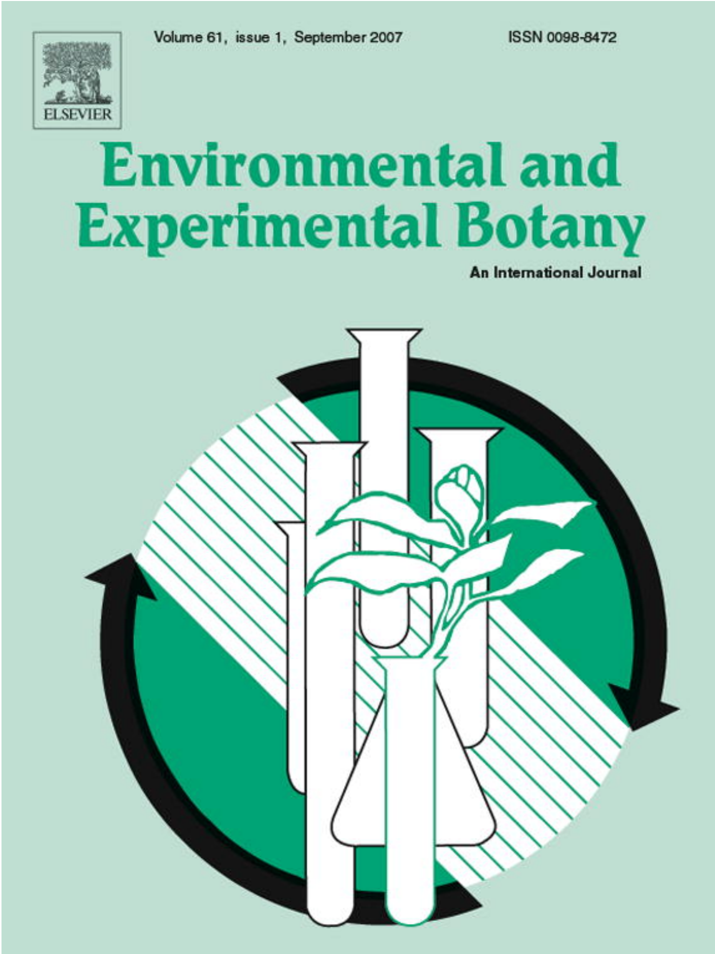
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Influence of pollen emission and weather-related factors on variations in holm-oak (*Quercus ilex* subsp. *ballota*) acorn production

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Abstract

In Iberian Mediterranean ecosystems holm-oak acorn production is of vital ecological and economic importance. Economically these fruits are the major component in the feeding systems of high-quality domestic pigs. As in most *Quercus* species, the chief feature of holm-oak acorn production is its high variability among individuals and years. Many hypotheses have been put forward to explain these fluctuations, but the variables influencing this alternating behavior remain unknown. From 1998 to 2003 we studied floral phenology, fruit production, fruit size, airborne pollen emission and meteorology in a holm-oak natural area of South Spain. The results obtained by using a Principal Components Factorial Analysis indicated that pollen emission, up to the day where maximum pollen data are recorded, was the most important factor determining final acorn harvest. With regard to the influence of the weather, temperature, relative humidity and rainfall of January, March and September were the most influencing variables. Our results support the "wind pollination" hypothesis proposed by other authors in some North-American *Quercus* studies. Integration of aerobiological, field phenological and meteorological data could represent an important step forward in forest fruit production research.

Keywords: Oak forest; *Quercus ilex* subsp. *ballota*; Holm-oak; Acorn; Pollen; Aerobiology; Phenology

1. Introduction

Quercus ilex subsp. *ballota* (Desf.) Samp (holm-oak) is one of the most abundant tree species in the Iberian Peninsula. In Spain, it covers a total of 2,489,000 ha. It is the dominant species in both Mediterranean forests and in the "dehesa", a semi-natural landscape for animal breeding. Both landscapes are found throughout the central and southern areas of Spain (Spanish Ministry of the Environment, 2002). Holm-oak acorn production is of vital ecological and economic importance (Cecich and Sullivan, 1999; Rodá et al., 1999) since the amount and the quality of the acorns produced are crucial factors in the development of new holm-oak stands. These fruits are a major component in the feeding systems of many Mediterranean wild animal species (Vazquez, 1998). In economic terms, they are the basic feed ingredients for domestically-bred high-quality meat pigs. They are currently one of the fastest-growing markets in Spain (Spanish Ministry of Agriculture and Fisheries, 2002).

