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A model to account for variations in holm-oak (*Quercus ilex* subsp. *ballota*) acorn production in southern Spain

Herminia García-Mozo, Eugenio Dominguez-Vilches, Carmen Galán

Department of Botany, Ecology and Plant Physiology, University of Córdoba, Spain

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Abstract

One of the characteristics of holm-oak acorn production is its high variability among individuals and years. To examine the main causes of this fact, a study was conducted from 1998-2010 in a natural area of holm-oak in southern Spain, where floral phenology, fruit production, fruit size, airborne pollen emission and meteorology factors were analyzed with the ultimate aim of developing a model for forecasting holm-oak yield. Pollen emission during flowering season was the main factor determining the final acorn harvest, but also some meteorological variables played an important role in explaining acorn crop variations, especially humidity and temperature during the months of April and September. The reliability of the proposed model was externally validated using data not included in its construction; validation yielded acceptable results, with a minimum error of estimation. Our results appear to be very useful for planning cropping and pig feeding strategies. Further research could extend the use of airborne pollen counts in forest studies relating to anemophilous species, in order to optimize agricultural policies.

Key words

acorn production, pollen, oak forest, model, holm oak, *Quercus ilex* subsp. *ballota*, aerobiology, phenology

INTRODUCTION

Mast seeding, or masting – the synchronous intermittent production of large seed crops [1] – is a characteristic feature of certain tree species, including many oaks [2, 3, 4, 5]. Mast seeding is widely reported in the holm oak, *Quercus ilex* subsp. *ballota* (Desf.) Samp. an anemophilous species forming the basis of the 'dehesa' ecosystem in southern Spain [6]. The 'dehesa' ecosystem consists of oak woodland with an understory composed of a mosaic of croplands, grasslands and shrublands, which together constitute a semi-natural agro-ecosystem of open woodland forest, created and maintained by humans for livestock breeding purposes [7, 8]. In Spain, this ecosystem spans an overall area of 2.3 million ha. [9]. Holm-oak acorn production is of vital ecological and economic importance in southern Spain, since the amount and quality of available acorns strongly influences feeding patterns, not only in wild animals, but also in domestically-bred, high-quality Iberian meat pigs which are fed largely on acorns. Given the commercial implications, a thorough understanding of acorn production patterns is essential to the sustainable management of this ecosystem.

Although a number of studies have focussed on various aspects of acorn production in the 'dehesa' ecosystem, the information available to date is still not sufficient to account for all the potential causes of mast-years. One question to which there is as yet no clear answer is whether these variations are completely random or whether they are governed by certain factors. If the latter, it would be useful to identify the factors involved. Several studies have addressed this issue: traditionally, three theories have been put forward to account for masting, known as the 'seed-dispersal', 'predator satiation' and 'wind pollination' hypotheses [10, 11, 12, 13, 14]. According to the first two theories, random production patterns are a strategy to guarantee species continuity. Recent research, however, has highlighted inconsistencies in the hypotheses regarding the first two theories, and has lent support to the third, the 'wind pollination' theory, which argues that acorn crop size is strongly influenced by flowering intensity, pollen production and weather conditions during flowering and fruiting [5, 15]. A previous study, carried out in the same area of the semi-natural 'dehesa' ecosystem in southern Spain [16], found that variations in holm-oak acorn production were largely accounted for by the combined influence of pollen release patterns and weather conditions. The present study sought to build on those results, using data collected over 13 years (acorn crops, pollen release and weather-related variables), to examine in greater detail the causes of variations, and to build a preliminary model which might account for production patterns in a holm-oak population in the north of Córdoba province (Andalusia, Spain). The results obtained provide the scientific basis for the development of a potential general model to be used in future acorn-crop forecasting in southern Spain.

MATERIAL & METHODS

Study area. The study was conducted over a 13-year period (1998-2010) at 'El Cabril', a 1,200-ha reserve located in the north of the Hornachuelos Natural Park in the province of Córdoba (Southern Spain), 38°4'N, 5°24'W (Fig. 1). Average elevation of the area ranges from 450-600 m a.s.l. This area

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Address for correspondence: Herminia García-Mozo, Departamento Botánica, Ecología y Fisiología Vegetal, Edif. Celestino Mutis (C4), Campus de Rabanales, Universidad de Córdoba, Córdoba 14071, Spain.
E-mail: bv2gamoh@uco.es

