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Environmental Factors Affecting Airborne Pollen Concentration in Anemophilous Species of *Plantago*

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Pollination of *Plantago* species in the Extremadura Region (SW of the Iberian Peninsula) was studied using three volumetric traps located in the cities of Badajoz, Mérida and Cáceres between 1994 and 1999. Variations in atmospheric concentration of *Plantago* pollen were analysed between locations, and annual, daily, and hourly variations recorded for each location. The highest concentrations of pollen were recorded at Cáceres, while the Mérida and Badajoz values were similar. This is explained by the nature of the surroundings of each city. Interannual variations in pollination levels were significantly correlated with autumn rains, which determine the extent of development of the populations. The hourly patterns of pollen capture were well-defined and similar for all three study sites. Maximum levels were reached between 1000 and 1200 h. Nocturnal concentrations were very low. Furthermore, this pattern was maintained throughout the flowering period, impling a very close link with the patterns of anthesis of the species. The three stations showed similar patterns of daily variation, which were significantly correlated with certain meteorological parameters. Pollen concentrations were affected positively by temperature, but negatively by relative humidity. The influence of wind direction also seemed to be explicable in these terms since the easterly winds, which are dry and hot in this region, had a positive influence, and the westerly winds which are moist and cool had a negative effect. The most relevant factor influencing levels of *Plantago* pollen in the atmosphere was wind speed, which was negatively correlated with pollen levels.

Key words: *Plantago*, aerobiology, reproduction, anemophily, pollen.

INTRODUCTION

The genus *Plantago* of the family Plantaginaceae is represented by eight species in the Extremadura Region (south-west of the Iberian Peninsula): *Plantago afra* L., *P. lagopus* L., *P. lanceolata* L., *P. major* L., *P. albicans*, *P. bellardii* All., *P. serraria* L. and *P. coronopus* L. Flowers are typically anemophilous, presenting reduced scarious corollas and stamens with developed filaments that expose the anthers to the action of the wind (Van Damme, 1992). Given the systematic position of the Plantaginaceae, this flower type has undergone a series of evolutionary transformations of the typically entomophilous corollas of the subclass Asteridae to adapt them to this system of pollination (Cronquist, 1988). However, some species, such as *P. lanceolata*, maintain a link with specific insects that might act as pollinators (Stelleman, 1978; Sharma *et al*., 1993).

The flowers exhibit protogyny; spikes mature from bottom to top and have a whorl of functionally female flowers above a whorl of functionally male flowers. The lag in growth and opening of the anthers with respect to the exsertion and onset of stigmatic receptivity is up to 4 or 5 d in the cases of *P. lanceolata* and *P. lagopus* (Sharma *et al*., 1993), and may be even longer when meteorological conditions are unfavourable for pollen release (Hyde and Williams, 1946). In some species this dichogamy is accompanied by a system of gametophytic self-incompatibility (Van Damme, 1992). In other species, however, there may be high rates of autogamy, as in the case of *P. major* (Wolff, 1991), and even of cleistogamy (Crompton, 1990; Sharma *et al*., 1993). This latter system, however, is not present amongst the European species of the genus (Van Damme, 1992).

Although the flowers of the species are described as hermaphrodite, gynodioecy is frequent in many species, caused by a cytoplasmic genetic factor of male sterility which determines the existence of three types of individual: hermaphrodite, female, and partially androsterile (Van Damme, 1983). The proportion of female and partially androsterile individuals varies between species and populations, with the former constituting up to 24 % of populations of *P. coronopus* (Van Damme, 1992; Koelewijn, 1996; Koelewijn and Van Damme, 1996) and up to 22 % in *P. lanceolata* (Van Damme and Van Delden, 1982). Androsterile individuals of *P. lanceolata* have more

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resources available for reproduction due to savings involved in the non-production of pollen. This compensates for the lack of any male contribution to the progeny, and explains why this type is maintained in the populations (see Poot, 1997). However, in other species such as *P. maritima*, the advantage of androsterile individuals has yet to be demonstrated (Dinnétz and Jerling, 1997), or has only been demonstrated with respect to the larger size of their stigmas (Dinnétz, 1997). The capacity of these individuals to be pollinated is, in any case, closely related to the distance from the nearest hermaphrodite plant (Sharma *et al*., 1993) on which their reproductive success will depend.