As in most *Quercus* species, the chief feature of holm-oak acorn production is its high variability, which ranges from 0.5 to 150 kg/tree. In addition to "year-on-year" variations in tree mass, there are marked variations in fruit production between individuals within the same year (Vazquez, 1998). Studies of acorn-production patterns in other *Quercus* species in eastern and central United States, highlight the alternation of periods of synchronous production or mast years with periods of very low production (Sork and Bramble, 1993; Koening et al., 1994; Cecich and Sullivan, 1999). However, little is known about either European *Quercus* reproductive patterns or holm-oak acorn production patterns, with the exception of isolated studies in south-western Spain that reported a random alternation of mast and low production years (Vázquez et al., 1990; Esparrago et al., 1992).

Although many hypotheses have been put forward, the variables influencing this alternating behavior remain unknown. In evergreen *Quercus* species, the resource-matching and seed-dispersal hypotheses have been scientifically ruled out by

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Koening et al. (1994). Other studies were generally consistent with the "predator satiation" and the "wind pollination" hypotheses (Docousso et al., 1993; Koening et al., 1994; Vazquez, 1998; Cecich and Sullivan, 1999).

Pollination is only one of the many events taking place in the plant development cycle; however, it is extremely important for yield where seed is required. Although successful fertilization depends on a number of environmental and endogenous factors, including climate and plant nutritional status, a sufficient quantity of pollen must reach the receptive stigma to enhance potential fertilization (Frenguelli, 1998). Moreover, in anemophilous plants a larger number of pollen grains are required to ensure pollination. Pollen production, which is genetically and physiologically controlled, largely determines the pollination process (Allison, 1990; Tormo et al., 1996; Hidalgo-Fernández et al., 2000; Gómez-Casero et al., 2004; Prieto-Baena et al., 2003). Although, theoretically, one pollen grain per ovule would be sufficient for fertilization, in several wind-pollinated plants the average number of pollen grains reaching the stigma ranges from 5 to 20 (Stefani, 1992). In *Q. ilex* subsp. *ballota* the ovule/pollen grain ratio has been reported to be as high as 1/400,000 (Tormo et al., 1996).

Numerous studies have indicated a close link between the quantity and quality of emitted pollen and fruit production in wind-pollinated plants (Campbell and Halama, 1993; Frenguelli, 1998). Thus, pollen data can provide information regarding the final fruit harvest several months in advance (Galán et al., 2004). This aerobiological application, which was initiated in the 1970s in France by Cour (1974), has been successfully tested in both anemophilous crops (Gonzalez-Minero et al., 1998; Moriondo et al., 2001; Galán et al., 2004; Besselat and Cour, 1990; Baugnent, 1991; Lletjos et al., 1993) and forest non-crop species (Allison, 1990; Cecich and Sullivan, 1999; Litschauer, 2000, 2001, 2003).

The main objective of the present study was to determine how and how much pollen emission and weather-related factors influence on annual holm-oak acorn production. The detailed steps of the present study were: (1) to analyze the possible correlation between holm-oak pollen emission and acorn production in a given area of south-western Spain; (2) to identify the meteorological parameters influencing holm-oak pollen emission and acorn production; (3) to detect the degree of influence of the different studied factors on the final annual acorn production.

2. Material and methods

2.1. Study area

The study was carried out from 1998 to 2003 at "El Cabril", a 1200-ha reserve located in the northern part of the Hornachuelos Natural Park in the province of Córdoba (southern Spain), 38°4′N, 5°24′W. Average elevation of the area ranges from 450 to 600 m a.s.l. This area has a sub-humid Mediterranean climate with virtually no rainfall in summer (June–August). The mean 50-year data indicates annual rainfall of 700 mm and a mean temperature of 16.8 °C (Pinilla et al., 1995).

