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Aerobiological behaviour of six anemophilous taxa in semi-arid environments of southern Europe (Almería, SE Spain)

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ABSTRACT

Airborne pollen records constitute a suitable bioindicator for evaluating physiological behaviour and resource conservation of vegetation responding to water deficit, reflected in pollination alterations (fluctuations in the dates of the beginning and end of the pollination period), or variation in total pollen production. The effects of extreme climatic conditions, such as increased inter-annual variability of rainfall and reduced rainfall, can be the limiting factors for pollen production and pollination patterns. We explore the effect that seasonal and inter-annual variation in climatic patterns (emphasizing the alteration of rainfall regimes) exert on pollination pattern in six anemophilous taxa located in the semi-arid area of Almería (SE Spain), which is considered to be one of the areas with the highest aridity index in Europe. The sampling in a temporal series of 8 years (1998–2005) showed the pulsed and discrete rainfall events interspersed with drought periods are closely related to the alteration of the pollination in certain species. This is manifested in: (i) delayed onset of flowering until reaching the minimum threshold of soil water, in the case of some annual plants (*Plantago*, *Rumex*, and Poaceae), or (ii) scant variability both in the flowering period in plants with drought tolerance (Chenopodiaceae and *Artemisia*) or plants often linked to soil-moisture availability (Urticaceae).

1. Introduction

Knowing the behaviour of vegetation subjected to extreme climatic episodes is of the utmost importance for understanding and estimating the response and evolution of ecosystems in future climatic scenarios. Most climate scenarios predict increased temperature and an overall decrease in rainfall in some regions of the globe such as the Mediterranean, with more rain events in winter, fewer rainy days, and longer drought periods between events, thus making rainfall patterns more extreme (Easterling et al., 2000; IPCC, 2007). The implications of these events will be particularly significant for areas currently subjected to a high degree of aridity stress (Peñuelas and Boada, 2003), such as south-eastern Spain, one of the European areas with an extreme aridity index. This area, included in the Mediterranean region, has already undergone progressive aridification over recent decades (Peñuelas et al., 2002; Peñuelas and Boada, 2003) and currently presents great geographical and temporal variability in precipitation and water availability (Peñuelas, 2001).

In arid and semi-arid ecosystems, water is the most important limiting resource, and thus temporal patterns of plant growth and reproduction have generally been related to its availability (Abd El-Ghani, 1997; Pavón and Briones, 2001). Sub-desert plants have had to develop many mechanisms to maintain a positive balance between assimilation and respiration by developing two basic strategies: (i) drought resistance; and (ii) drought evasion (e.g. Pavón and Briones, 2001). The two strategies coexist in the semi-arid environments and differ in the degree to which their biological activity is geared to rainfall pulses, as well as water reserves (Noy-Meir, 1973). Plant life form has also been related to phenological pattern in sub-desert plants (Bertiller et al., 1991; Abd El-Ghani, 1997; Pavón and Briones, 2001; Peñuelas et al., 2004).

Many works have examined the implications of such changes for arid and semi-arid lands, emphasizing the impact of drought on growth (Körner et al., 2005), survival (Macias et al., 2006), and distribution (Peñuelas and Boada, 2003). However, the effects of altered seasonal rainfall patterns (IPCC, 2007) have been poorly explored (Fay et al., 2000); so far, few researches have addressed

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the ecosystem responses to changes in seasonal precipitation distribution (e.g., Svejcar et al., 1999; Suttle et al., 2007) and pulsed rain events (e.g., Chesson et al., 2004; Schwinning and Sala, 2004). For an understanding of responses of plant communities to climate change, it is important to address flowering phenology – including from an aerobiological standpoint. Previous aerobiological studies have used the measurement of biological particles to complement studies on the dynamics and alteration of terrestrial ecosystems, providing data of great interest concerning the response of vegetation to global warming (e.g. Vliet et al., 2002; Cariñanos et al., 2004; Galán et al., 2004; Gehrig, 2006; Recio et al., 2009).

In the present work, we explore the effect that seasonal and inter-annual variation in climatic patterns (emphasizing alteration of rainfall regimes) exert on the pollination pattern in some anemophilous sub-desert plants. Our hypothesis states that airborne pollen records constitute a suitable bioindicator for evaluating physiological behaviour of vegetation responding to water deficit, reflected in alterations in length of the pollination period and pollen production. We expected that both flowering-time and pollen production would be related to the capacity of these species to respond to seasonal pulses of water and rainfall quantity.

2. Materials and methods

2.1. Study area and surroundings

The study area is within the province of Almería, (SE Iberian Peninsula). The rich and varied flora and vegetation in the south-eastern Spain is a result of a complex orography and an extensive altitudinal gradient (0–3400 m asl), giving rise to the abrupt climatic contrasts. This diversity can be divided into three biogeographic provinces (Rivas-Martínez et al., 2002) and diverse series of vegetation (Valle, 2003), as reflected in Fig. 1 and Appendix 1.

The two climatic zones, according to the UNESCO aridity index (UNESCO, 1979), are also displayed in Fig. 1. According to this classification, the study area belongs to semi-arid zone ($0.20 \leq P/PET \leq 0.50$), and in fact this area is located in one of the driest regions in Europe. The aridity index was calculated using Pennman's formula: P (Precipitation values) and PET (Potential Evapotranspiration); mean values (P and T) supplied by regional government of Andalusia (www.juntadeandalucia.es/medioambiente/).

The aerobiology study was made in the city of Almería. This zone (36°50′ N; 02°28′ W) is bordered to the south by the Mediterranean Sea, and towards the interior by the Baetic Mountain Range. The Baetic Range rings the large semi-arid areas called Tabernas sudesert, Campos de Nijar, and Campos de Dalías. In this study, we established an area of 40 km in diameter as the potential zone of influence for the aerobiological particle trap according to the direction of the prevailing winds of the area. This potential zone circumscribes the three semi-arid zones and some Baetic mountains (Fig. 1). The dominant vegetation are shrubs such as *Zizyphus lotus, Maytenus senegalensis, Periploca laevigata, Chamaerops humilis*, often giving way to brush such as esparto grass (*Stipa tenacissima*), *Artemisia* sp. or halophytes of the family Chenopodiaceae. Some sub-desert plants are exclusive of the study area and others are also found in North Africa. It is remarkable that in this semi-arid environment, therophytes are the life form best adapted to this habitat, followed by hemi-cryptophytes, dwarf chamaephytes and low phaneorophytes, and finally geophytes and helophytes (Merlo et al., 2004).

The ombrothermic diagram (Bagnoul and Gaussen, 1957) shows the temperature and precipitation values during the period

