 1.8×10^5 pollen grains per flower; Tormo Molina et al. 1996), olive pollen is the most abundant in the city of Granada (Díaz de la Guardia et al. 1993, Alba & Díaz de la Guardia 1996), in other neighbouring cities (Dominguez et al. 1993, Candau et al. 1994, Recio et al. 1996), and in other Mediterranean countries (Gellerbenstein et al. 1996, Safadi 1999). Furthermore, this type of pollen has been considered by several authors (D'Amato & Lobefalo 1989, Macchia et al. 1991, Liccardi et al. 1996) as being the primary cause of pollen related allergies in the Mediterranean region as a whole.

An average diurnal pattern of pollen concentrations through the main pollen season has been proposed by some authors (Galán et al. 1988, Díaz de la Guardia et al. 1993, Recio et al. 1996). However, since olive pollen emission and dispersal is governed by turbulence and wind patterns, and that the distribution of this species is uneven in the area surrounding Granada (Fig. 1), the hypothesis that, along the main pollen season, there could be distinct diurnal patterns of pollen concentrations has been put forward. Indeed, it is more than probable that pollen from different sources, carried by different wind speeds, will reach Granada at different time periods.

Moreover, if the existence of these different patterns can be shown, it would necessary mean, according to our

hypothesis, that relationships between them and either hourly values of the most important meteorological variables governing pollen emission and dispersal, or the distribution and phenology of the sources in relation to topography, would be significant. These two objectives are the main topics of this paper.

Study area

The city of Granada is located in the S-SE of the Iberian Peninsula (37°11' N and 3°35' W), and lies in the Intra-Baetic trench that divides the Baetic Mountains into two main geological units (Fig. 1): the Peni-Baetic Mountains (Sierra Nevada, Sierra de la Almiñara, Sierra de Lújar, Sierra de la Contraviesa), and the Sub-Baetic Mountains (Sierra de Loja and Sierra Arana). These mountain ranges act as natural barriers for the dispersal of olive pollen in such a way that a regional area of pollen influence having a radius of approximately 50 km around the pollen sampling station can be delimited.

Regional climate

According to Capel Molina (1981), Granada has a continental Mediterranean climate, characterised, at the time of the olive flowering season (from the last days of April to the first half of July), by warm mean monthly air temperatures (13.5–25.4°C), sharp intradiurnal temperature variations (up to 16°C), a mean of 366 hours of sunshine per month and between 8 to 10 hours of sunshine per day. The rainfall pattern is similarly uneven, with heavy rains in April—usually in the form of torrential downpours—and a

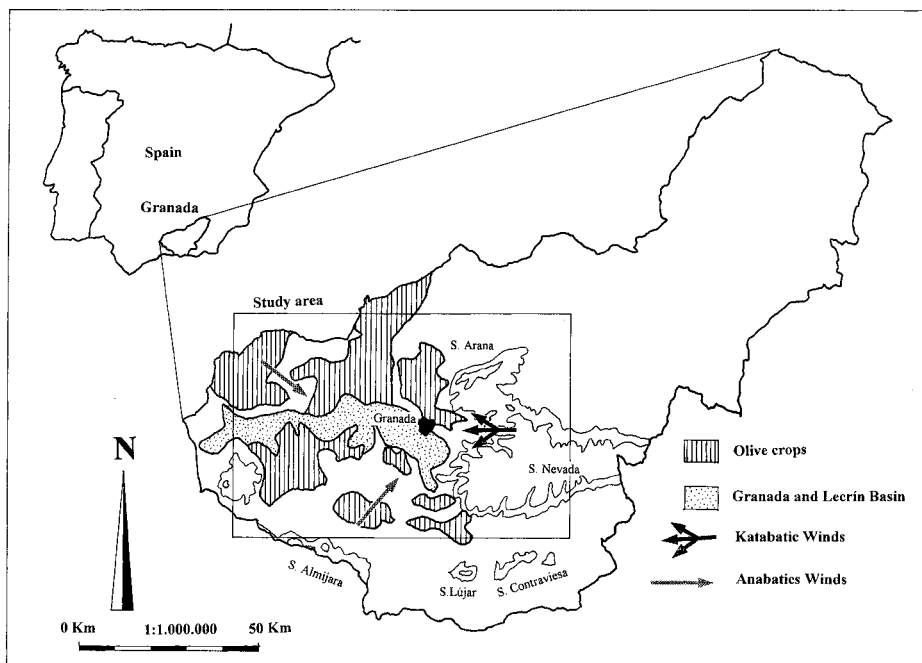


Fig. 1. Geographical location of Granada and the distribution of olive groves around the pollen sampling station.

notable drought in July. The atmospheric relative humidity falls steadily during the course of the olive pollen season, with maximum values at night and minimum values in the afternoon.