As in most areas of southern Spain, the holm-oak is the dominant tree species in the reserve. Other *Quercus* species including *Quercus suber* L., *Quercus coccifera* L. and *Quercus faginea* Lamk. can be found in the Hornachuelos Natural Park, but not in the reserve studied.

In 1998, 30 oaks within a radius of 2–3 km from the spore-trap were tagged and sampled. Ten individuals (numbered 1–10) were on a south-facing slope, other 10 (numbered 11–20) in a flat non-exposed area; and the last 10 (numbered 21–30) on a north-facing slope. All the study individuals belong to the same population. It is not easy to determine the exact age of the Mediterranean holm-oak due to locally absent rings and false bands are quite frequent in this species (Hidalgo-Fernández and Heras, 2003). Nevertheless, their age was estimated to be in a range of 50–70 years in base to their size and trunk's radio (Hidalgo-Fernandez, 1998, personal communication).

2.2. Acorn censuses

2.2.1. Acorn harvest estimates

From 1998 to 2003, acorn production (AP) from the selected trees was estimated. From 1998 to 2000, AP was measured by collecting acorns from the selected trees using the traditional method of beating down fruits with long poles. Harvest took place in mid-autumn, between mid-October and early November, just prior to acorn fall. Acorns were collected on a special plastic blanket spread out below the trees. Additionally, from 1998 to 2003, the abundance of acorns was also estimated using three visual methods: (1) two observers scanned the area of the tree canopy and counted as many acorns as possible in 15 s. The average value for each tree was taken as the "15 s value" estimation, modified from Koening et al. (1994); (2) two observers scanned the area of the tree canopy and counted as many acorns as possible in 1 min. The average value of those counts was taken as the "1 m value" estimation; (3) the relative abundance of acorns was categorized in five levels using the visual scale method proposed by Graves (1980), with the following categories: 0 (no acorns), 1 (a few seen after close scrutiny), 2 (a fair number), 3 (a good crop), and 4 (a bumper crop, many acorns seen almost everywhere on the tree).

2.2.2. Acorn measurement

To determine year-on-year variations in acorn size and weight, a sample of 30 acorns was taken from each selected tree. Thus, a total of 900 acorns was weighed and measured each year in the laboratory.

2.3. Phenological data

Floral phenological observations were performed in the field using the phenophase system developed by Gomez-Casero (2003): eight phenological phases for male flowers, designated by upper-case letters, and eight phenological phases for female flowers, designated by lower-case letters, from flower budding to fruiting. Phenological surveys were carried out weekly over the study period in the selected trees.

2.4. Airborne pollen data

Airborne pollen concentration data were collected over the 6-year period (1998–2003) using a volumetric Hirst-type spore-trap (Hirst, 1952), the Burkard® 7-day recording volumetric spore-trap model. The standard sampling procedures proposed by the Spanish Aerobiology Network (REA) were employed (Galán, 1998). The volumetric trap was located on a 300-m hill in the middle of the valley where the selected holm-oaks were located. The trap was placed 5 m above ground level. This sampling trap, which continuously worked 24 h/day during the study period, consists of two parts: a lower compact unit with built-in vacuum pump and an upper mobile part with a winged portion that positions the trap slit opening into the wind. The trap absorbed a constant air-flow volume ($10\,l\,min^{-1}$). Airborne solid particles stack to a Melinex® tape placed over a drum connected to a clock. Adhesive tape was changed weekly, cut in daily samplings and stained with fuchsine; pollen grains were analyzed under a light microscope (400× magnification). The Pollen Index (PI) used here represents annual sum of daily airborne pollen concentrations.

2.5. Meteorological data

Meteorological monitoring was carried out using a weather station placed 10 m from the spore-trap. Mean, maximum and minimum temperature, rainfall, relative humidity and wind direction and velocity were measured daily. Annual rainfall ranged from 207 mm in 1999 to 617 mm in 2003, while annual mean temperature ranged from 13.9 °C in 2003 to 18 °C in 1998. The dominant wind directions in the area during Spring were NW and SE. The 6-year average wind speed in Spring was 3 m/s.