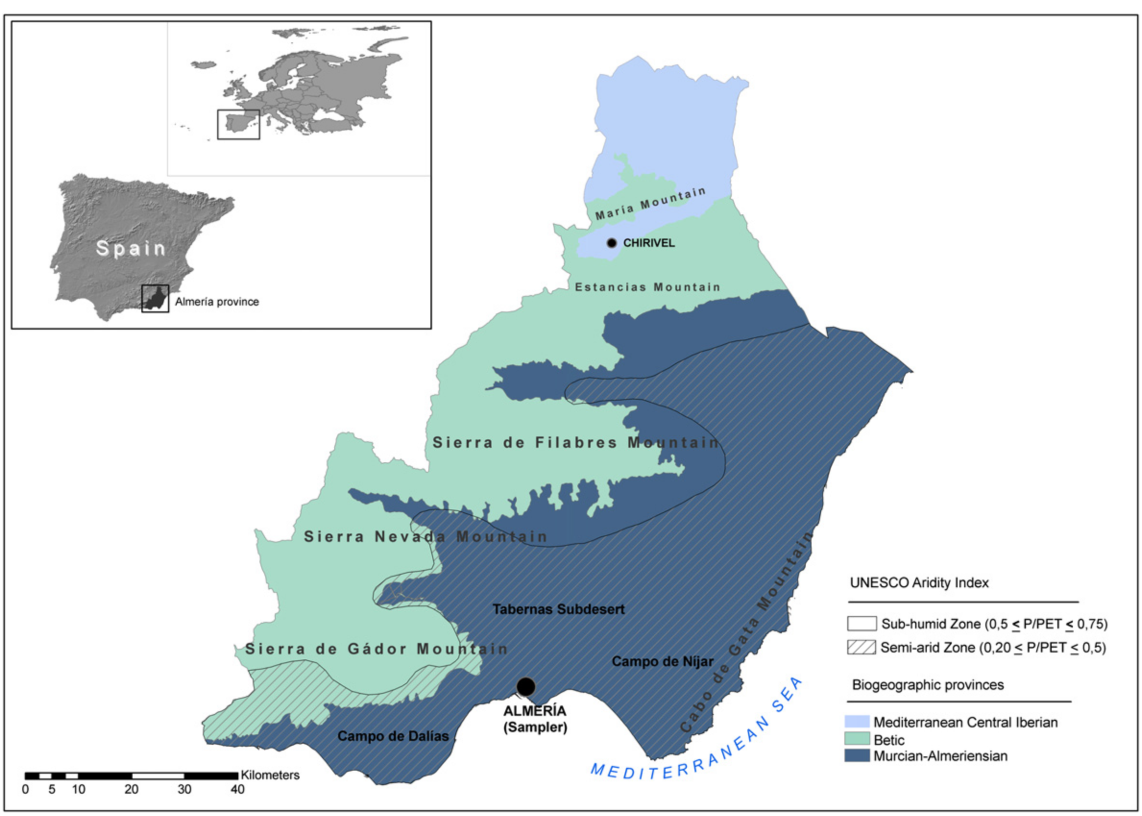


Fig. 1. Geographical location of Almería city and position of the pollen-sampling station in relation to the Biogeographic provinces (Rivas Martinez et al., 2002) and the climatic zones according to the UNESCO aridity index (UNESCO, 1979).

1971–2000 (Appendix 2A). The rainfall time-series 1971–2001 from the Almería airport weather station averaged 196 mm yearly (www.aemet.es); the latter data contrasts with those reported by Roldán (1988) for the previous period 1941–1970 (230 mm). The rainfall distribution pattern is typically Mediterranean; the mean annual temperature fluctuates between 16 and 18 °C, while in the dry season, the maximum temperature is over 30 °C, this situation accentuating the drought conditions. The water-balance diagram (Thornthwaite and Mather, 1957) shows a water deficit throughout most of the year, peaking in summer. The diagram also displays the period of water reserves utilized by the plants (January–March) and water surplus was not detected (Appendix 2B).

2.2. Methods

For aerobiological analysis a volumetric Hirst-type spore trap (Lanzoni VPPS 2000) was used (Hirst, 1952) for 8 years (1998–2005). The trap was placed in Almería city at an altitude of 23 m above soil level. For collecting and handling data, the protocol of REA (Spanish Aerobiology Network; Galán et al., 2007) was used. The data were expressed as mean daily pollen grains per cubic meter of air (grains/m^3).

Appendix 3 lists the annual mean percentage of the 38 pollen morphotypes sampled in Almería. In addition, the total annual values (or pollen production index) as well as the mean percentage of the six selected taxa (*Artemisia*, Chenopodiaceae, *Plantago*, Poaceae, *Rumex* and Urticaceae) are shown in Table 1. As a means of exploring the relationship between flowering phenology and meteorological variables, the pollination periods of the six anemophilous taxa were coupled with seasonal variation in meteorological patterns (mean, maximum, and minimum temperature; and total precipitation); also, both data series were shown year-by-year in separate graphs (Figs. 2 and 3A–F) and expressed in 10-day values; i.e. temperature values for 10-day means (°C), precipitation data in 10-day totals (mm) and the concentrations of airborne pollen in 10-day means (grains/m^3). The length of the pollination period (number of days), also called main pollen season (MPS) was determined at 95% of the annual pollen recorded, following Nilsson and Persson (1981).

Following Díaz de la Guardia et al. (2003), for estimating the influence of temperature and rainfall regarding the onset of pollination, a *Spearman's* correlation between the series of meteorological parameters mentioned above (cumulative values) and the series of airborne pollen records (daily values) was used (Table 2). The cumulative meteorological values were calculated using the cumulative sum for the daily data; the above-mentioned algorithm is specific for each taxon/year, and the starting date for accumulating daily values is one-month (30 days) preceding the start date of the pollen season (Emberlin et al., 1993). Finally, to test the hypothesis that the inter-annual and seasonal precipitation variability has more influence on the pollination patterns than inter-annual temperature, the non-parametric *Kruskal-Wallis* one-way analysis of variance by ranks was applied to our data set (Appendix 4).

3. Results

3.1. Climatic data

3.1.1. Inter-annual variation of the precipitation and temperature

In general terms, Fig. 2 shows that autumn and spring are the rainiest periods, with longer drought episodes during the summer. However, the most important elements of the annual precipitation pattern are discrete rainfall events alternating with drought periods. In relation to annual records, we noted an extreme drought in 1998 (66 mm), as well as in 2001 and 2005 (115 and 136 mm, respectively), but under normal conditions these values range between 218 mm (1999) and 308 mm (2002). The mean annual temperature remained quite stable over the 8 years, ranging from 19.0 °C (2004) to 19.3 °C (1999). The highest seasonal values were reached during the summer (27–28 °C) and the lowest during January and February (13 °C), with quite moderate temperature fluctuations both daily as well as annually.

3.2. Pollen spectrum

3.2.1. Pollen data

Over the 8 years sampled, 38 pollen morphotypes were identified in Almeria, 20 from woody species and 18 from shrubs/herbaceous ones (Appendix 3). Furthermore, sporadically morphotypes appeared, these coming from entomophilous species (*Cruciferae, Fabaceae, Umbelliferae*, etc.), from taxa scarcely represented in the area *(Acer, Alnus, Populus, Ulmus,* etc.), or from widely distributed halophyte but entomogamous plants, such as *Zygophyllum, Thymelaea,* Tamarix (Appendix 3). The inter-annual means for the six most representative taxa (shrubs/herbaceous species) and the total inter-annual pollen records are shown in Table 1. The latter records reflect great inter-annual fluctuation, from 13,096 grains (1998) to 25,114 grains (2001), registering the highest annual pollen intensity throughout the period 2001–2005.

3.2.2. Inter-annual pollination behaviour

Fig. 3 reflects the inter-annual length of the six herbaceous-taxa pollen season (MPS) as well as the pollen production. In general terms, the pollination patterns shift year-by-year, especially in relation to the onset and length of flowering, and pollen production. We should clarify that the negative influence of rainfall during the pollination process is a global finding in aeropalynological studies. This is explained by the sedimentation of the grains and the corresponding increase in relative humidity.

Artemisia (Fig. 3A) presented slightly heterogeneous pollen production index, which is visibly affected not only by the drought

Table 1
Annual pollen production index (expressed in number of grains/year), sum of the pollen grains recorded (total pollen) and mean percentage values (%) of the six herbaceous/shrub taxa studied (*Artemisia*, Chenopodiaceae, *Plantago*, Poaceae, *Rumex* and Urticaceae) in Almería over 8 years (1998–2005). The yearly pollen spectrum (total pollen grains/year) is also shown.