The mountains surrounding the city act as a screen to block dynamic winds, generally related to depressions. However, the same mountains favour the existence of local mountain-valley winds, whose origin is exclusively thermal. These winds occur throughout the day in the Sierra Nevada and in the Granada Plain–Lecrín Valley (Fig. 1), simultaneously forming anabatic winds in the afternoon and katabatic winds, when the colder, denser air from the Sierra Nevada move downwards to the city of Granada.

MATERIAL AND METHODS

Pollen monitoring was performed from January 1993 to December 1996 using a Hirst-type volumetric sampler (Burkard 7-day-recording spore-trap), set at approximately 23 m above ground level on the roof of the University of Granada Faculty of Sciences, located in the centre of Granada. For the daily pollen count estimations, four longitudinal sweeps per microscope slide were made at a 40 $\times$ -magnification; the hourly counts were obtained along the same sweeps with the aid of a small ruler impressed on acetate paper stuck to the reverse of the slide, following the method recommended by the Spanish Aerobiology Network (Dominguez et al. 1991). Mean daily and hourly pollen concentrations are expressed as grains per cubic metre of air.

The main pollen season (MPS) was determined by taking 95% of the annual sum, using cumulative values (Pathirane 1975). Over the 4 years of the study, we were able to extract 149 days that could be defined as being part of the olive MPS. Each one of these daily counts can be represented as a diurnal pattern by using the distribution of the hourly percentage values of the daily total. After comparing the aerobiological behaviour of the olive pollen in the course of the day over these 149 days, we were able to classify these

diurnal patterns into 4 categories (Pattern A, B, C, and D). For a given day to be included in one of these categories, a specific threshold of the pollen concentration in a specific hours range must be encountered (Table I); when this could not be achieved, the daily pattern was classified as “irregular”.

Each of these diurnal patterns of airborne pollen (Figs. 2 to 5), except the irregulars (Fig. 6) were graphically compared to the average daily meteorological conditions, including mean air temperature, sunshine hours, humidity level, wind speed, frequency of periods of calm and wind direction (winds from the 1st, 2nd, 3rd and 4th quadrants are from 1–90°, 91–180°, 181–270° and 271–360° respectively), and total precipitation observed on the same days. The meteorological data used were registered three kilometres south of the sampling station. Spearman’s correlation coefficients were used to establish the relationship between the hourly pollen count and the corresponding hourly meteorological parameters for each day included in each pattern (Tables II to V).

In order to test the hypothesis outlined above, i.e. the existence of specific diurnal patterns, it is necessary to test the relative proportion of the intra- and inter-variability of the different patterns over the 149 days analysed. To do so, a Kruskal–Wallis one-way analysis of variance by ranks was applied to our data set (Table VI). This test is useful to decide whether our diurnal pattern categories really constitute different populations of hourly percentage values of the daily total. In order to analyse the differences between specific pairs of diurnal patterns, the Mann Whitney *U* test was used (Table VII). The Mann Whitney test is the most useful alternative to the Student’s *t* test when the measurement is weaker than interval scaling and when at least ordinal measurement can be achieved.

RESULTS

Pattern A (Fig. 2, Table I)

Days that show a type-A pattern are characterised by presenting 35% of the daily total concentration between

Table I. Threshold criteria used to differentiate intradiurnal dispersal patterns for *Olea* pollen and the descriptive statistics of each pattern.

	Definition of patterns				Observed values			
	Sub-pattern labels	Hours Range	% of the Total Concentration	Number of cases	Mean (%)	Maximum	Minimum	Std. Dev.
Pattern A	A1	1.00–12.00	<35	28	20.20	24.38	16.03	10.76
	A2	13.00–24.00	>65	28	79.93	84.11	75.75	10.77
Pattern B	B1	1.00–12.00	>65	18	68.76	78.19	65.33	12.96
	B2	13.00–24.00	<35	18	25.68	34.60	21.80	10.30
Pattern C	C1	19.00–7.00	<40	18	36.25	39.86	29.63	13.31
	C2	8.00–18.00	>60	18	63.75	70.372	60.13	13.31
Pattern D	D1	19.00–7.00	>60	17	67.52	72.42	62.61	9.54
	D2	8.00–18.00	<40	17	32.48	37.39	27.58	9.54

01.00 hours and 12.00 hours (A1) and the remaining 65% between 13.00 and 24.00 hours (A2). Maximum hourly values generally occur between 17.00 and 22.00 hours. Only 20% of the days included in this pattern had precipitation events, and these were significant only in the A1 phase. During the A2 phase, there was a major increase in temperature (19–26°C), sunshine (up to 10.8 hours) and wind speed (up to 9.3 km/h), whereas the relative humidity fell to 41%. Winds were predominantly from the 4th quadrant and to a lesser degree the winds from the 3rd quadrant. Periods of calm and winds from the 1st and 2nd quadrants had little influence on the appearance of this pattern.