2.6. Statistical analysis

The Spearman non-parametric correlation test was applied to visual and actual acorn-production data due to the number of observation. Sixty-one monthly meteorological data (average mean, maximum and minimum temperature; relative humidity and total rainfall) and the Pollen Index (PI) were analyzed to determine their influence on acorn production. Rainfall of July was not used because no variability was detected, no rainfall during the whole study period. Given the number of observations, 6 years, a Principal Components and Factor Analysis (PCFA) was performed to detect structure in the relationships between variables and to classify variables according to their influence on dependent variable's variation (Tipping and Bishop, 1999). The advantage of this non-parametric analysis is its hardiness when the number of variables is high but there are a scarce number of observations (Sabatier et al., 1989). The statistical software used was STATISTICA 6 for Windows.

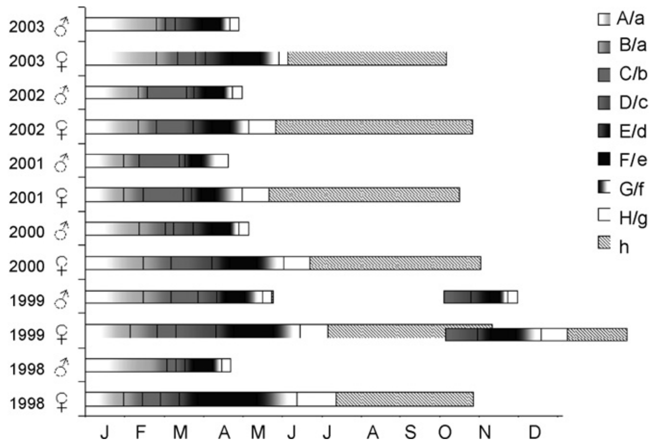

Fig. 1. Floral phenological data chartt. Male phenological phases for catkins are named after capital letters: A, closed buds; B, differentiated buds; C, young catkin; D, longed catkin; E, flowering start; F, full flowering; G, flowering end; H, death catkins. Female flower phenological phases named after lower case letters: a, closed buds; b, young female flowers; c, anthesis; d, growing of flowers; e, mature flowers; f, fertilized flowers; g, differentiated cup; h, fruit maturation.

3. Results

Fig. 1 charts the phenological development of floral structures in the 30 trees selected. Although both male and female flowers displayed eight phenological phases, nine different patterns were used to represent the various flowering stages by combining both types of flower. In general, budburst (Phenophase B) started in February and full flowering (Phenophase F) tended to occur in April. Fig. 2 shows the pollination curves plotted on the basis of airborne pollen data obtained from the spore-trap. The main pollination periods matched the phenological data obtained in the field, confirming that most *Quercus* pollen grains detected by the trap came from holm-oak trees in the study area. Interestingly, in 1999 local holm-oaks had a second flowering period in autumn.

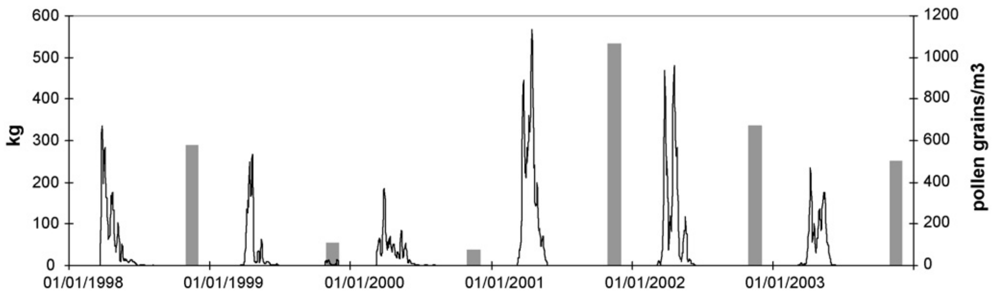

Fig. 2. Daily pollen variation (5-day running mean) during the study period (1998–2003) is showed in black line. Grey histograms represent acorn production expressed in kilograms.