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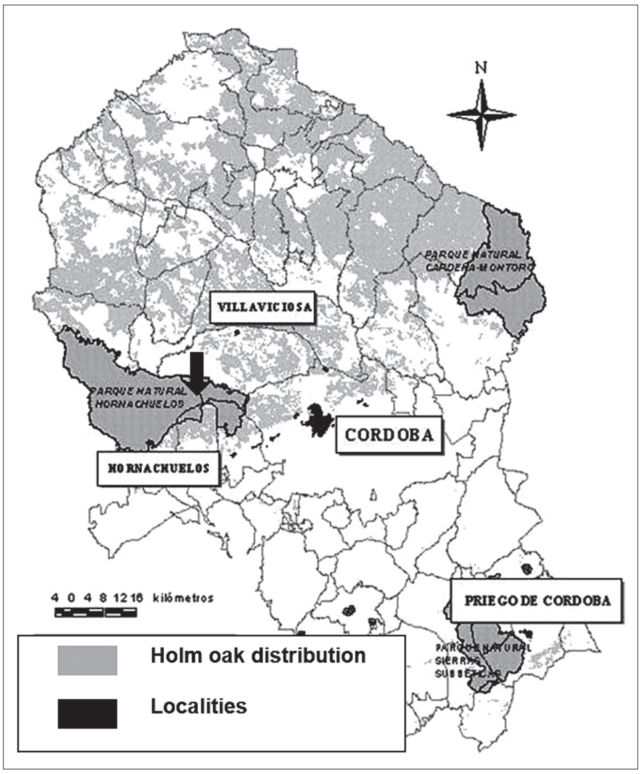

Figure 1. Map of Cordoba province. Holm oak distribution is shown in grey. The arrow marks the location of the study population: the "El Cabril" reserve in the Hornachuelos Natural Park

has a sub-humid Mediterranean climate with virtually no rainfall in summer (June-August). Mean annual rainfall over the last 50 years is 700 mm, and mean temperature 16.8°C [17].

As in most areas of southern Spain, the holm oak is the dominant tree species in the reserve. Other *Quercus* species found in the Hornachuelos Natural Park include cork oak (*Quercus suber* L.), kermes oak (*Quercus coccifera* L.), and the portuguese oak (*Quercus faginea* Lamk.), but these are not present in the study area.

In 1998, 30 holm oaks growing within a radius of 2-3 km from the site where a pollen trap was placed were tagged and periodically sampled. Ten individuals (numbered 1 – 10) were on a south-facing slope, a further 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 trees belonged to the same population. It is not easy to determine the exact age of the Mediterranean holm oak, since locally absent rings and false rings are fairly common in this species [18]. However, their age was estimated in the range 50-70 years, judging by tree size and trunk radius.

Acorn production estimates. Acorn Production (AP) by the selected trees was estimated over the whole study period. For the first 3 years (1998-2000), AP was measured by collecting acorns from the selected trees using the traditional method of beating down fruits with long poles. Harvesting took place in mid-autumn, between mid-October – early November, just prior to acorn fall. Acorns were collected on a specially-designed plastic blanket spread out below the trees. Acorn abundance was also estimated using 3 different methods in order to identify the most accurate for the trees studied. The so-called '15 s value' displayed the closest statistical correlation to AP [16], and it was therefore used to estimate AP over the 13-year-period. This method offers the average value given by 2 persons counting during 15 s. Finally, the weight and size of a random sample of 30 acorns were measured over the first 6 years of the study.

Airborne pollen data. Airborne pollen counts were recorded over the whole study period using a Hirst-type volumetric spore-trap [19], specifically, the Burkard 7-day model. The trap was placed 5 m above ground level, on a 300-m hill in the middle of the valley where the selected holm oaks were located. The standard sampling procedures recommended by the Spanish Aerobiology Network (REA) were used [20]. Pollen Index (PI) represents the annual sum of daily airborne pollen counts; Pre-Peak Index (PPI) represents the sum of daily airborne pollen counts from the start of the season up to the peak day (i.e. the day recording the maximum pollen count).

Phenology. Floral and fruit phenological observations were performed weekly in order to obtain additional information about potential sources of airborne pollen. *In situ* observations for selected trees were recorded using the holm-oak phenophase system developed by Gómez-Casero et al. [21].

Meteorological data. Weather patterns were monitored by a weather station placed 10 m from the Hirst-type spore-trap. Mean, maximum and minimum temperature, wind speed and direction, relative humidity and rainfall were measured daily. Annual rainfall ranged from 207 mm in 1999 to 617 mm and 611 mm in 2003 and 2006, respectively. 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 average wind speed in spring was 3 m/s.

Statistical analysis. Spearman's non-parametric correlation coefficients were calculated for different variables in order to chart correlations between PI, AP and monthly weather-related variables (mean, maximum and minimum temperature; relative humidity and rainfall).