		1998	1999	2000	2001	2002	2003	2004	2005	Total pollen	%
Shrubs/herbaceous species	*Artemisia*	1140	547	969	745	1262	1024	430	704	6820	5
	Chenop./Amaranth.	1630	1551	1846	1890	2228	1869	1929	2121	15,063	10
	Plantago	186	97	301	352	292	329	132	232	1921	1
	Poaceae	527	420	857	1505	1914	1064	1570	576	8433	6
	Rumex	124	45	77	123	120	113	88	27	717	1
	Urticaceae	1565	1392	1881	2635	1781	1656	1283	1700	13,892	9
	Other taxa	7924	10,314	10,985	17,865	13,019	13,391	11,233	18,024	102,755	67
	Yearly pollen spectrum	13,096	14,365	16,916	25,114	20,616	19,446	16,665	23,384	149,601	100

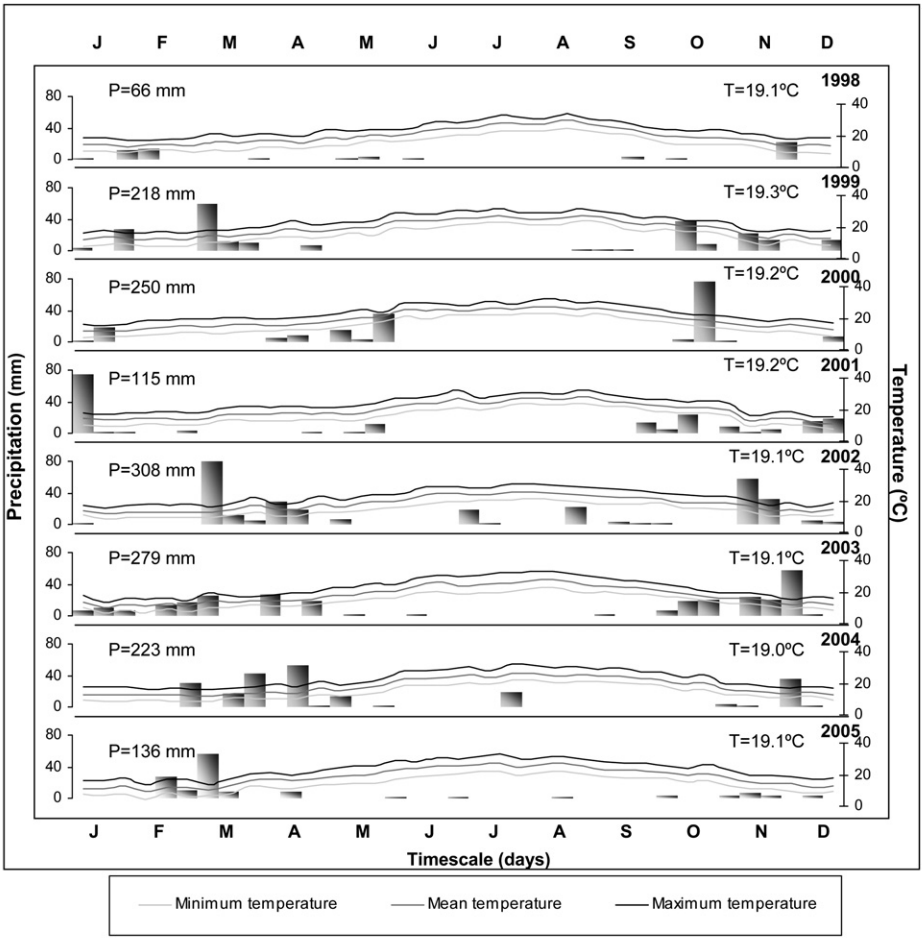


Fig. 2. Seasonal variation in meteorological patterns (maximum, mean and minimum temperature; and total precipitation) over the study period (1998–2005). The data series are expressed in 10-day values: temperature values for 10-day means (°C) (see line chart) and precipitation data in 10-day totals (mm) (see bar graphs). One day is the minor unit in the timescale of the *x*-axis. P, total annual precipitation; T, mean annual temperature.

periods but also by the presence of rainfall during pollination. The peak years for pollen records (1998: 1140 grains, and 2002: 1262 grains) coincided with highly uneven periods in terms of precipitation quantify and distribution (see Table 1 and Fig. 2). *Artemisia* presented a seasonality in two well-differentiated periods, summer due to the pollination of *Artemisia campestris* and winter to early spring due to *Artemisia barrelieri*. It bears emphasizing that these taxa have a very long flowering period (153–203 days) and that the beginning and ending date barely fluctuated throughout the study period. Chenopodiaceae presented uniform seasonality over the 8 years of sampling (Fig. 3B). This morphotype pollen also exhibited a very long MPS (>220 days) and the length remained almost invariable over the study period. In relation to the annual pollen concentration, this taxon showed less fluctuation than did *Artemisia*, so that the records ranged between 1551 grains (1999) and 2228 (2002) grains (Table 1).

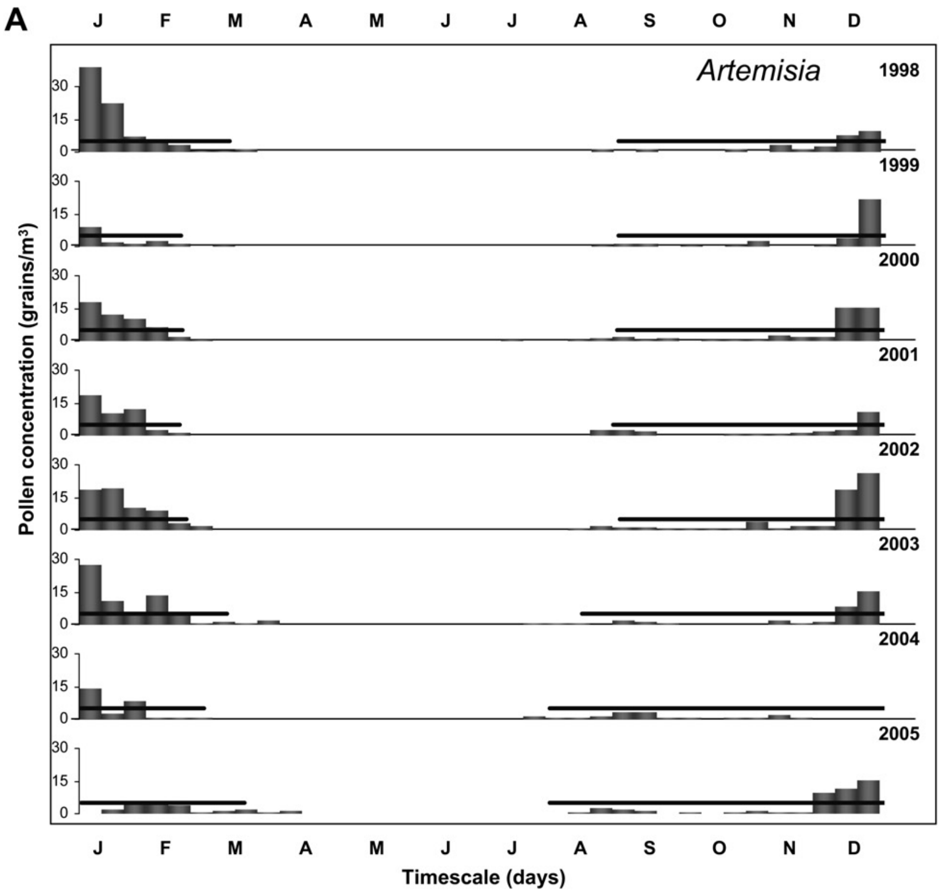
On the contrary, *Plantago* and *Rumex* (Fig. 3C and E) presented an irregular pollen production pattern, both in annual and inter-annual periods, high airborne pollen concentrations alternating with very low values. When the rainfall events were concentrated in the winter and early spring months (Fig. 2), *Plantago* and *Rumex* had a positive response, and the lag times between the water pulse and their response were relatively short. Under these conditions, airborne pollen values were significantly higher for *Plantago* and sometimes for *Rumex* (2000–2003). Clearly, rain events during the pollination process negatively affect the pollen released – see *Rumex* season during 1998 and 2005 (Fig. 3E). Additionally, the onset of flowering dates, as well as the duration of pollination displayed a great inter-annual disparity (Fig. 3C and E).

The total annual records of Poaceae (Fig. 3D and Table 1) oscillated widely over the study period. It seems that the annual Poaceae pollen production index is related to the rainfall quantity, for example in drought years, and when the pre-seasonal rainfalls were scarce (1998, 1999 and 2005) the pollen production indexes were relatively low (527, 420, and 576 grains, respectively). Contrary, the phenological response was favourable during rainy years as well as precipitation prior to flowering success – see the Poaceae season during 2000, 2003 and 2004 (Fig. 3D) and annual pollen production (Table 1). In general terms, the Poaceae pollen season has shown a heterogeneous inter-annual pattern.