As anemophilly is the main pollination mechanism in the genus *Plantago*, this study aims to investigate how environmental factors affect airborne pollen concentration. Although it is obvious that environmental factors should be taken into account when determining the success and relative abundance of these species at different sites, airborne pollen concentration is also an outcome of this success.

MATERIALS AND METHODS

The pollination dynamics of *Plantago* were studied by calculating pollen concentrations in the atmosphere at three locations in SW Spain: Badajoz, Mérida and Cáceres. These cities form a triangle with sides of between 60 and 90 km in length. All three locations belong to the same Mesomediterranean bioclimatic classification and the same biogeographical province of Luso-Extremadurense (Ladero, 1987). While they are surrounded by a similar percentage of cropland (Badajoz: 66·4 %; Mérida: 70·32 % and Cáceres: 66·27 %), there is a difference in the system of agriculture used. Badajoz and Mérida benefit from the presence of the River Guadiana by having 31·3 and 11·9 %, respectively, of their area under irrigation while in Cáceres this figure is only 1·8 % (MAPA, 1984, 1985*a*,*b*). The most abundant species in the vicinity of the sporetrap sites are *P. lanceolata*, *P. coronopus* and *P. afra*; they are ruderal plants and weeds of nitrophilous and wet ground, and Cáceres is the site in which these species are most abundant. The next most abundant species are *P. lagopus* found on sandy ground, and *P. major*, requiring more humid ground, e.g. the irrigated crops near Badajoz city. *P. albicans* only appears in calcareous ground around sporetrap sites in Cáceres and Mérida. *P. serraria* and *P. bellardii* are scarce in the area.

A Burkard model volumetric trap was installed at each of the three sites to monitor concentrations of airborne particles continuously (Hirst, 1952). The study period was from 1994 to 1999 for Badajoz, and from 1996 to 1998 for Mérida and Cáceres. There were gaps in sampling due to infrastructure problems from 28 Apr. to 1 May 1995 in Badajoz, from 28 May to 6 Jun. 1996 in Mérida, and from 17 to 24 Jun. 1996 and 10 to 17 Mar. 1998 in Cáceres. The Badajoz sporetrap was 6 m above ground level on the periphery of the city in a semiurban environment; the Cáceres sporetrap was further from the city near a meadow with holm-oak and 6 m above ground level; the Mérida sporetrap was in the city, 12 m above ground level.

The data were used to calculate, firstly, the hourly rates of variation in *Plantago* pollen concentrations at each station. These were obtained by taking the arithmetic mean of the hourly concentrations for all the days on which this type of pollen was recorded in each site's atmosphere. The 95 % confidence intervals were calculated for these averages. We also calculated the daily concentrations of each pollen type for each year and each site. From the resulting patterns of daily variation, we calculated the principal pollination periods using the method of Nilsson and Persson (1981), which defines this period as from the day on which the cumulative concentrations reach 5 % of the year's total to the day on which they reach 95 %. The statistical package used was SPSS for Windows, standard version 6.1.2 of 1995.

We used the following daily meteorological data for each site: mean, minimum, and maximum temperatures (°C), relative humidity (%), rainfall (mm), wind speed (km h^{-1}), and periods of calm air and of winds from quadrants 1 (NE), 2 (SE), 3 (SW) and 4 (NW) (in h d^{-1}). For the last five parameters the data are times (numbers of hours per day, up to 24) that the wind blows from the four principal directions or times of calm. The data were provided by the Centro Meteorológico Territorial of Extremadura from the meteorological observatories corresponding to the three sampling locations. No relative humidity or wind data were available for Mérida in the *Plantago* pollination period of 1997. We studied the possible correlations between the daily meteorological parameters and *Plantago* pollen concentrations during the principal pollination periods by calculating the Spearman correlation coefficients (r) and the probability (P) that $r = 0$, taking as significant those correlations with $P < 0{\cdot}05$.

RESULTS

Although *Plantago* pollen is present in the atmosphere of the three stations at least sporadically throughout the year, pollination showed a marked phenology in all years of study. Concentrations rose during March, and from the middle of this month to June *Plantago* pollen was habitually present in the atmosphere at concentrations above 50 grains m^{-3}. The concentrations were low from July to the beginning of October, and from then on only appeared sporadically in the samples.