Multiple regression analysis was performed to identify relationships among variables and establish the degree of variance in AP accounted for by independent variables (pollen counts and monthly weather-related variables), as the first step in constructing a preliminary model to account for variations in AP. Stepwise multiple regression analysis was performed to measure the combined or individual influence of each independent variable. A 13-year crop, aerobiological and meteorological database (1998 – 2010) was used for correlation analysis, but a 12-year database (1998-2009) was used for the regression analysis for the model. Data for 2010 were excluded from the model, and used for external validation. All statistical tests were performed using the STATISTICA 6.0 for Windows software package.

RESULTS

Meteorology. Climate data for the area during the study period are shown in Figure 2. Intra-annual variations in average monthly temperature, relative humidity and rainfall are indicated in Figure 2a. The data reflect to a Mediterranean

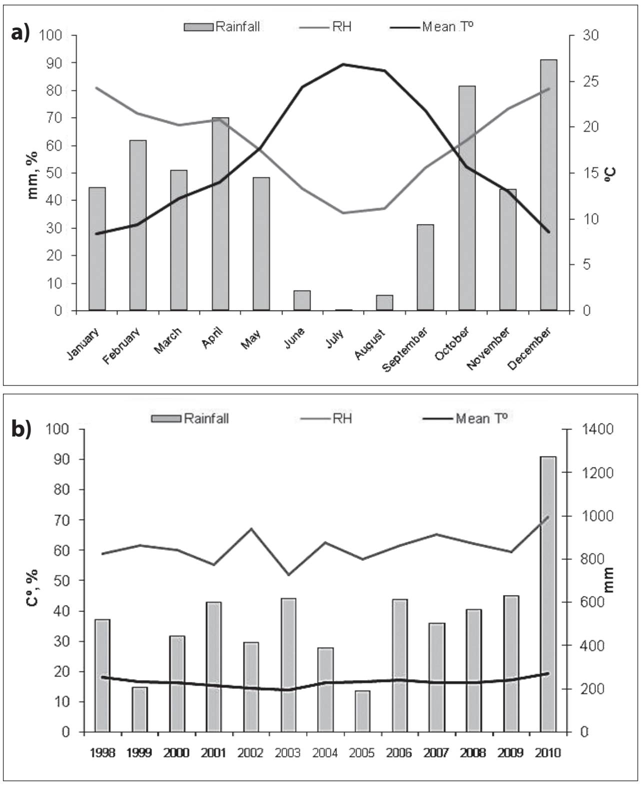

Figure 2. Meteorological data for the study period (1998-2010): a) average data for monthly Mean Temperature (Mean Tª), Rainfall and Relative Humidity (RH), b) average data for annual Mean Temperature (Mean Tª), Rainfall and Relative Humidity (RH)

climate, with scarce rainfall and very high temperatures in summer, higher rainfall in spring and autumn, and colder temperatures in winter. Annual variations in major weather-related parameters in the study areas are shown in Figure 2b. 1999 and 2005 marked the 2 driest years. In fact, those years were the driest years recorded in Spain over the past 50 years. The warmest year was 1998, whereas the lowest temperature was recorded in 2003.

Phenology. The seasonal development of average floral phenophases was similar at all sites throughout the study period, except in 1999 and 2006, when a second flowering period was recorded during autumn. In early spring, male flower budburst usually started in February, and the full flowering stage was reached around mid-April. A high percentage of fruit abortion was recorded, particular in the driest years.

Airborne pollen dynamics. Every year, the pollen-season curve was plotted on the basis of average daily airborne pollen data, obtained from the Hirst type spore-trap. A single-peak curve was generally recorded, and analysis of the main pollination periods over the study period revealed a close match with *in situ* phenological data. The results confirmed that most *Quercus* pollen grains detected by the trap came from holm oak trees in the study area.

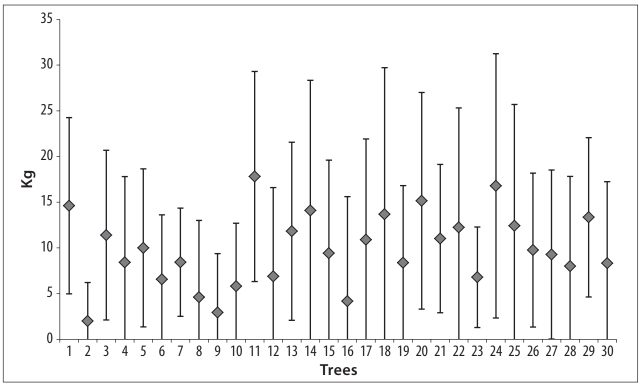

Figure 3. Average acorn production per tree, expressed in kilograms (1998-2010). Standard deviation is also shown