Urticaceae airborne pollen was detected practically every day of the year (Fig. 3F) and its presence in the samples was continuous. Certain periods (August–November) registered low concentrations (1–10 grains/m^3) whereas the higher levels (10–30 grains/m^3) were reached in the months of March and April. The pollen production as well as the length of the flowering period increased when the pluviometric conditions were favourable (e.g. winter 2000–spring 2001). The onset of the pollen season, generally in October, appeared to be related to the beginning of the rainy period in Almería.

3.3. Analysis of pollen records versus climatic variables

The correlation coefficients between the accumulated climatic variables and the daily levels of pollen sampled (Table 2) revealed



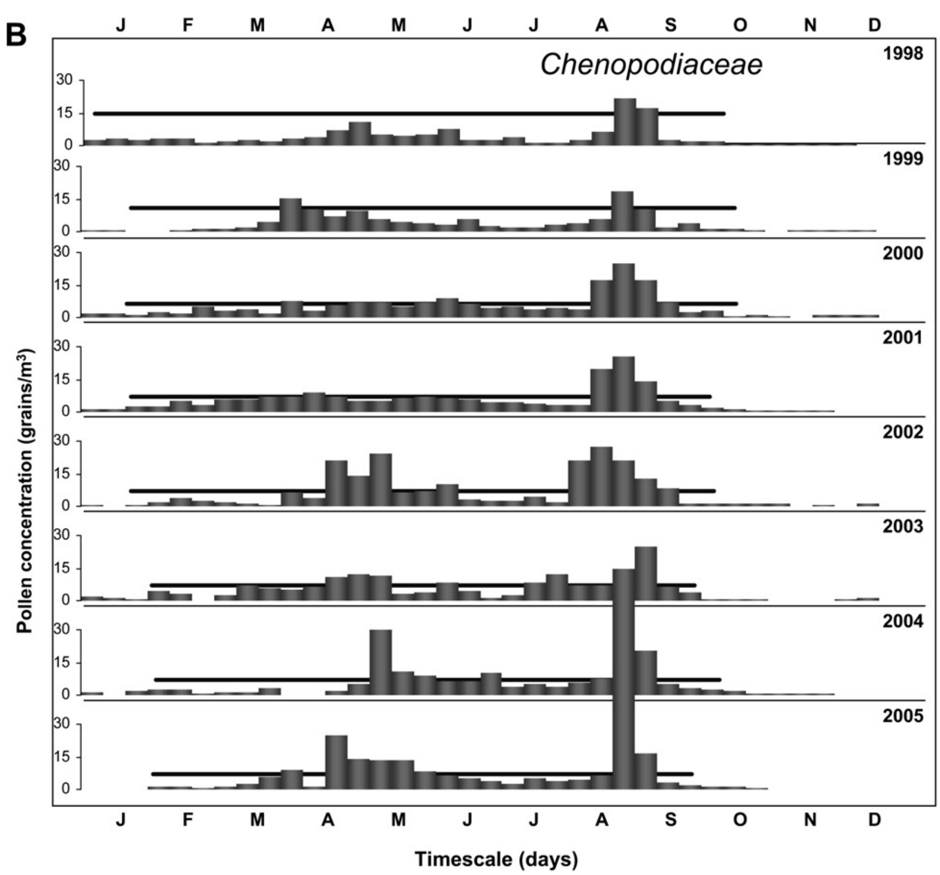


Fig. 3. The pollination periods of the six anemophilous taxa studied are shown year-by-year. Firstly, the concentrations evolution of airborne pollen is expressed in 10-day means (grains/m^3) (see bar graphs). Secondly, the length of the main pollination period (Nilsson and Persson, 1981), expressed in number of days, is displayed by means of a horizontal line. One day is the minor unit in the timescale of the *x*-axis. (A) *Artemisia*, (B) Chenopodiaceae, (C) *Plantago*, (D) Poaceae, (E) *Rumex* and (F) Urticaceae .

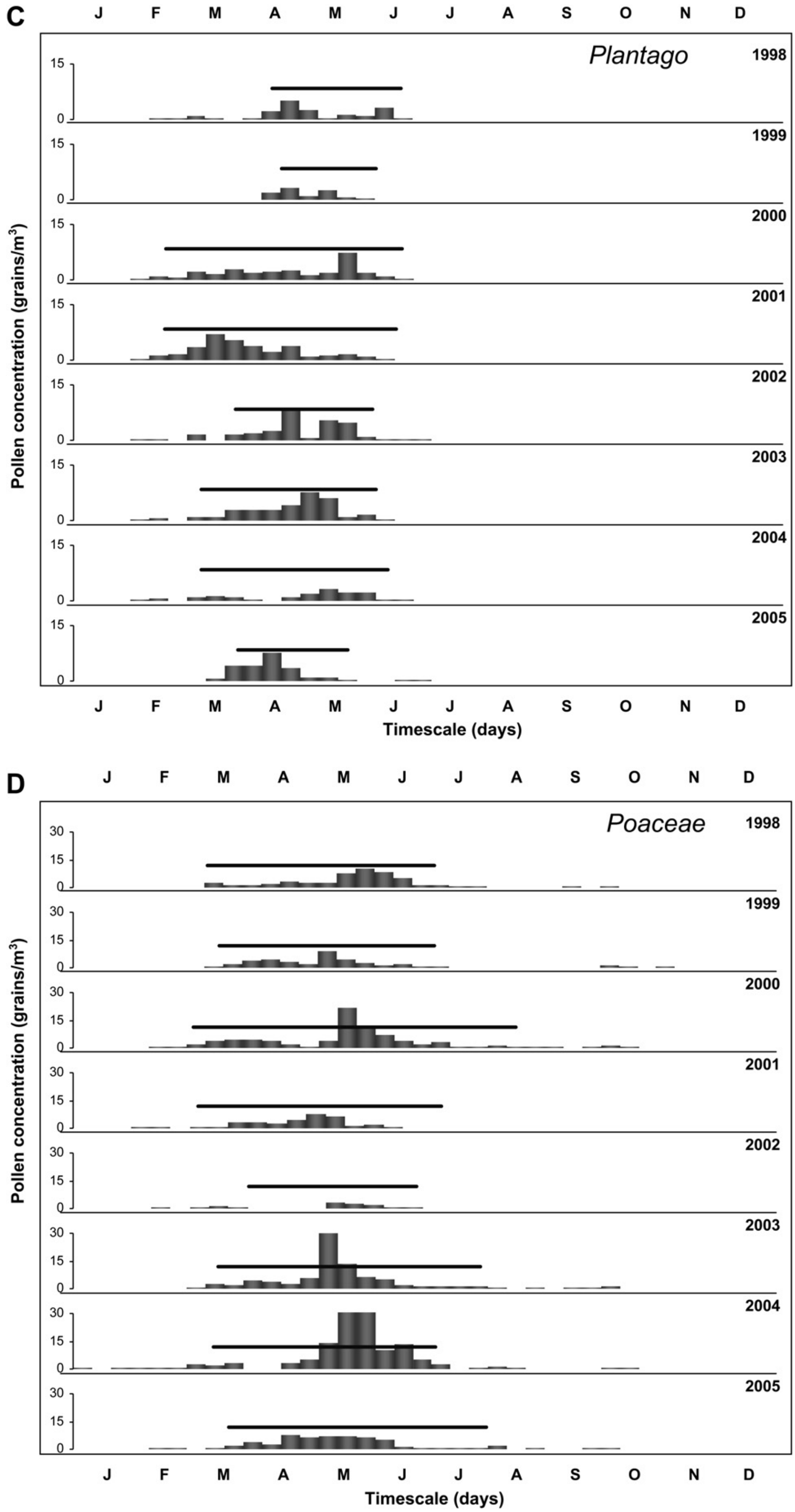
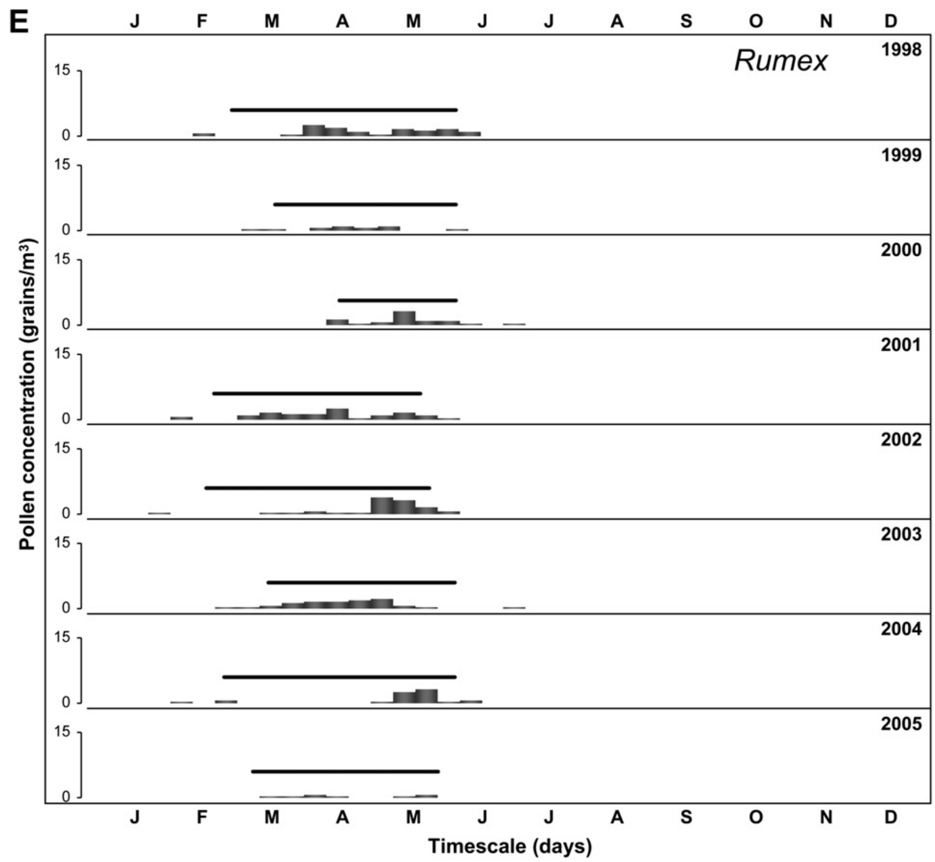