Figure 1 shows the principal pollination period identified in the study; this period is centred on May for all the stations, with the beginning and end of the period varying from the second half of March to the first half of April and from the second week in June to the second week in July, respectively. The shortest periods in the three stations were found in 1996: 67 d in Badajoz, 64 d in Mérida, and 61 d in Cáceres. The longest periods were recorded in 1997: 107 d in Badajoz, 111 d in Mérida, and 106 d in Cáceres.

With respect to the magnitude of pollination, Fig. 1 also shows the total cumulative *Plantago* pollen concentrations for each year and each site. There are differences between sites: while Badajoz and Mérida have similar pollination

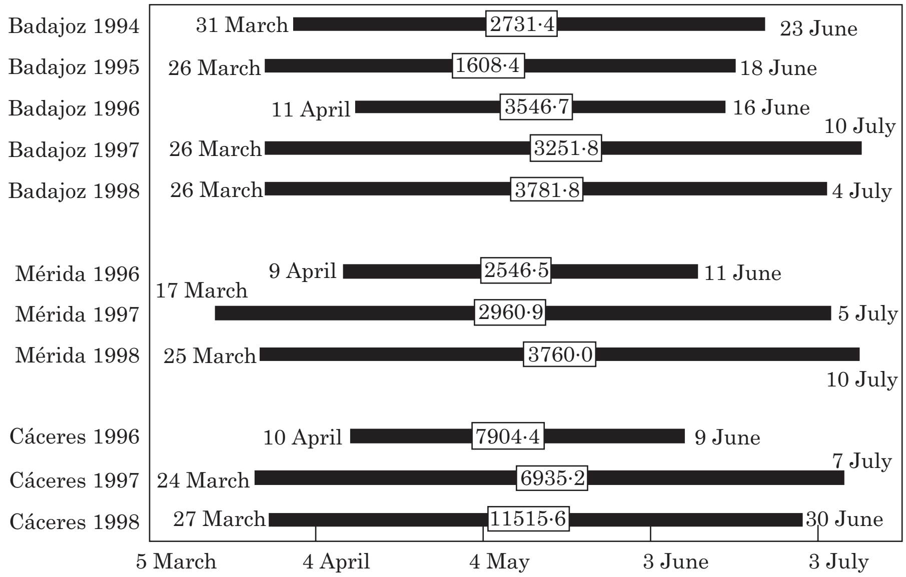

FIG. 1. Dates of the beginning and end of the principal *Plantago* pollination periods at the three study sites, and the total cumulative concentration for each year in grains m^{-3}.

TABLE 1. *Correlations between total annual concentrations of* Plantago *pollen in Badajoz and the beginning and end of the principal pollination period (expressed as the number of days since 1 January) with rainfall and mean temperatures during autumn, winter and spring, corresponding to each pollination period*

	Concentration		Begining		End	
	r	*P*	*r*	*P*	*r*	*P*
Rain						
Autumn	>0·9999*	0·000	0·1118	0·858	0·2000	0·747
Winter	0·3000	0·624	0·8944*	0·041	−0·3000	0·624
Spring	0·4000	0·505	0·6708	0·215	−0·1000	0·873
Temperature						
Autumn	0·6000	0·285	0·2236	0·718	−0·5000	0·391
Winter	0·5000	0·391	−0·7826	0·118	0·6000	0·285
Spring	−0·6000	0·285	0·1118	0·858	−0·6000	0·285

The values of the Spearman correlation coefficient (r) and the probability (P) of $r = 0$ are given. *$P < 0·05$ ($n = 5$).

levels, Cáceres has values that are at least twice as large. There are also interannual variations: in Badajoz the annual concentrations varied between 1068.4 grains m^{-3} in 1995 and 3781·8 grains m^{-3} in 1998, this latter year being that in which Cáceres and Mérida also showed maximum concentrations. Table 1 gives the results of the correlation analysis for the total annual concentrations and the dates of the beginning and end of the principal pollination period in Badajoz with respect to rainfall and mean temperature in the autumn, winter and spring. There is a significant positive correlation between the autumn rains and the level of annual pollination, and a similar correlation between the winter rains and the beginning of the principal pollination period. There is also a notable absence of any significant correlation with the mean temperatures of the different seasons.