Spearman's correlation analysis (Table II) shows that the intradiurnal concentrations present significant negative correlation coefficients with relative humidity, total rainfall, frequency of calm and winds from 1st and 2nd quadrants. Positive significant coefficients were obtained with temperature, sunshine hours, wind speed and winds from the 3rd and 4th quadrants; furthermore, there were positive associations between these two quadrants and temperature or wind speed-related variables.

Pattern B (Fig. 3, Table I)

The intradiurnal variations that fit this pattern show the opposite dispersal pattern than the one described above (Pattern A), with more than 65% of the total daily concentration from 01.00 to 12.00 hours (B1) and less than 35% of the total daily concentration from 13.00 to 24.00 hours (B2). The hourly peaks generally appeared between 02.00 and 09.00 hours. When this profile is found, the variation between the maximum temperature values (26°C) and the minimum values (9°C) is at its peak, while the relative humidity, accumulated sunshine hours and wind speed are low. Precipitation was observed only sporadically after 12.00 hours. During the first hours of the day there is a high frequency of periods of calm, and from 12.00 to 24.00 hours winds from the 3rd and 4th quadrants are predominant.

Spearman's correlation coefficients (Table III) indicate that pollen counts rise when the periods of calm are frequent and when relative humidity values are high; and fall when

sunshine hours, rainfall and wind-speed increase and winds are from the 3rd and 4th quadrants.

Pattern C (Fig. 4, Table I)

The days included within this pattern meet the criterion of 40% of the total daily pollen concentration being reached during the period between 19.00 and 07.00 hours (C1), while the remaining 60% of the olive pollen was found between 08.00 and 18.00 hours (C2). The most significant difference between this profile and pattern A is that the maximum peak occurs earlier (between 12.00 and 16.00 hours). At the time of the daily pollen maximum, temperatures are high, with maximum values of 28°C (at 16.00 hours), thereby favouring wind speeds of up to 8.6 km/h and low relative humidity levels (34%). None of the days included in this pattern registered precipitation events. Winds from the 3rd quadrant were predominant during the second half of the day, and those from the 4th quadrant—while less frequent—presented a higher frequency during the morning (9.00–13.00).

Spearman's correlation coefficients (Table IV) indicate that *Olea* pollen is dispersed to the Granada city centre when temperature, wind speed and winds from the 3rd and 4th quadrants increase, whereas transport decreases as relative humidity and periods of calm increase.

Pattern D (Fig. 5, Table I)

The type-D pattern presents the opposite dynamics as the one described for pattern C. During the period between 19.00 and 07.00 hours (D1), maximum pollen counts are recorded (accounting for more than 60% of the total daily concentration), while between 08.00 and 18.00 hours (D2) less than 40% of the total daily counts are recorded. The average meteorological parameters concomitant with this pattern present wide variations throughout the day in both temperature (8.5–24.5°C) and relative humidity (37–89%). Maximum values for wind speed (10 km/h) and accumulated sunshine (10 hours) were recorded at 19.00 hours. Precipitation was observed in 12% of the days included in this pattern and were present only in D2 phase. Periods of calm and winds from the 2nd quadrant are predominant for the