Fig. 3. (*continued*).



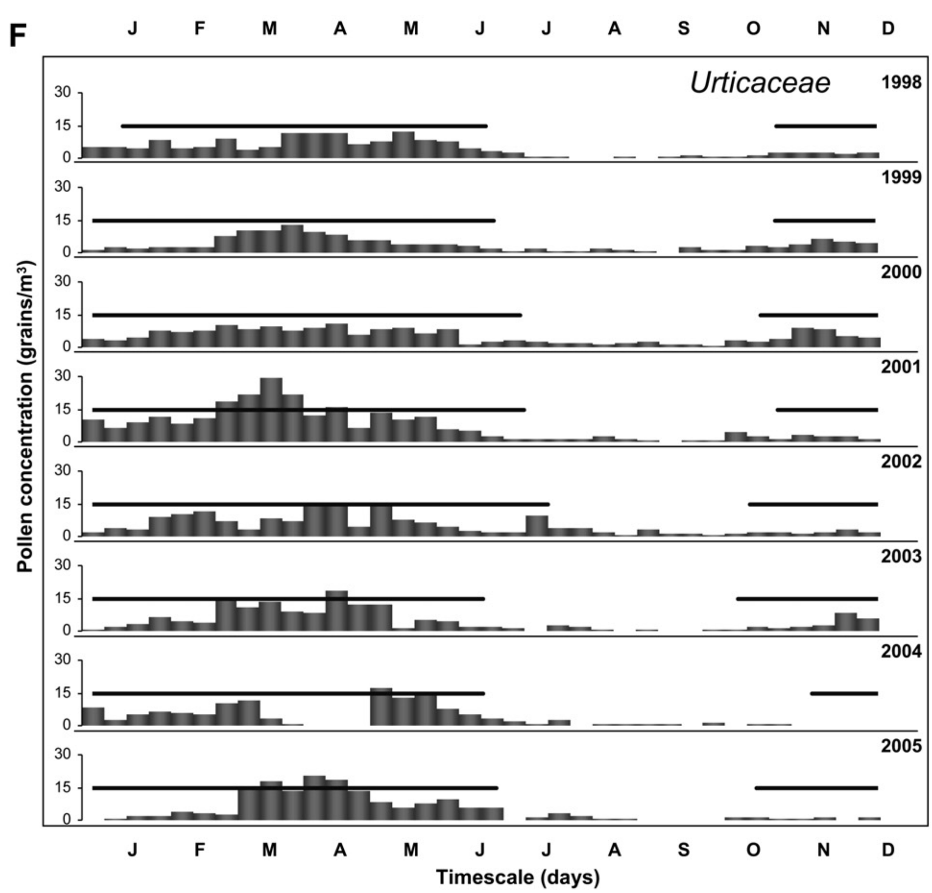


Fig. 3. (*continued*).

Table 2
Spearman correlation coefficients between the daily observations of pollen (daily values of pollen expressed in grains/m^3 during the main pollen season (MPS) taxa-specific) and cumulative meteorological values – i.e. cumulative mean temperature (CT) and cumulative rainfall (CP).

Taxa	1998		1999		2000		2001		2002		2003		2004		2005	
	CT	CP	CT	CP	CT	CP	CT	CP	CT	CP	CT	CP	CT	CP	CT	CP
Artemisia	0.427**	0.398**	0.628**	0.580**	0.429**	0.355**	0.475**	0.472**	0.323**	0.398**	0.528**	0.450**	0.489**	0.255**	0.485**	0.372**
Chenopodiaceae	0.121*	0.151*	0.025	0.092	0.372**	0.340**	0.099	0.071	0.111*	0.141*	0.026	0.123	0.352**	0.340**	0.299*	0.171*
Plantago	0.900*	0.203*	0.671**	0.253*	0.123*	0.313**	0.251*	0.105*	0.690*	0.103*	0.651**	0.353*	0.153*	0.213**	0.267*	0.105*
Poaceae	0.467**	0.432**	0.056	0.253*	0.150	0.255*	0.314**	0.339**	0.567**	0.452**	0.056	0.253*	0.150	0.205*	0.314*	0.349**
Rumex	0.332**	0.182**	0.400**	0.201**	0.421**	0.208**	0.207**	0.126*	0.327**	0.182**	0.420**	0.201**	0.431**	0.218**	0.207*	0.121*
Urticaceae	0.503**	0.502**	0.462**	0.453**	0.367**	0.317**	0.545**	0.543**	0.613**	0.602**	0.562**	0.453**	0.467**	0.217**	0.555**	0.443**

$^*P \leq 0.05$; $^{**}P \leq 0.01$.

that the degree of association were generally positive and significant with all the taxa. This fact could reflect a relationship between meteorological variables prior to the pollination season with the onset of flowering and the pollen production index. An exception would be Chenopodiaceae, which seem relatively independent of rain and temperature prior flowering.

The *Kruskal-Wallis test* (Appendix 4) showed no significant differences among the temperature (maximum, mean and minimum) series ($0.123 \leq P \leq 0.152$) over the 8 years, so that the temperature profile was relatively stable during the study period. On the other hand, the *Kruskal-Wallis test* supports the hypothesis that seasonal precipitation distribution follows an irregular pattern; this test shows significant differences among the median ranks in the mean profile of each pattern ($P \leq 0.001$). The *Kruskal-Wallis test* results could support the hypothesis that the inter-annual and seasonal variability of the rainfall has more influence on the pollination patterns than does the inter-annual temperature.