The hourly variations of *Plantago* pollination at the three sites (Fig. 2) present a similar pattern, at least in Badajoz and Mérida, characterized by very low nocturnal concentrations before dawn, with minima at 0600 h. After daybreak, there is a progressive and rapid rise beginning at 0800 h to reach a maximum concentration at 1100 h. There is then a gradual decline during the afternoon and evening. Although the pattern is similar at Cáceres, there is an apparent advance on the above pattern. Thus the nocturnal minimum is reached at 0200 h, and the morning rise begins at 0700 h, reaching its maximum at 1000 h—1 hour before Badajoz and Mérida. Since the pollination period covers various months, Fig. 3 shows the hourly variation patterns from March to July for the Badajoz data. It is apparent that the pattern repeats itself in the months of March to June, with the concentration levels varying according to the existing pollination. In July, however, the pattern is different, being flat with uniform concentrations for all hours of the day.

Daily variations showed similar patterns for all three sites (Fig. 4) The coincidence in dates of the different annual maxima is clear. Correlations between the daily

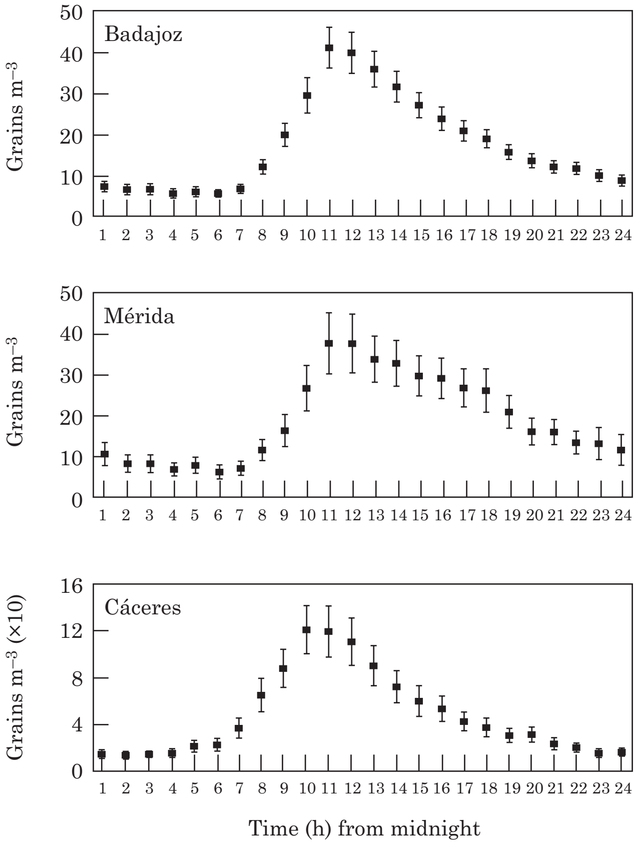

FIG. 2. Hourly variations in *Plantago* pollen concentrations at the three study sites, showing the means and 95 % confidence intervals of the values reached on days when *Plantago* pollen was observed.

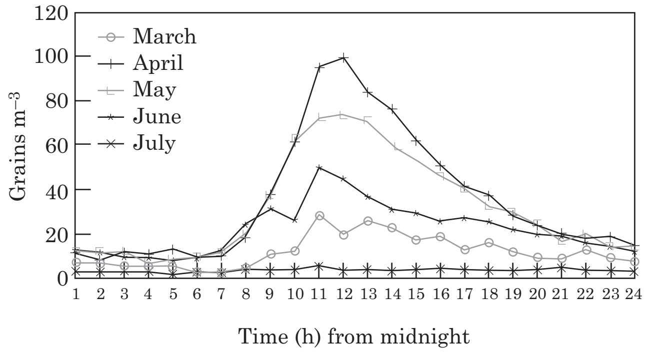

FIG. 3. Hourly variation in *Plantago* pollen concentrations in Badajoz from March to July, showing the means of the values reached on days when this pollen type was observed for all the years of the study.

concentrations recorded at the three sites during the common principal pollination periods of these three years were always significant and positive (Table 2).