Acorn production. Average acorn production per tree, expressed in kilograms (1998-2010) is shown in Figure 3. Considerable year-on-year variations are evident in histograms, which also indicate standard deviation. In some trees, production remained very low throughout the study period; in most years, virtually no acorns were found. The lowest production per tree was recorded on the south-facing slope. By contrast, both acorn production and standard deviation were higher in the flat, non-exposed area (individuals 11-20). Variations in acorn size and weight for each tree over the study period were very limited; greater variation was recorded between individual trees. Acorn size by tree scarcely varied from one year to another, remaining within the range of 30 mm length/10 mm width to 40 mm length/15 mm. Year-on-year weight variations were also small. Regarding the total production of the area, the year 2000 acorn harvest was the smallest of the whole period, while the 2001 harvest was the largest, with over 500 kg of acorns.

In Figure 4, which shows variations in AP, PI (Fig. 4a) and PPI (Fig. 4b) over the study period (1998-2010), it is possible to observe the relationship between airborne pollen and

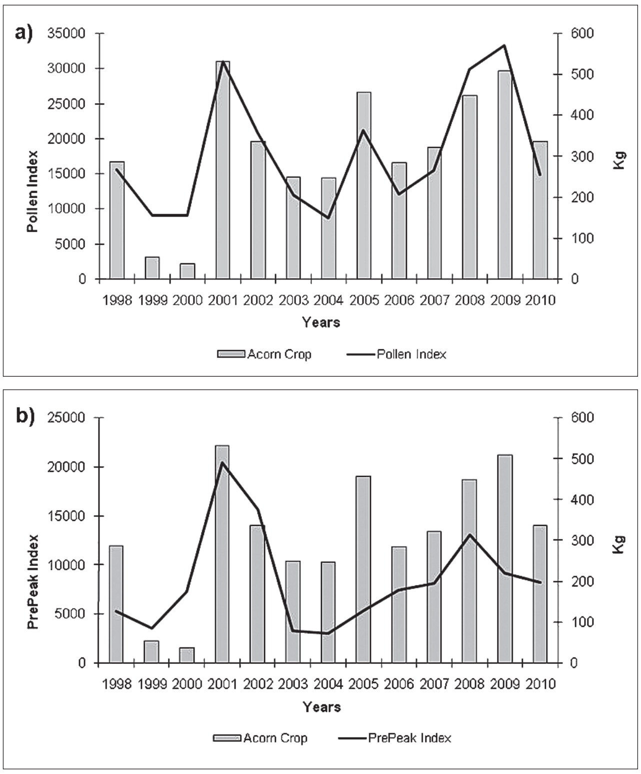

Figure 4. a) Annual Acorn Production vs. annual Pollen Index b) Annual Acorn Crop Production vs. Pre-Peak Index (pollen detected from the start of the season up to the day when the maximum concentration was recorded

fruit production. Although marked year-on-year variations in acorn production were observed, no alternating pattern was apparent over the study period, in general, years with more intense pollination seasons also displayed higher acorn productions. The link between these variables was analyzed using Spearman's correlation test, which yielded a significant R coefficient of 0.69 p< 0.01 for AP and PPI; the correlation between AP and PI was also significant but even stronger, with an R coefficient of 0.91 p< 0.00 (Tab. 1). Significant correlations were also observed for other variables influencing both PI and AP. January rainfall and April relative humidity were identified as the major factors governing PI. Whilst higher January rainfall exerted a positive influence on pollen counts, higher relative humidity in April prompted a decrease in pollen dispersal. The variable which increased AP the most – apart from PI – was increased September rainfall. High April relative humidity and high May minimum temperature exerted a negative influence.

Table 1. Significant correlations (Spearman's test; $p<0.05$) between Pollen Index (PI), Pre Peak Index (PPI), Acorn Production (AP) and monthly meteorological data. **Rf J**: Rainfall in January; **RH Ap**: Relative Humidity in April; **Min My**: Minimum temperature in May; **Rf S**: Rainfall in September

		N	Spearman R	t(N-2)	p-level
PI	& Rf J	13	0.57	2.01	0.04
PI	& RH Ap	13	-0.60	-2.42	0.03
PPI	& Rf J	13	0.63	2.60	0.02
AP	& PI	13	0.91	7.22	0.00
AP	& PPI	13	0.69	3.03	0.01
AP	& RH Ap	13	-0.69	-3.09	0.01
AP	& Min My	13	-0.33	-1.12	0.02
AP	& Rf S	13	0.64	2.63	0.02