4. Discussion

The significant increase in global temperature is visible in long-term phenological observation series (Menzel et al., 2001; Vliet et al., 2002). However, for arid and semi-arid zones, the accepted argument is that flowering phenological patterns are intimately related to the availability of water (Bertiller et al., 1991; Friedel et al., 1994). Climate change is expected to accentuate the drought conditions and alter the seasonal patterns of rainfall distribution, exerting major effects over the short and middle term in the functioning and structure of ecosystems (Miranda et al., 2009).

Aerobiological analysis provides a complementary tool for determining how sub-desert plants respond to water resources. The sampling made in a temporal series of 8 years (1998–2005) showed water availability to be closely related to the alteration of the pollination in certain species (Figs. 2 and 3 and Appendix 4). These species-specific responses in the timing of flowering produced different reproductive responses in each of the species studied. In general terms, this fact is manifested in: (i) delayed onset of flowering until reaching the minimum threshold of soil water, in the case of some annual plants (*Plantago*, *Rumex,* and Poaceae), or (ii) scant variability in the flowering period in plants with drought tolerance (Chenopodiaceae and *Artemisia*) or plants often linked to soil-moisture availability (waterways, crops, etc.) (Urticaceae). Pollination patterns observed in this study could indicate that these species living in semi-arid areas differentially exploited the resources available in the community (Van Schaik et al., 1993).

4.1. Pulse dynamics in annual plants

This study indicates that the water availability in south-eastern Spain is highly pulsed, and discrete rainfall events interspersed with drought periods are important components of the annual water supply (Fig. 2). According to Noy-Meir (1985) and Miranda et al. (2009), plants inhabiting in semi-arid regions respond not only to rainfall quantity but also to variations in time (Lázaro et al., 2001), so that relatively small changes in rainfall frequency (i.e., pulsed inputs) can have strong effects on flowering.

Each species needs a threshold of water prior to beginning its annual growth cycle (Seghieri et al., 1995) and therefore the lack of predictability in rainfall timing during some periods causes uncertainty in the behaviour of plants (Rathcke and Lacey, 1985). If so, this must be particularly true in unpredictable environments – as Southern eastern Spain – where length and quality of the growing season vary drastically from year-to-year. This fact could cause irregular pollination patterns (Sarmiento, 1983); for example, in the present study, we observed that the annual plants pollinate in pulses associated with rainfall over certain thresholds. In general, *Plantago* and *Rumex* and some Poaceae species adjusted their flowering-onset date to the availability of soil water resources (Aronson et al., 1992), responding positively to rainfall from the previous weeks (Table 2). Rainfall probably has only a short-term effect on these annual herbaceous species. Based on the threshold concept, Ogle and Reynolds (2004) suggest that plant functional types may be distinguished by their phenological responses to soil moisture and the lag times between pulse and response.

Comparing the onset of pollen season between Mediterranean (e.g. Tavira Muñoz et al., 1998; Ruiz et al., 2002; Díaz de la Guardia et al., 2003) and semi-arid Mediterranean populations (*Plantago, Rumex* or Poaceae), we observed that plants living in semi-arid zones flowered earlier than Mediterranean populations, even in winter. So it seems that sub-desert populations show high plasticity in the timing of flowering adjusted it to rainy period (Figs. 2 and 3C–E). The latter observation is supported by Aronson et al. (1992), who stated that some annual plants have adapted to arid or semi-arid environments through changes in their phenological development as well as in plasticity in the timing of the flowering phenophase, synchronizing with the rainy period, i.e. winter. If so, this must be particularly important in unpredictable environments – as South-eastern Spain – where the length of the rainy season and quantity of rain could vary drastically from year-to-year, besides causing confusion in the flowering patterns. Other aerobiological studies also point out that flower phenology in grass species varies year-to-year (Emberlin et al., 1994; Fernández-González et al., 1999; García-Mozo et al., 2009, 2010), supporting the idea that water availability is one of the most important factors for the onset of flowering.

The pollen production index also supports the argument that species coexistence in semi-arid zones may be due to differences in resource utilization (Polis, 1991; Pavón and Briones, 2001). Annual plants such as *Plantago*, Poaceae, and *Rumex* showed, from 1999, a trend, although irregular, to increase their annual pollen production. Recent aerobiological studies have also highlighted the influence of rainfall on grass pollen-season intensity (Sánchez-Mesa et al., 2005; Smith and Emberlin, 2006). This is also attributable to an immediate response to the increase in annual rainfall (Table 2) but more fundamentally immediately prior to flowering (Tormo Molina et al., 2001; García-Mozo et al., 2009).

4.2. Stable dynamics in some perennial plants

Curiously, despite that in semi-arid environments water seems to be the most important force driving ecosystem dynamics (Noy-Meir, 1985), in the present study the pollination behaviour of some perennial plants did not always depend on rainfall patterns. Chenopodiaceae and *Artemisia* species are well adapted to drought and capable of colonizing degraded, nitrified, and saline terrain. Thus, these species show stress only during prolonged periods of drought (Cariñanos et al., 2004). A relatively stable and prolonged flowering period was noted in Chenopodiaceae and *Artemisia*, which showed optimal pollination evolution even during unfavourable and drought periods (1998, 2001 and 2005). Similar findings have been reported by other authors (Gehrig, 2006), this may indicate their tolerance to water stress or other climatic variables might govern flowering (Pavón and Briones, 2001). Analogous results have been presented by Miranda et al. (2009) on changing patterns of the water supply in an experimental zone in Almería; these authors reported that decreased water amount and frequency, and accentuated seasonality did not change the flowering phenology.

In relation to pollen-season intensity, many authors have reported that *Artemisia* and Chenopodiaceae are strongly influenced by rainfall in the previous weeks (Munuera et al., 1999; Muñoz-Rodriguez et al., 2000; Stach et al., 2007). We observed that these taxa presented a slight increase in pollen production during rainy years (e.g. 2002). However, in semi-arid environments, these species maintained an optimal index even in highly unfavourable periods (1998); this behaviour could be due to the development of a drought-resistant strategy, in which the physiological adaptations enable them to maintain growth under water stress (Cariñanos et al., 2004). Meanwhile, the above study (Miranda et al., 2009) pointed that species from semi-arid environments are opportunistic 'water spenders', which maximize water uptake when it is abundant and are able to adjust their growth rate to water supply.

The family Urticaceae includes many species, both annuals and perennials. The aerobiological study of these herbaceous species tends to be more complex due the different life forms often linked to phenological pattern (Boot et al., 1986; Abd El-Ghani, 1997; Peñuelas et al., 2004).

The effect of meteorological variables on the Urticaceae pollen season is a recurrent topic in aerobiology literature, although results have been quite contradictory. In relation to climate change, opposing results are reported; that is, Spieksma et al. (2003) found a trend for increasing the production index in north-western Europe, while, on the contrary, Clot (2003) found no significant increasing trend in Switzerland. With regard to pollination period, Recio et al. (2009) reported a trend to advance the end of the MPS along the Iberian Mediterranean coast, while a delayed pollination start has been detected on the Atlantic coast. According to the latter authors, it is clear that the influence of climate change on Urticaceae flowering phenology must be studied locally.

Because some of these populations are generally linked to soil-moisture availability, in the present study, we observed that both the inter-annual pollen season and production index presented a relatively stable pattern. Nevertheless, the pollination period lengthened and the concentrations increased when rainfall events occurred (Table 2). Similar results were found by Gehrig (2006) and Alcázar et al. (2009), supporting the idea that the species forming part of this family need a threshold of soil moisture in order to flower (Guardia and Belmonte, 2004; Alcázar et al., 2009), so that the onset of MPS, generally in October, appears to be related to water surplus.

4.3. Pollen spectrum

The aridity prevailing in the study area (Fig. 1) also makes it possible for the pollen spectrum to be qualitatively unique, as features characteristic of the Mediterranean region are shared with aspects typical of an arid or semi-arid climate (Bicakci et al., 2003). Furthermore, elements typical of semi-arid zones rich in salt as well as gypsum substrates appeared, such as *Zygophyllum*, *Thymelaea*, *Tamarix*, Chenopodiacea, some of these (e.g. *Zygophyllum*) being reported only in other locations with features similar to those of southern Spain (e.g. Moreno-Grau et al., 1998; Munuera et al., 2002).