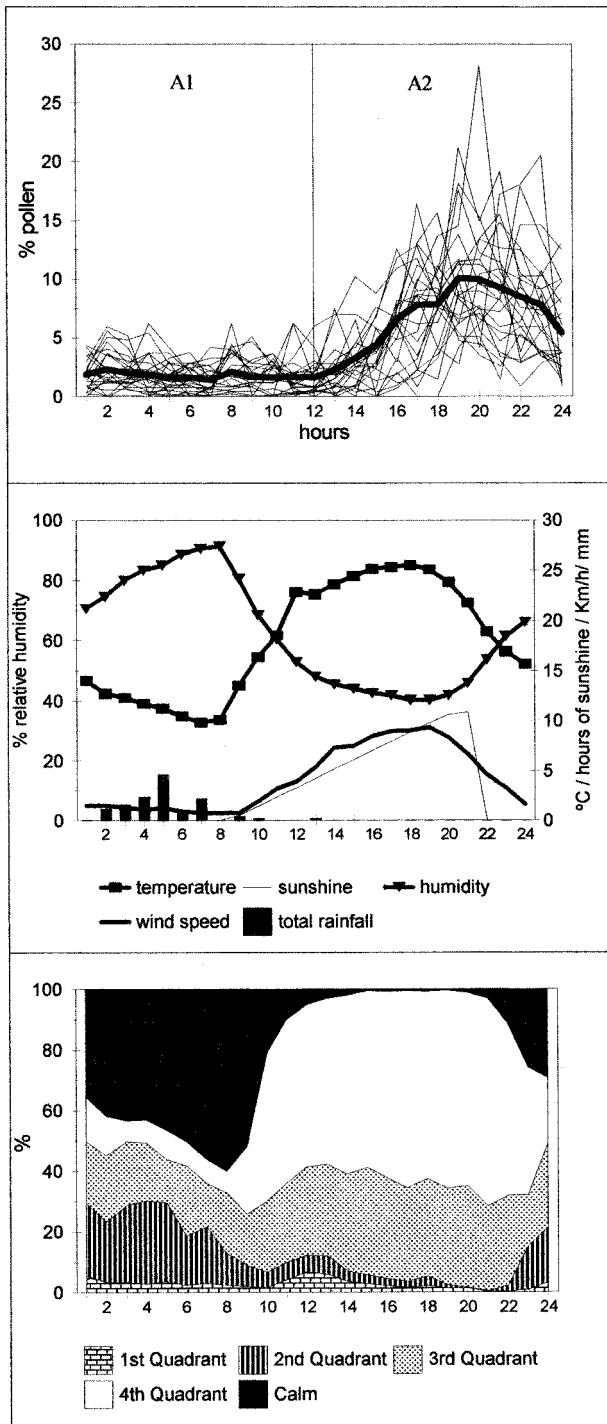


Fig. 2. Mean intradiurnal variation of *Olea* pollen and meteorological values corresponding to dispersal pattern "A".

first 8 hours, while winds from the 3rd and 4th quadrants are predominant for the remainder of the day.

The correlation analysis performed (Table V) reveals that pollen counts presented significant correlation with temperature, wind speed and winds from the 4th quadrant. However, the positive association between temperature and wind speed with winds from the 3rd and 4th quadrants, and

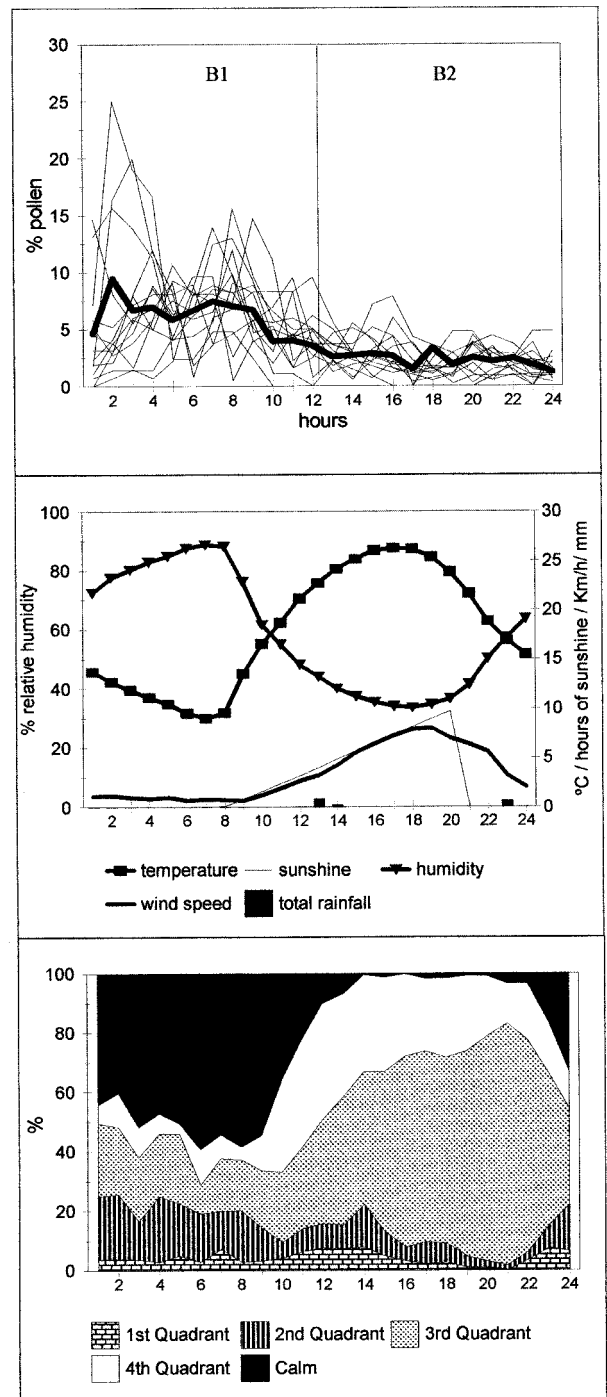


Fig. 3. Mean intradiurnal variation of *Olea* pollen and meteorological values corresponding to dispersal pattern "B".

those between humidity and periods of calm with winds from the 1st and 2nd quadrants provides valuable information about pollen dispersal during the D1 interval.