Table 3 shows correlations between the pollen concentrations and the daily meteorological parameters. Wind speed showed the most correlations being significantly negatively correlated with the daily pollen concentrations for almost every year and every site. With respect to the remaining parameters, rainfall was significantly negatively correlated in ten of the 12 cases, and relative humidity was also negatively correlated in nine of the 12 cases. Of the thermal parameters, there were significant positive correlations in nine cases with the daily maximum temperatures, and in eight cases with the mean temperatures. It is noteworthy that, with respect to the minimum temperatures, there were significant correlations in only three cases, two of which were negative. As well as wind speed, there were significant correlations with other wind parameters: periods of calm were correlated with pollen concentrations in nine cases—the correlation being positive (and thus opposite to that for wind speed, as expected). With respect to wind direction, periods of winds from the NE were always positively correlated with pollen concentration (significant in eight cases), SE winds were positively correlated (significant in seven cases), SW winds showed nine significantly negative correlations, but NW winds only showed three statistically significant correlations; these were negative.

DISCUSSION

Pollen concentrations in the atmosphere may be taken as a measure of the intensity of the transport of an anemophilous plant's pollen. Thus the results of the present study have to be discussed in terms of the pollination system, and their interpretation sought in the functionality of the biological processes.

The first point for discussion has to be the differences found in pollination intensity at the different sites and for the different years of the study, together with their phenology. With respect to the former, there was a great similarity between the annual behaviour in Mérida and Badajoz, whereas Cáceres showed more intense pollination. An explanation of this phenomenon lies in the surroundings of each city and their environmental conditions; in Cáceres, the trap was located on the outskirts of the city in a location where *Plantago* species were much more abundant than at the Badajoz or Mérida sites. With respect to the interannual

TABLE 2. *Correlations (Spearman) of the* Plantago *pollen concentrations recorded between the three sites, using in each year the common principal pollination period (1996: 9 April to 6 June; 1997: 17 March to 10 July; 1998: 25 March to 10 July)*

	1996			1997			1998		
	r	*P*	*n*	*r*	*P*	*n*	*r*	*P*	*n*
Badajoz–Mérida	0·6307	0·0001	49	0·7980	0·0001	116	0·8570	0·0001	107
Badajoz–Cáceres	0·7109	0·0001	58	0·7552	0·0001	116	0·8174	0·0001	107
Mérida–Cáceres	0·7555	0·0001	49	0·6847	0·0001	116	0·8106	0·0001	108

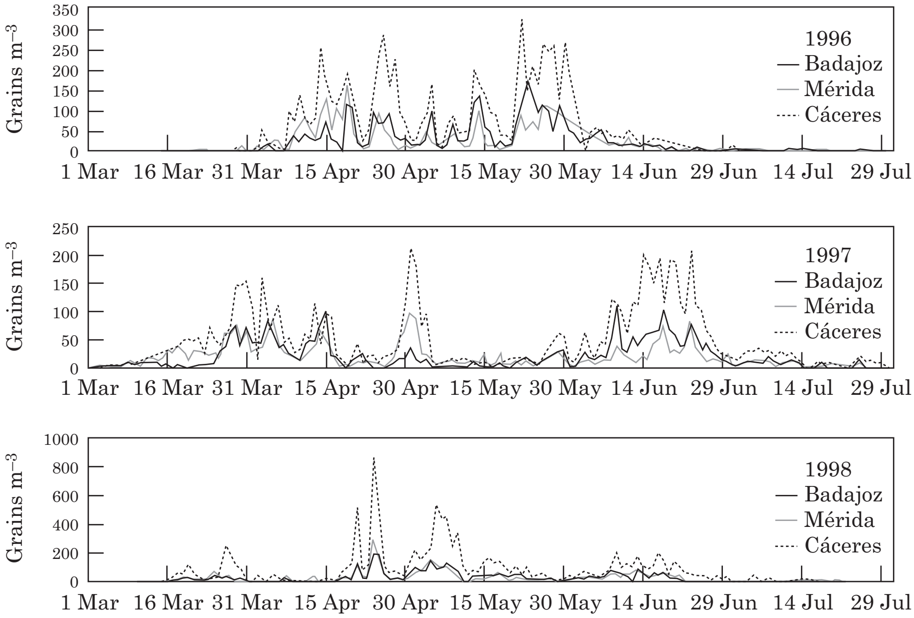

FIG. 4. Variations in daily *Plantago* pollen concentrations during 1996, 1997 and 1998 for the three study sites.