However, pollen production of some taxa, which also inhabit nearby localities within the Mediterranean climate, was appreciably lower – i.e. Granada (Alba et al., 2000), Jaén (Ruiz et al., 2002), or even in Chirivel (Fig. 1), northern Almería province (Cariñanos et al., 2004). The pollen production index was more similar to that reported in other localities with a high aridity index, such as Ankara or Bursa in Turkey (Inceoglu et al., 1994; Bicakci et al., 2003). The rapid response to water availability has been noted since 1999, when a gradual increase in the rainfall as well as the recharging of water reserves (www.igme.es) caused a pollen production recovery both of trees and of herbaceous plants.

5. Conclusions

The strong effect of drought on flowering phenology and pollen production found in this study supports the idea that water availability has an important role in determining year-to-year shifts in these parameters among species adapted to semi-arid zones. The results show that changes in rainfall patterns and water availability can cause complex phenological changes with likely far-reaching consequences for ecosystem and biosphere functioning and structure. Further studies are needed in areas currently with a high aridity index in order to ascertain the extent, impact, and risks facing the ecosystems that are currently not under water deficit. Aerobiological analysis provides a complementary tool for studying future drier and warmer conditions affecting flowering.

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Supplementary material

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.jaridenv.2010.06.005.

References

Abd El-Ghani, M.M., 1997. Phenology of ten common plant species in western Saudi Arabia. Journal of Arid Environments 35, 673–683.
Alba, F., Díaz de la Guardia, C., Sabariego, S., 2000. Aerobiología en Andalucía: estación de Granada. REA 6, 31–34.
Alcázar, P., Stach, A., Nowak, M., Galán, C., 2009. Comparison of airborne herb pollen types in Córdoba (Southwestern Spain) and Poznan (Western Poland). Aerobiologia 25, 55–63.
Aronson, J., Kigel, J., Shmida, A., Klein, J., 1992. Adaptive phenology of desert and Mediterranean populations of annual plants grown with and without water stress. Oecologia 89, 17–26.
Bagnoul, F., Gaussen, H., 1957. Les climats biologiques et leur classification. Annales de Géographie 66, 193–220.
Bertiller, M.B., Beeskow, A.M., Coronato, F., 1991. Seasonal environmental variation and plant phenology in arid Patagonia (Argentina). Journal of Arid Environments 21, 1–12.
Bicakci, A., Tatlidil, S., Sapan, N., Malyer, H., Canitez, Y., 2003. Airborne pollen grains in Bursa, Turkey, 1999–2000. Annals of Agricultural and Environmental Medicine 10 (1), 31–36.
Boot, R., Raynal, D.J., Grime, J.P., 1986. A comparative study of the influence of drought stress on flowering in *Urtica dioica* and *U. Urens*. Journal of Ecology 74, 485–495.
Cariñanos, P., Galán, C., Alcázar, P., Domínguez, E., 2004. Airborne pollen records response to climatic conditions in arid areas of the Iberian Peninsula. Environmental and Experimental Botany 52, 11–22.
Chesson, P., Gebauer, R.E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S.K., Sher, A., Novoplansky, A., Weltzin, J.F., 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. Oecologia 141, 236–253.
Clot, B., 2003. Trends in airborne pollen: an overview of 21 years of data in Neuchâtel (Switzerland). Aerobiologia 19, 227–234.
Díaz de la Guardia, C., Alba, F., Nieto, D., Sabariego, S., 2003. Diez años de control aerobiológico en la atmósfera de la ciudad de Granada: calendario polínico (1992–2001). Polen 13, 251–260.
Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R., Mearns, L., 2000. Climate extremes: observations, modelling and impacts. Science 289, 2068–2074.
Emberlin, J., Jones, S., Bailey, J., Caulton, E., Corden, J., Dubbels, S., 1994. Variation in the start of the grass pollen season at selected sites in the United Kingdom 1987–1992. Grana 33, 94–99.
Emberlin, J., Savage, M., Jones, S., 1993. Annual variations in grass pollen seasons in London 1961–1990: trends and forecast models. Clinical and Experimental Allergy 23, 911–918.
Fay, P.A., Carlisle, J.D., Knapp, A.K., Blair, J.M., Collins, S.L., 2000. Altering rainfall timing and quantity in a mesic grassland ecosystem: design and performance of rainfall manipulation shelters. Ecosystems 3, 308–319.
Fernández-González, D., Valencia-Barrera, R.M., Vega, A., Díaz de la Guardia, C., Trigo, M.M., Cariñanos, P., et al., 1999. Analysis of grass pollen concentrations in the atmosphere of several Spanish sites. Polen 10, 123–132.
Friedel, M.H., Nelson, D.J., Sparrow, A.D., Kinloch, J.E., Maconochie, J.R., 1994. Flowering and fruiting of arid zone species of *Acacia* in central Australia. Journal of Arid Environments 27, 221–239.
Galán, C., Cariñanos, P., Alcázar, P., Dominguez-Vilches, E., 2007. Manual de Calidad y Gestión de la Red Española de Aerobiología. Universidad de Córdoba, Córdoba.
Galán, C., García-Mozo, H., Vázquez, L., Ruiz, L., Díaz de la Guardia, C., Trigo, M.M., 2004. Heat requirement for the onset of the Olea europaea L. pollen season in several sites in Andalusia and the effect of the expected future climate change. International Journal of Biometeorology 49 (3), 184–188.
García-Mozo, H., Galán, C., Alcázar, P., de la Guardia, C., Nieto-Lugilde, D., Recio, M., Hidalgo, P., Gónzalez-Minero, F., Ruiz, L., Domínguez-Vilches, E., 2010. Trends in grass pollen season in southern Spain. Aerobiologia 26 (2), 157–169.
García-Mozo, H., Galán, C., Belmonte, J., Bermejo, D., Candau, P., Díaz de la Guardia, C., Elvira, B., Gutiérrez, M., Jato, V., Silva, I., Trigo, M.M., Valencia, R., Chuine, I., 2009. Predicting the start and peak dates of the Poaceae pollen season in Spain using process-based models. Agriculture and Forest Meteorology 149, 256–262.
Gehrig, R., 2006. The influence of the hot and dry summer 2003 on the pollen season in Switzerland. Aerobiologia 22, 27–34.
Guardia, R., Belmonte, J., 2004. Phenology and pollen production of *Parietaria judaica* L. in Catalonia (NE Spain). Grana 43, 57–64.
Hirst, J.M., 1952. An automatic volumetric spore trap. Annals of Applied Biology 39, 257–265.
Inceoglu, Ö., Pinar, N.M., Sakiyan, N., Sorkun, K., 1994. Airborne pollen concentration in Ankara, Turkey 1990–1993. Grana 33, 158–161.
IPCC, 2007. Intergovernmental Panel on Climate Change, Climate Change 2007: Synthesis Report, Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva.
Körner, C., Sarris, D., Christodoulakis, D., 2005. Long-term increase in climatic dryness in the East- Mediterranean as evidenced for the island of Samos. Regional Environmental Change 5, 27–36.
Lázaro, R., Rodrigo, F.S., Gutiérrez, L., Domingo, F., Puigdefábregas, J., 2001. Analysis of a thirty year rainfall record (1967–1997) from semi-arid SE Spain: a plant ecological perspective. Journal of Arid Environment 48, 373–395.
Macias, M., Andreu, L., Bosch, O., Camarero, J.J., Gutiérrez, E., 2006. Increasing aridity is enhancing silver Fir *Abies Alba* (Mill.) water stress in its south-western distribution limit. Climatic Change 79, 289–313.
Menzel, A., Estrella, N., Fabian, P., 2001. Spatial and temporal variability of the phenological seasons in Germany from 1951–1996. Global Change Biology 7, 657–666.
Merlo, E.J., Rodríguez-Tamayo, M.L., Cabello-Piñar, J., Lázaro, R., 2004. Adaptaciones de la flora y vegetación: implicaciones del clima y biotipos. In: Mota, J., Cabello, J., Cerrilo, M.I., Rodríguez-Tamayo, M.L. (Eds.), Subdesiertos de Almería: naturaleza de cine. Junta de Andalucía, pp. 227–247, 461 pp.
Miranda, J.D., Padilla, F.M., Pugnaire, F.I., 2009. Response of a Mediterranean semiarid community to changing patterns of water supply. Perspectives in Plant Ecology, Evolution and Systematics 11, 255–266.
Moreno-Grau, S., Bayo, J., Elvira-Rendeules, B., Angosto, J.M., Moreno, J.M., Moreno-Clavel, J., 1998. Statistical evaluation of three years of pollen sampling in Cartagena, Spain. Grana 37, 41–47.
Munuera, M., Carrión García, J.S., García Sellés, J., 1999. Aerobiology of Artemisia airborne pollen in Murcia (SE Spain) and its relationship with weather variables: annual and intradiurnal variations for three different species. Wind vectors as a tool in determining pollen origin. International Journal of Biometeorology 43, 51–98.
Munuera, M., Carrión, J.S., Navarro, C., 2002. Seasonal fluctuations of the pollen spectrum in Murcia (SE Spain). Some peculiarities in the pollen calendar. Aerobiologia 18, 141–151.
Muñoz-Rodriguez, A.F., Silva, I., Tormo, R., Moreno, A., Tavira, J., 2000. Disperal of Amaranthaceae and Chenopodiaceae pollen in the atmosphere of Extremadura (SW Spain). Grana 39, 56–62.
Nilsson, S., Persson, S., 1981. Tree pollen spectra in the Stockholm region (Sweden), 1973–1980. Grana 20, 179–182.
Noy-Meir, I., 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4, 25–52.
Noy-Meir, I., 1985. Desert ecosystem structure and function. In: Evenari, M., Noy-Meir, I., Goodall, D.W. (Eds.), Hot Desert and Arid Shrublands. Ecosystems of The World 12A. Elsevier, Amsterdam, pp. 93–101.
Ogle, K., Reynolds, J.F., 2004. Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds, and delays. Oecologia 141 (2), 282–294.
Pavón, N.P., Briones, O., 2001. Phenological patterns of nine perennial plants in an intertropical semi-arid Mexican scrub. Journal of Arid Environments 49, 265–277.
Peñuelas, J., 2001. Cambios atmosféricos y climáticos y sus consecuencias sobre el funcionamiento y la estructura de los ecosistemas terrestres mediterráneos. In: Zamora, R., Pugnaire, F.I. (Eds.), Ecosistemas mediterráneos Análisis funcional. CSIC-AEET Press, Granada, pp. 423–455.