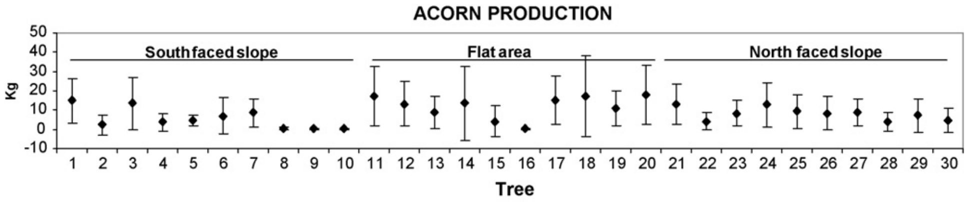

Fig. 3. Average acorn production by each tree expressed in kilograms (1998–2003). Standard deviation is also showed.

After the first 3 years of the study, one of the three visual methods tested was selected by comparing estimated results with actual data. The "15 s value" was chosen for correlation testing for the remaining years, since it yielded a higher correlation coefficient and greater probability over the period 1998–2000.

A considerable year-on-year variation on acorn production can be observed in the histograms of Fig. 2. The most productive year was 2001, while the harvest per tree in 2000 was very poor. In Fig. 2, the close match between the two variables was apparent. Both pollen and acorn production displayed considerable year-on-year variations, although neither displayed repetition of any particular pattern over the study period. Fig. 3 details differences in acorn production per tree as an average over the 6-year period. In some trees (2, 8, 9, 10, 16, 28, 29 and 30), no acorns were virtually found. The average standard deviation was very high (±8.48). Both acorn production and standard deviation were higher in the flat non-exposed area (individuals 11–20); the south-facing area recorded the lowest production per tree.

The variation in acorn size and weight was greater among individual trees in a given year than year-on-year for each tree. Acorn size for each tree scarcely varied from 1 year to another, remaining within the range of 30 mm length/10 mm width to 40 mm/15 mm. Considerable differences were found for acorn weight between trees, as shown in Fig. 4. However, year-on-year weight variations were small.

A Factor Analysis was used as a classificatory method of more influencing variables on AP. PI displayed a positive significant correlation with relative humidity and rainfall of January and rainfall of March; it showed negative correlation with relative humidity of April. The correlation between AP and PI was highly significant (0.95). The weather-related variables that most positively influence AP were: minimum temperature, relative humidity and rainfall of January; rainfall of March, relative humidity of April, mean temperature of June and rainfall of September. Variables coordinates of the five-dimensional extracted factors analysis represent the variables exerting highest loading in the extracted factors. The bi-dimensional Factorial Loadings Graphical Analysis indicated that PI, relative humidity of January and the rainfall recorded in September were the variables with highest loadings and nearest to AP. In a second order, we found rainfall of January and March and mean temperature of June.

4. Discussion

Acorn production in the genus *Quercus* showed considerable annual fluctuations, mast years tending to alternate with years of low production. Although many hypotheses have been put forward, a clear and unassailable explanation for this behavior has still to be found (Koening and Knops, 1995; Sork, 1992; Cecich and Sullivan, 1999; Vázquez et al., 1990). According to one of the most widely accepted hypotheses, masting in wind-pollinated species such as *Quercus* has evolved due to a proportional increase in pollen emission, fertilization and seed set during mast years (Koening et al., 1994). Accordingly, a higher concentration of airborne pollen in mast years would favor wind pollination efficiency (Nilsson and Wästljung, 1987; Norton and Kelly, 1988). In species adapted to changeable Mediterranean climate, the advantages of investing in mast years increase in years with favorable weather conditions (Smith et al., 1990; Sork and Bramble, 1993).

Given the difficulty and the ecological damage involved in establishing total acorn production, several visual estimation methods have been used in this sort of study (Graves, 1980; Koening et al., 1994; Vazquez, 1998). In view of the lack of literature on *Q. ilex* subsp. *ballota*, various traditional methods were tested. Comparison analysis between actual and visual estimation indicated the "15 s method", modified from Koening et al. (1994), as the most appropriate. The use of this method could facilitate to establish an acorn forecast model by increasing both the number of study years and individuals.