differences at a given site, the analysis performed on the Badajoz data seems to indicate that the explanation might lie in the autumn rains which, as with other herbaceous groups studied in the same location (Silva *et al*., 1998*a*,*b*), influence the development of the populations and hence the pollination levels. With respect to the differences in the beginning and end of the principal pollination periods, we found a significant positive correlation only between the winter rains and the start of the principal pollination period. There seems to be no biological reason that would explain why these rains would delay the onset of the pollination period. In this regard, it is also necessary to take into account the observations of Poot (1997), who indicated that, in *P. lanceolata*, different individuals show considerable variation in phenology, even under homogeneous conditions.

The hourly patterns of pollen capture at the three sites are centred around midday. The regularity of this model, and its maintenance throughout flowering, reveal a certain lack of dependence on the physical factors of atmospheric transport, but a very close relationship with the timing of anthesis of the *Plantago* species. Hyde and Williams (1946) also observed that opening of the anthers of *P. lanceolata* is centred around the hours of midday, coinciding with their observations of airborne pollen capture. Recio *et al*. (1997) also found a pattern of hourly variation that was constant over a number of years in Málaga, and clearly centred between 1200 and 1400 h. Von Wahl and Puls (1991) found peaks towards midday in Essen, but in Córdoba, Galan *et al*. (1991) observed a pattern that was shifted towards the afternoon hours.

There are variations in the daily levels of *Plantago* pollen concentration within each year's pollination period. These give rise to distinct pollination peaks that might, in certain cases, be interpreted as the successive flowering of different species of the genus, as occurs with other anemophilous taxa whose species succeed each other in anthesis. In the present study, however, the variations can be interpreted on the basis of the daily variations in meteorological parameters. Some of these have a known influence on the concentrations of airborne pollen. For instance, relative humidity generally has a negative effect in Spanish aeropalynological studies (Herrero and Fraile, 1997), and in particular is in accord with the observations of Hyde and Williams (1946) on *P. lanceolata* anthesis in Cardiff, Wales. The positive influence of temperature on pollen concentrations is a frequent finding in these studies. Thus, in the particular case of the Iberian Peninsula, Fernández *et al*. (1993) and Martín *et al*. (1990) showed the positive effect of thermal parameters on plants whose pollination occurs before summer; and for *P. lanceolata*, Hyde and Williams (1946) observed that the flowers may remain in a stationary state, with no pollen release, when the temperatures fall during the pollination period, even when the female phase of the flowers has already been initiated. The existence of a significant negative correlation between the daily *Plantago* pollen concentrations and the maximum temperatures in 1995 in Badajoz could be explained by the abnormal conditions that occurred in this year, when the maximum temperatures were the highest recorded during the study period (the mean maximum temperature in May 1995 was 4°C hotter than in the other years), and consequently the mean relative humidity of these months was the lowest (Muñoz *et al*., 2000*a*). Our findings were not merely a local phenomenon since even in Málaga, 340 km away, there was also a notable decline in pollen concentration in 1995 (Recio *et al*., 1997). According to Koelewijn and Van Damme (1996), when the temperatures rise above 15–20°C, there is an increase in the percentage of sterile anthers in *P. coronopus*.

The negative influence of rainfall on airborne pollen grains is a global finding in aeropalynological studies. This is explained on the basis of the sedimentation of the grains and the corresponding increase in relative humidity. This

TABLE 3. *Correlations between the daily pollen concentrations and the meteorological parameters within the respective principal pollination periods*