Irregular pattern (Fig. 6)

This pattern includes those daily pollen profiles whose intradiurnal variations did not fit easily into any of the

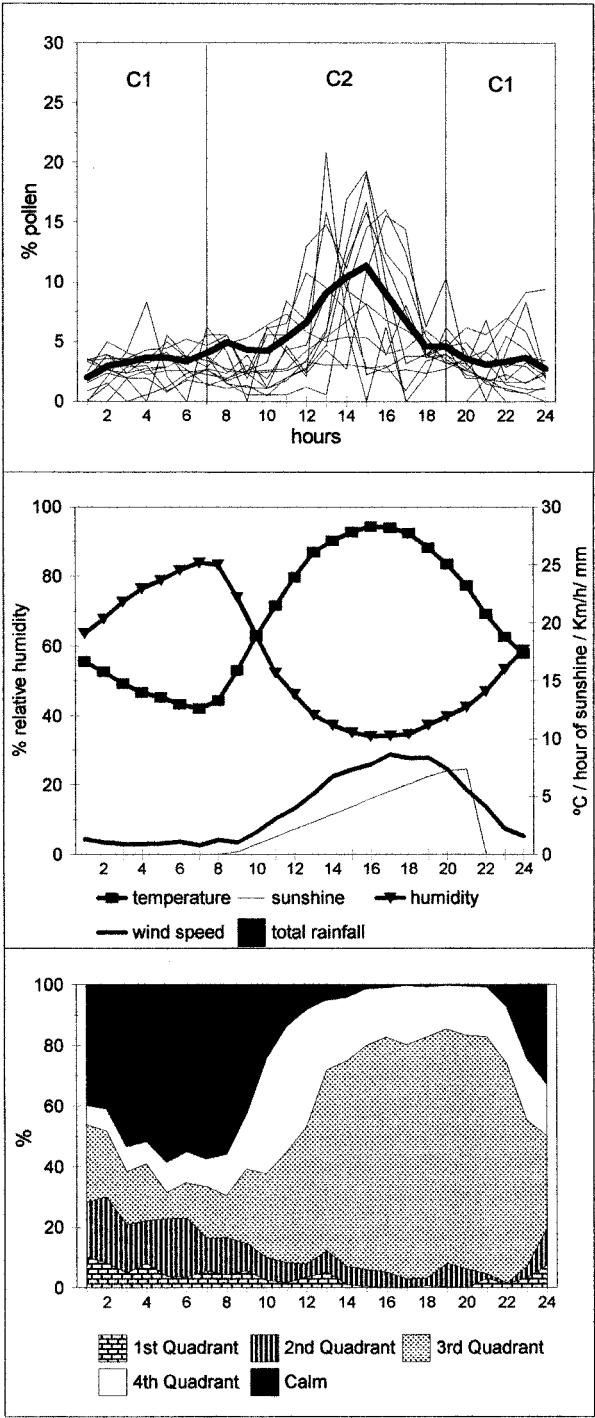


Fig. 4. Mean intradiurnal variation of *Olea* pollen and meteorological values corresponding to dispersal pattern "C".

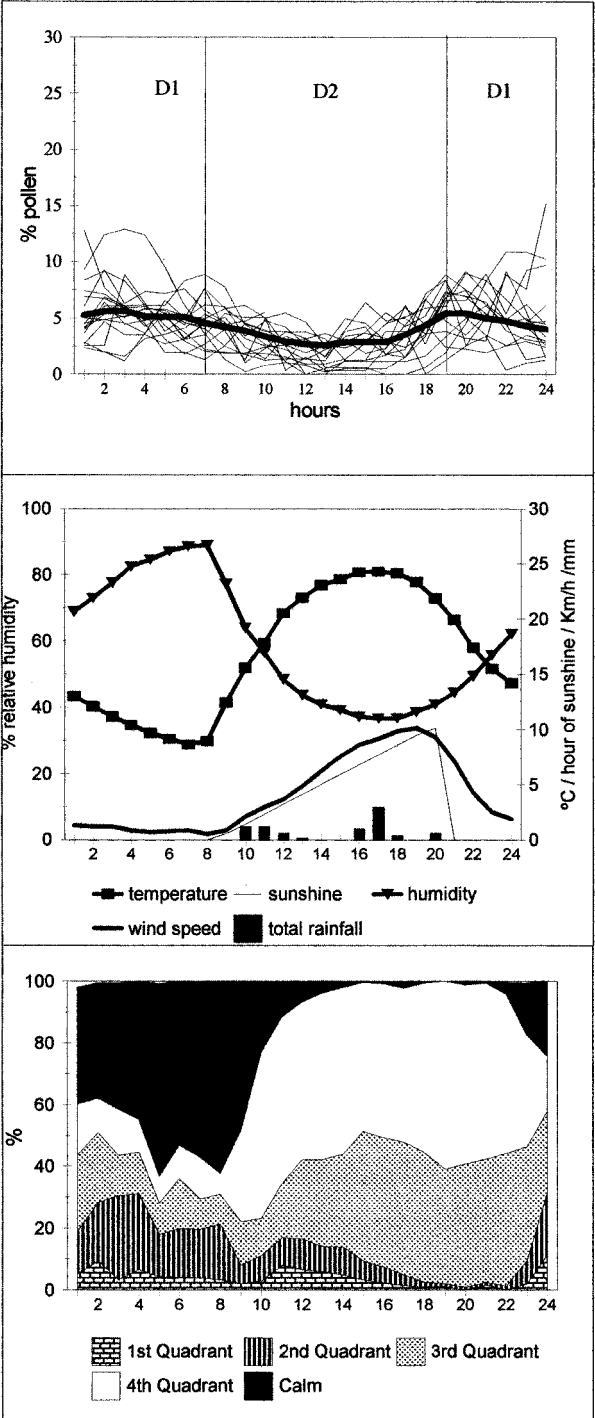


Fig. 5. Mean intradiurnal variation of *Olea* pollen and meteorological values corresponding to dispersal pattern "D".