Year-on-year variations in acorn size and weight were very small which seems to indicate that they are genetically determined. Therefore, variations in harvests over the 6-year study period were due to differences in the number of acorns per tree rather than differences in single acorns size and weight. Despite considerable variations in acorn production, there was no evidence of regular masting cycles in the study population. Other

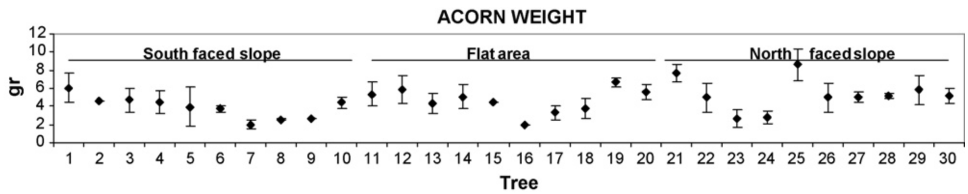

Fig. 4. Average acorn weight by each tree expressed in grams (1998–2003). Standard deviation is also showed.

studies have argued that *Quercus* reproductive dynamics display a particular periodicity (Sork and Bramble, 1993). However, the results of the present study – albeit over a relatively short period – support the view that variations in *Quercus* fruit production do not follow any given pattern (Docousso et al., 1993; Koening et al., 1994).

It is impossible to exactly determine the area of influence of an aerobiological sampler; nevertheless, the physical characteristics of *Quercus* pollen grains give them a relative short pollen dispersal capability (Jato et al., 2002; Gomez-Casero, 2003). Moreover, field floral phenological results confirmed that airborne pollen detected clearly reflected the reproductive behavior of the selected holm-oaks located at a short distance from the sampler.

A positive correlation was observed between the amount of airborne holm-oak pollen released to the atmosphere and the size of the acorn harvest. The close match between annual acorn yields and airborne pollen data agrees with the "wind pollination" hypothesis favored by many authors (Docousso et al., 1993; Koening et al., 1994; Cecich and Sullivan, 1999). Winter weather conditions influence spring pollen production, which has been shown to have a marked influence on acorn production. Therefore, weather-related parameters such as relative humidity and rainfall of January and rainfall in March were decisive factors for both PI and AP. Key events in the floral phenological cycle take place in these months; budburst usually occurs in February, and a cold, very dry atmosphere in January can lead to bud freezing. Results here showed a strong positive correlation between January minimum temperature and AP. Similarly, the final stage in catkin development occurred in the first half of March, and the availability of water in a dry Mediterranean area could increase the rate of final pollen production and hence AP. By contrast, rainfall occurring during the main pollen season, as in the spring of 2000, prompted a drop in airborne pollen due to the wash-out effect on the atmosphere, leading to a lower rate of acorn production. High relative humidity during flowering had an adverse effect on pollen dispersal; however, it has been shown that low humidity at the time of male flowering may result in higher rates of acorn production (Wolgast and Stout, 1977).

It is often asked whether fruit production in natural populations is pollen- or resource-limited (Campbell and Halama, 1993). Our results for *Q. ilex* subsp. *ballota* suggest this is not a strict dichotomy. Studies in Mediterranean *Quercus* species have demonstrated the relationship between acorn production and either pollen availability (Koening et al., 1994) or weather-related factors (Cecich and Sullivan, 1999), but have not investigated the interplay of these factors. The current study recorded large increases in fruit production both with increased pollen availability and with favorable weather conditions, including water availability. Acorn production and standard deviation were both highest in the flat, non-exposed area, probably due to greater variations in soil water availability.

The Principal Components and Factor Analysis results lead us to propose PI as a reliable bio-indicator of holm-oak acorn harvest, as already demonstrated for other anemophilous species (Galán et al., 2004; Litschauer, 2003; Koening et al., 1994). Moreover, factor analysis could be applied in a future extended study as a variable reduction method in order to obtain acorn production forecast models. The present work sheds some light on holm-oak, major species in the Iberian Peninsula, fruit-production behavior and overall on the biological and meteorological factors influencing acorn production pattern. Integration of aerobiological, field phenological and meteorological data could represent an important step forward in forest fruit production research.

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