	Mean temperature	Max. temperature	Min. temperature	Relative humidity	Rain	Wind	Calm periods	NE wind	SE wind	SW wind	NW wind
BADAJOZ											
1993	−0·1493	−0·0280	−0·3449**	−0·0877	−0·0732	−0·3029*	0·3099*	0·2128	0·1719	−0·1060	0·0376
($n = 60$)	0·255	0·832	0·007	0·505	0·578	0·019	0·016	0·103	0·189	0·420	0·776
1994	0·3424**	0·5392***	0·0684	−0·8242***	−0·5103***	−0·4667***	0·3246**	0·6758***	0·3059**	−0·4503***	−0·0105
($n = 85$)	0·001	0·000	0·534	0·000	0·000	0·000	0·002	0·000	0·004	0·000	0·924
1995	−0·1389	0·0887	−0·3399***	−0·2911**	−0·2563**	−0·3132**	0·2004	0·5036***	0·3932***	−0·3659**	−0·2274*
($n = 81$)	0·216	0·431	0·002	0·008	0·021	0·004	0·073	0·000	0·000	0·001	0·041
1996	0·1911	0·2061	−0·0058	−0·1529	−0·2663*	−0·3515**	0·1459	0·1509	0·1019	−0·1678	0·0724
($n = 67$)	0·121	0·094	0·963	0·217	0·029	0·004	0·239	0·223	0·412	0·175	0·561
1997	0·3299**	0·5190***	−0·0104	−0·4007***	−0·3864***	−0·2677**	0·2886**	0·3470***	0·2583**	−0·3522***	−0·0429
($n = 107$)	0·001	0·000	0·915	0·000	0·000	0·005	0·003	0·000	0·007	0·000	0·661
1998	0·2487*	0·3241**	0·1209	−0·3167**	−0·2152*	−0·3489***	0·2450**	0·5417***	0·3851***	−0·4000***	−0·0338
($n = 101$)	0·012	0·001	0·228	0·001	0·031	0·000	0·014	0·000	0·000	0·000	0·737
CÁCERES											
1996	0·3809**	0·4278**	0·1522	−0·3735**	−0·2845*	−0·5763***	0·3933**	0·4012**	0·1159	−0·2821*	0·2852*
($n = 61$)	0·002	0·001	0·241	0·003	0·026	0·000	0·002	0·001	0·374	0·028	0·026
1997	0·5049***	0·5751***	0·2706**	−0·3833***	−0·3314**	−0·2399*	0·1975*	0·2449*	0·1197	−0·3526***	0·2783**
($n = 106$)	0·000	0·000	0·005	0·000	0·001	0·013	0·042	0·011	0·222	0·000	0·004
1998	0·3274**	0·4225***	0·1588	−0·4121***	−0·1763	−0·3993***	0·3690***	0·4513***	0·4034***	−0·3737***	−0·0481
($n = 91$)	0·001	0·000	0·122	0·000	0·086	0·000	0·000	0·000	0·000	0·000	0·641
MÉRIDA											
1996	0·5645***	0·6387***	0·1920	−0·6246***	−0·4013**	−0·3309*	0·3683**	0·1324	0·2742*	−0·2996*	−0·0817
($n = 54$)	0·000	0·000	0·164	0·000	0·003	0·016	0·006	0·340	0·045	0·028	0·557
1997	0·2320*	0·5298***	−0·1334	−0·9487	−0·2812**	−0·9487	0·7746	0·9487	0·7746	−0·8000	0·4000
($n = 111$)	0·014	0·000	0·163	0·051	0·003	0·051	0·225	0·051	0·225	0·200	0·600
1998	0·1089	0·2673**	−0·1071	−0·4998***	−0·3443***	−0·3661***	0·3599***	0·5678***	0·3925***	−0·6546***	0·1716
($n = 108$)	0·262	0·005	0·270	0·000	0·000	0·000	0·000	0·000	0·000	0·000	0·076

The values of the Spearman correlation coefficient (r), the probability (P) that $r = 0$, and the number of data points (n) are given. $^*P < 0{\cdot}05$, $^{**}P < 0{\cdot}01$, $^{***}P < 0{\cdot}001$.

generalized influence was regularly and significantly manifest in the present study. In this regard, it is worth noting the observations of Hyde and Williams (1946) who observed no reductions in pollination rate or floral anthesis during rainy days.