Pattern differentiation

The Kruskal-Wallis test (Table VI) supports the hypothesis that *Olea* pollen is dispersed differently over the 149 studied days (H = 252.85; P < 0.0001). Moreover, there was a significant difference between the median ranks achieved by the mean profile of each pattern (H = 52.81; P < 0.0001); whereas there was no significant difference between the days

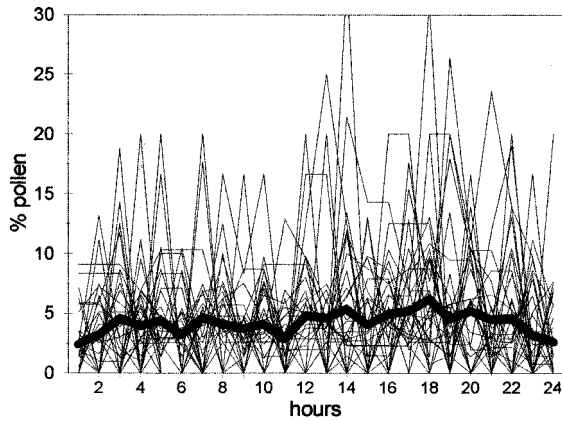


Fig. 6. Mean intradiurnal variation of *Olea* pollen corresponding to the "irregular" dispersal pattern.

included in a single pattern ($0.1377 < p < 0.9962$). This analysis of variance confirms that our definition of patterns A, B, C and D corresponds to significant differences in behaviour. The intra-variability of the irregular pattern, with a H of 126.04 associated to a $P < 0.0001$, confirms that this last category is indeed a mix of irregular dynamics. A

detailed analysis using the Mann-Whitney *U* test (Table VII) reveals significant differences between the medians of the intradiurnal variations of *Olea* pollen included in a given pattern and those included in the remaining models (except in the case of pattern B against D).

Frequencies

Pattern A was the most frequent to appear (in 28 days or 19% of the MPS), followed by Patterns B and C (both found in 18 days or 12% of the MPS), and Pattern D (17 days or 11% of the MPS). 68 days (or 46% of the MPS days analysed) did not match any of the fixed pollen-count thresholds, and therefore could not be assigned to one of the pre-established patterns, but rather presented a highly irregular intradiurnal profile.

DISCUSSION

A number of studies of airborne pollen transport at a regional scale (Tampieri et al. 1977, Mandrioli et al. 1980, 1984; Cabezudo et al. 1997, Di-Giovanni et al. 1996, Comtois 1997) have shown that distant pollen sources may have a considerable effect on the atmospheric pollen content if the local weather conditions are favourable for transport.

Table II. Spearman's correlation coefficients for the intradiurnal variations in *Olea* pollen and the meteorological parameters included in pattern "A". (*) $P \leq 0.05$, (**) $P \leq 0.01$.

PATTERN A (n = 672)									
Temperature	0.527**								
Sunshine	0.384**	0.522**							
Humidity	-0.510**	-0.924**	-0.636**						
Rainfall	-0.206**	-0.191**	-0.149**	0.210**					
Wind speed	0.221**	0.599**	0.662**	-0.647**	0.039				
Calm	-0.204**	-0.615**	-0.622**	0.679**	0.011	-0.930**			
1 st Quadrant	-0.152**	-0.094*	-0.093*	0.005	-0.007	-0.117**	0.168**		
2 nd Quadrant	-0.227	-0.320**	-0.345**	0.291**	-0.002	-0.374**	0.241**	0.588**	
3 rd Quadrant	0.133**	0.259**	-0.029	-0.247**	-0.044	0.227**	-0.326**	-0.197**	-0.097**
4 th Quadrant	0.182**	0.349**	0.598**	-0.385**	0.025	0.758**	-0.550**	0.038	-0.279**
Intradiurnal Pollen		Temperature	Sunshine	Humidity	Rainfall	Wind speed	Calm	1 st Quad	2 nd Quad
								3 rd Quad	

Table III. Spearman's correlation coefficients for the intradiurnal variations in *Olea* pollen and the meteorological parameters included in pattern "B". (*) $P \leq 0.05$, (**) $P \leq 0.01$.