Peñuelas, J., Boada, M., 2003. A global change-induced biome shift in the Montseny mountains (NE Spain). Global Change Biology 9, 131–140.
Peñuelas, J., Filella, I., Comas, P., 2002. Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. Global Change Biology 8, 531–544.
Peñuelas, J., Filella, I., Zhang, X., Llorens, L., Ogaya, R., Lloret, F., Comas, P., Estiarte, M., Terradas, J., 2004. Complex spatio-temporal phenological shifts as a response to rainfall changes. New Phytologist 161, 837–846.
Polis, G.R., 1991. Desert communities: an overview of patterns and processes. In: Polis, G.R. (Ed.), Ecology of Desert Communities. University of Arizona Press, Tucson Arizona, pp. 1–25, 456 pp.
Rathcke, B., Lacey, E.P., 1985. Phenological patterns of terrestrial plants. Annual Review of Ecology and Systematics 16, 179–214.
Recio, M., Rodríguez-Rajo, F.J., Jato, M.V., Trigo, M.M., Cabezudo, B., 2009. The effect of recent climatic trends on Urticaceae pollination in two bioclimatically different areas in the Iberian Peninsula: Malaga and Vigo. Climatic Change 97, 215–228.
Rivas-Martínez, S., Díaz, T.E., Fernández-González, F., Izco, J., Loide, J., Lousã, M., Penas, A., 2002. Vascular plant communities of Spain and Portugal. Addenda to the Syntaxonomical checklist of 2001. Itinera Geobotanica 15, 5–922.
Roldán, A., 1988. Notas para una climatología de Almería. Ministerio de transporte, turismo y comunicaciones, 28 pp.
Ruiz, L., Díaz de la Guardia, C., Cano, E., 2002. Aerobiología en Andalucía: Estación de Jaén (2000–2001). REA 7, 77–82.
Sánchez-Mesa, J.A., Galán, C., Hervás, C., 2005. The use of discriminant analysis and neural networks to forecast the severity of the Poaceae pollen season in a region with a typical Mediterranean climate. International Journal of Biometeorolology 49 (6), 355–362.
Sarmiento, G., 1983. Patterns of specific and phenological diversity in the grass community of the Venezuelan tropical Savannas. Journal of Biogeography 10 (5), 373–391.
Schwinning, S., Sala, O.E., 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia 141, 211–220.
Seghieri, J., Floret, C., Pontanier, R., 1995. Plant phenology in relation to water availability: herbaceous and woody species in the savannas of northern Cameroon. Journal of Tropical Ecology 11 (2), 237–254.
Smith, M., Emberlin, J., 2006. A 30-day-ahead forecast model for grass pollen in north London United Kingdom. International Journal of Biometeorolology 50 (4), 233–242.
Spieksma, F.T.M., Corden, J.M., Dentandt, M., Millington, W.M., Nikkels, H., Nolard, N., Schoenmakers, C.H.H., Wachter, R., Weger, L.A., Willems, R., Emberlin, J., 2003. Quantitative trends in annual totals of five common airborne pollen types (Betula, Quercus, Poaceae, Urtica, and Artemisia), at five pollen-monitoring stations in western Europe. Aerobiologia 19, 171–184.
Stach, A., García-Mozo, H., Prieto-Baena, J.C., Czarnecka-Operacz, M., Jenerowicz, D., Silny, W., Galán, C., 2007. Prevalence of artemisia species pollinosis in Western Poland: impact of climate change on aerobiological trends, 1995–2004. Journal of Investigational Allergology and Clinical Immunology 17 (1), 39–47.
Suttle, K.B., Thomsen, M.A., Power, M.E., 2007. Species interactions reverse grassland responses to changing climate. Science 315, 640–642.
Svejcar, T., Angel, R., Miller, R., 1999. Fixed location rain shelters for studying precipitation effects on rangelands. Journal of Arid Environments 42, 187–193.
Tavira Muñoz, J., Tormo Molina, R., Muñoz Rodríguez, A.F., Silva Palacios, I., Gonzalo Garijo, M.A., 1998. Calendario polínico de la ciudad de Cáceres. Revista Española de Alergología e Inmunología Clínica 13 (5), 288–293.
Thornthwaite, C.W., Mather, J.R., 1957. Instructions and tables for computing potential evapotranspiration and the water balance. Drexel Institute of Technology, Laboratory of Climatology. Publications in Climatology 10, 185–311.
Tormo Molina, R., Silva Palacios, I., Muñoz Rodriguez, A.F., Tavira Munoz, J., Moreno Corchero, A., 2001. Environmental factors affecting airborne pollen concentration in anemophilous species of Plantago. Annals of Botany 87, 1–8.
UNESCO, 1979. Aridity Definition (UN Documents). United Nations Educational, Scientific and Cultural Organization, New York.
Valle, F., 2003. Mapa de Series de Vegetación de Andalucía. Rueda, Madrid.
Van Schaik, C.P., Terborgh, J.W., Wright, S.J., 1993. The phenology of tropical forest: adaptive significance and consequences for primary consumers. Annual Review of Ecology and Systematics 24, 353–377.
Vliet, A.J.H.V., Overeem, A., Groot, R.S.D., Jacobs, A.F.G., Spieksma, F.T.M., 2002. The influence of temperature and climate change on the timing of pollen release in the Netherlands. International Journal of Climatology 22, 1757–1767.