With respect to the influence of wind direction, the positive relationships with winds from quadrants 1 and 2, both with an easterly component, for all three sites might, in principle, be interpreted as a contribution of pollen from a localized source. The distribution of the genus in the study region, however, lends little support to this hypothesis. On the contrary, there is a proven relationship between the direction of the wind and its thermal and humidity characteristics in this zone of the Iberian Peninsula: the westerly winds are cool and moist, while the easterly winds are hot and dry (Font, 1983). The influence of wind direction has therefore to be explained as a reflection of its temperature and humidity.

Of all the meteorological parameters studied, wind speed has the most influence in all years and for all study sites. By way of example, Fig. 5 shows the evident negative influence of this factor on the pollination phenology in Badajoz during 1996, a pattern that was repeated at the other locations. There are two phenomena that might explain the negative effect of wind speed: (1) it might have a negative effect on pollen capture; or (2) it might directly affect pollen release by the flowers. With respect to the former, in previous studies carried out at the three sampling sites, only pollen from the Chenopodiaceae and Amaranthaceae has shown this negative relationship with wind speed. The explanation proposed is that transport and dilution is caused by the movement of the air, since these sources of pollen are centred in the immediate vicinity of the sampling sites, so that the wind dilutes and carries off the pollen accumulated in the zone (Muñoz *et al*., 2000*b*). This is not such an adequate explanation for *Plantago*, however, since the pollen sources are scattered throughout the region, and such a close relationship reveals a direct effect of increasing wind speed on lowering pollen concentrations. Glassheim *et al*. (1995) also found a negative relationship between wind speed and pollen from weed species, but did not consider individual pollen types, explaining this as a 'wind scrubbing' effect at higher wind velocities.

Wind might also affect the units of dispersion, impeding them from reaching the traps. Studying genetic dispersion via pollen in *P. lanceolata* using a wind tunnel with a constant wind speed of 4·5 km h^{-1}, Tonsor (1985) concluded that the unit of genetic flux in this species is the release of pollen grains in masses, but that beyond 1·2 m most of the grains travel singly. In the present work, most of the grains for all three sites and in all the years were not clustered. It might be supposed that their capture represented the remnant left over from the intrapopulational pollination by clusters of pollen grains, as assumed by Tonsor. Therefore, any factor that leads to more grains being released in masses, such as increased wind speed which would violently strip the grains from the anthers in relatively heavy clusters that are unable to travel great pollination distances, would lead to a reduction in pollen capture in the traps.

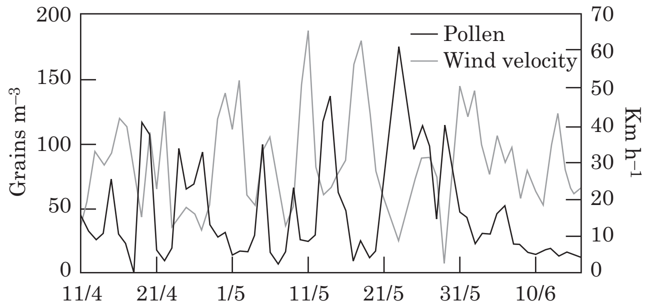

FIG. 5. Variations in the daily *Plantago* pollen concentrations in the atmosphere at Badajoz and daily wind speed for the principal pollination period of 1996.

This direct action of wind speed on pollination levels could also be explained as a negative effect on pollen release. In principle, this would be somewhat strange for an anemophilous plant in which one would suppose that wind would favour the dispersion of its pollen. It would also contradict observations on *P. lanceolata* by Hyde and Williams (1946), who found that low wind speeds led to a lack of pollen release from the anthers. It must be noted, however, that their observations were made in light and gentle breezes, below 4 on the Beaufort scale (less than 20 km h^{-1}). These speeds are less than those that reduced the pollen concentrations in the present study.

In any case, the decrease in pollen capture rate as wind speed increased is evidence for the reduction in pollen transport between populations under these conditions, whether because intrapopulational pollination is favoured by heavy pollen clusters, or because anther opening is repressed. It therefore seems that the wind conditions that favour pollination of these species are those that guarantee high levels of pollen concentration within the populations. This is concordant with the existence of gynodioecy in this genus, since the establishment of androsterile plants, carriers of the androsterility factor, is based on their reproductive success. This would only be so if there was a guarantee of the fecundity of their surplus of seminal primordia, in response to the greater allocation of resources that these plants enjoy as compensation for their lack of pollen production (Poot, 1997).

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