PATTERN B (n = 423)									
Temperature	-0.090								
Sunshine	-0.358**	0.580**							
Humidity	0.189**	-0.885**	-0.651**						
Rainfall	-0.143**	-0.117**	0.019	0.139**					
Wind speed	-0.343**	0.513**	0.584**	-0.602**	0.034				
Calm	0.307**	-0.590**	-0.690**	0.661**	0.001	-0.938**			
1 st Quadrant	-0.029	-0.132**	-0.060	0.141**	-0.022	-0.086	0.177**		
2 nd Quadrant	-0.051	0.279**	-0.169*	0.245**	0.035	-0.045	0.113*	0.596**	
3 rd Quadrant	-0.143**	0.592**	0.449**	-0.643**	-0.079	0.484**	-0.602**	-0.401**	-0.264**
4 th Quadrant	-0.159**	0.106*	0.226**	-0.131**	0.089	0.383**	-0.281**	0.258**	-0.018
Intradiurnal Pollen		Temperature	Sunshine	Humidity	Rainfall	Wind speed	Calm	1 st Quad	2 nd Quad
								3 rd Quad	

Table IV. Spearman's correlation coefficients for the intradiurnal variations in *Olea* pollen and the meteorological parameters included in pattern "C". (*) $P \leq 0.05$, (**) $P \leq 0.01$.

PATTERN C										
(n = 432)										
Temperature	0.279**									
Sunshine	-0.062	0.307**								
Humidity	-0.217**	-0.851**	-0.525**							
Rainfall	-	-	-	-						
Wind speed	0.131*	0.523**	0.597**	-0.705**						
Calm	-0.154**	-0.592**	-0.607**	0.738**	-	-0.925**				
1 st Quadrant	-0.052	-0.232**	-0.122*	0.246**	-	-0.150**	0.224**			
2 nd Quadrant	-0.017	0.162**	-0.078	0.124*	-	0.002	0.116*	0.695**		
3 rd Quadrant	0.133*	0.656**	0.311**	-0.670**	-	0.530**	-0.671**	0.449**	0.321**	
4 th Quadrant	0.212**	-0.039	0.315**	-0.065	-	0.303**	-0.218**	0.296**	0.144**	-0.269**
Intradiurnal Pollen		Temperature	Sunshine	Humidity	Rainfall	Wind speed	Calm	1 st Quad	2 nd Quad	3 rd Quad

In the present study, we have observed that the translation of olive pollen at a regional scale is found when a series of factors have an additive effect on the pollen concentrations. Temperatures of 19–26°C and more than 10.8 sunshine hours are associated with winds from the 4th quadrant (and 3rd quadrant) of moderate speed (<10 km/h). These factors stimulate the release of pollen in the air (Subba Reddi & Reddi 1985) and facilitate the optimal dispersal of the released pollen from the main olive-growing areas of the Province, located to the W-NW, towards the city of Granada (Fig. 1). The diurnal pattern then found will be of type A. The lag found between the anthesis hours 12.00–14.00 (Comtois: Personal observation) and the maximum airborne pollen concentration in the afternoon (17.00–22.00) can be related to the time needed between emission and capture in central Granada (a 50 km distance at a wind speed of 10 km/h will involve a 5 hours lag). High levels of relative humidity or presence of precipitation on the days included in pattern A will lead to a deposition of the airborne olive pollen in the first hours of the day (01.00–12.00).

This dispersal model could also be frequent in urban areas located in valleys, where anabatic currents on warm afternoons largely favour the transport of pollen from the surrounding crops towards the pollen trap; wind speed,

pollen release time and distance of the vegetation will be the main parameters that will determine the hours when the pollen count will be at its highest value.

However, the airborne pollen detected during any given day is not always the direct result of release from its original source, but rather, as Norris-Hill & Emberlin (1991) suggest, some pollen peaks are related to the time at which temperature fluctuations disappear, thereby allowing pollen particles that had been suspended in the air to fall to lower levels. This phenomenon is probably responsible for the correlation coefficients found for pattern B (Table III), where an increase in periods of calm—and even in relative humidity—during the night favours a high airborne *Olea* pollen count. In the afternoons, although winds from the 3rd and 4th quadrants (anabatic currents) are predominant, the decrease in temperature (which impedes optimal pollen release; Richard 1985), low wind speeds (which hinders airborne transport) and occasional precipitation will lead to a major decrease in airborne pollen levels.

In addition, we have observed that significant amounts of olive pollen can be found in Granada's atmosphere in the morning hours 9.00–13.00 (Fig. 4, Table IV), a time setting in contradiction with a concomitant release of olive pollen by the anthers. This could probably be related to

Table V. Spearman's correlation coefficients for the intradiurnal variations in *Olea* pollen and the meteorological parameters included in pattern "D". (*) $P \leq 0.05$, (**) $P \leq 0.01$.

PATTERN D										
(n = 408)										
Temperatu	0.223**									
Sunshine	-0.045	0.494**								
Humidity	0.019	-0.794**	-0.654**							
Rainfall	-0.060	0.091*	-0.070	-0.075						
Wind speed	-0.109*	0.503**	0.599**	-0.704**	-0.026					
Calm	0.083	-0.526**	-0.680**	0.721**	0.027	-0.922**				
1 st Quadrant	0.016	-0.078	0.215*	0.134**	-0.052	-0.217**	0.241**			
2 nd Quadrant	0.002	-0.271**	-0.2923*	0.255**	-0.072	-0.313**	0.323**	0.678**		
3 rd Quadrant	-0.015**	0.399**	0.188*	-0.415**	0.054**	0.235**	-0.314**	0.043	0.202**	
4 th Quadrant	-0.090*	0.168**	0.490**	-0.354**	-0.037	0.628**	-0.558**	0.061	-0.114**	0.044
Intradiurnal Pollen		Temperature	Sunshine	Humidity	Rainfall	Wind speed	Calm	1 st Quad	2 nd Quad	3 rd Quad

Table VI. *Kruskal-Wallis test values and associated probabilities for all studied days (a), the different patterns (b) and the days associated with each pattern (c–d).*

	Number of cases	D.F.	H	P
a All days studied (4 MPSs)	149	148	252.85	0.0000
b All Patterns	5	4	52.81	0.0000
Pattern "A"	28	27	31.45	0.2528
Pattern "B"	18	17	20.50	0.2494
c Pattern "C"	18	17	23.64	0.1377
Pattern "D"	17	16	6.57	0.9962
d Pattern "irregular"	68	67	126.04	0.0000

resuspension, especially since there was no significant correlation between temperature and these winds (Table IV). Indeed, Mandrioli et al. (1980) and Cepeda & Candau (1990) claim that sometimes most of the pollen detected has its origin in re-flotation phenomena. In addition, since this time pattern is also associated with winds from the 4th quadrant, the pollen detected could be released from the olive groves of the S-SW of the Province i.e. from groves located in fairly close proximity to the trap. In both cases, the maximum daily peak will be recorded earlier than in pattern A. When different phenomena favouring pollen dispersal occur together in a short period of time, the airborne pollen count increases steadily and a type C pattern is found, with maximum airborne concentrations of pollen in the middle part of the day.

In this discussion, we have seen that thermal flows play an important role in the supply of particles to the atmosphere of Granada. On many occasions, the pollen count recorded in the early hours of the morning (01.00–07.00 hours) can be related to katabatic winds from the slopes of the Sierra Nevada, and the pollen recorded during the evening and

night-time (18.00–24.00 hours) to anabatic winds from the olive groves located to the W-NW. When we are capturing pollen of both local and regional sources at the same time a type D pattern is encountered. When this behaviour occurs, the exposure to pollen is low and more or less continuous. However, the relative importance of morning and afternoon concentrations makes this pattern similar to the type B pattern (Table VII), i.e. that the net result is similar to pollen re-suspension.

CONCLUSIONS

We have confirmed our hypothesis that there is not a single intradiurnal pattern for *Olea* pollen in the city of Granada but rather that, throughout the main pollen season (MPS), a number of different patterns of intradiurnal airborne pollen transport can be identified. By considering only the average diurnal pattern, we are only visualising the average behaviour of pollen release in the atmosphere, and our understanding of anemophilous pollination is very incomplete. The diversity of intradiurnal patterns is mainly due to the distribution of the olive groves around the sampling station and to the phenological state of this species at the time of sampling. Moreover, the whole dispersal process is considerably affected by the diurnal variability of the major meteorological parameters. Over the four years of this study, only 54.4% of the observed days fitted any pre-determined dispersal pattern. On the remaining days of the MPS (45.6%), mostly at the start and end dates of the MPS, the pollen dispersal is highly irregular. The MPS is generally defined on the basis of a percentage of the annual pollen contribution of a species. From the point of view of pollen dispersal behaviour, however, we should think of a more restricted definition.

Table VII. *Mann Whitney U test for the paired comparisons of the dispersal patterns*

	Mean Rank	N° of cases	U	Z	2-tailed P
pattern "A" vs Pattern "B"	521.74 600.35	672 432	124482.0	−4.0597	0.0000
pattern "A" vs pattern "C"	546.63 561.63	672 432	141209.5	−2.7865	0.0016
pattern "A" vs pattern "D"	541.01 626.19	672 408	137430.5	−4.3307	0.0000
pattern "A" vs pattern "irregular"	987.87 1171.93	672 1632	437685.5	−6.2072	0.0000
pattern "B" vs pattern "C"	458.18 406.82	432 432	82217.5	−3.0481	0.0023
pattern "B" vs pattern "D"	470.06 444.30	432 408	97822.5	−1.4757	0.1400
pattern "B" vs pattern "irregular"	998.88 995.84	432 1632	335932.5	−1.9971	0.0326
pattern "C" vs pattern "D"	430.97 479.47	432 408	92652.5	−2.7890	0.0053
pattern "C" vs pattern "irregular"	891.81 1025.49	432 1632	291733.0	−4.2794	0.0000
pattern "D" vs pattern "irregular"	962.47 1038.35	408 1632	346547.5	−2.4684	0.0136

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