The feasibility of using annual PI and monthly meteorological data from 1998-2009 as predictive variables was tested by multiple regression analysis. The results (Tab. 2) were statistically significant, with an adjusted R^2 value of 0.99 given the probability value $p<0.00$. Moreover, the t value calculated for each variable indicated that all the associated coefficients were significant. The main positive variables for predicting AP were rainfall and relative humidity in September. Negative variables were rainfall, relative humidity, and maximum and minimum temperature in April; minimum temperature in May; and minimum temperature in September. Using the validation data for 2010, the model forecast an AP of 319 kg in the study area; the actual crop was 336 kg, giving an acceptable error of 5%. Moreover, this model enabled production to be forecast up to 5 months prior to the end of harvesting. Given the strong influence of PI on the final AP, preliminary forecasts could even be made as early as 8-9 months before harvest.

Table 2. Regression model to forecast Acorn Production**. Min My**: Minimum temperature in May; **Rf Ap**: Rainfall in April; **Min S:** Minimum temperature in September; **Max Ap**: Maximum temperature in April; **RH S**: Relative Humidity in September; **Rf S**: Rainfall in September; **RH Ap**: Relative Humidity in April

	Beta	Std.Err.	B	Std.Err.	t(value)	p-level
Intercept			1106.25	136.02	8.13	0.00
PI	0.85	0.04	0.01	0.00	19.33	0.00
Min My	-0.39	0.03	-25.34	2.21	-11.43	0.00
Rf Ap	-0.33	0.02	-0.81	0.07	-11.20	0.00
Min S	-0.57	0.07	-31.91	4.15	-7.68	0.00
Max Ap	-0.51	0.08	-16.76	2.68	-6.24	0.00
Rf S	0.11	0.03	0.59	0.15	3.73	0.03
RH S	0.17	0.05	8.83	0.86	3.27	0.04
RH Ap	-0.10	0.05	-1.56	0.85	-1.83	0.16

Regression Summary for Dependent Variable: Acorn Crop Production.
Adjusted R^2= .99, p<0.00 Standard Error of Estimate: 10.71
F(8,3)=278.02

DISCUSSION

Little research has addressed the reasons for acorn crop variations in the *Quercus* genus. Long-term studies of acorn-production patterns in North American species highlight the apparently-random alternation of periods of low production with periods of synchronous production or mast years [4, 5, 22]. Although few studies have focused on Iberian acorn production, Vázquez et al., [13] and Esparrago et al., [23] have also reported a random alternation of mast and low-crop years in southern Spain. Generally speaking, the resource-matching and seed-dispersal hypotheses advanced to account for mast crops in the holm oak have been discarded by the scientific community. Recent studies tend to support the 'predator satiation' and 'wind pollination' theories [10, 11, 12, 14, 15].

There is a close link between airborne pollen counts and final seed yields in anemophilous species. The use of pollen content in the air as a bio-indicator of final harvest is a tool of proven utility in several species, such as *Olea europaea* L. [24, 25, 26], *Vitis vinifera* L. [27], *Corylus avellana* L. [28] and *Betula* [29]. In *Quercus*, a higher concentration of airborne pollen in mast years would favour pollination efficiency, as reported in other tree species [30, 31].

Apart from the 'wind pollination' hypothesis, a number of authors [32, 33, 34] have highlighted the key role of weather-related factors in acorn ripening. Montserrat-Martí et al. [35] and Misson et al. [36] report that summer drought constrains acorn yields in the holm oak. Other factors, such as the combined effect of pruning and weather conditions, have also been investigated: yield variations have been found to depend on the weather patterns specific to each year, but tend to be independent of pruning intensity [32, 37].

Annual pollen emission is a measure of flowering intensity, and may thus indicate the intensity of crop yields. However, fruit development may be strongly influenced by weather-related parameters, especially in the highly-changeable climate of the Mediterranean area. In this climate, extreme climatic events, i.e. episodes in which the acclimatory capacity of organisms or populations is substantially crossed, triggering non-linearities [37, 38], are common

Various methods have been tested to estimate acorn production in a given area, including qualitative or indirect methods and quantitative or direct methods, based on visual surveys [39]. Over the first 3 years of the study, the quantitative method used was based on direct correlation with total harvest [16]. Considerable year-on-year variations were observed not only in acorn production, but also in airborne pollen counts. Since there was little change in acorn size and weight within a given tree, changes in yield must have been due to variations in the number of acorns per tree.

Despite these variations, no regular AP cycle was observed in the study population; similar findings are reported by [11, 12], although Abrahanson & Layne [22] noted regular cycles of acorn production in North American oak species.

In an earlier study [16], attention was drawn to the influence of PI on AP in holm oaks in southern Spain. In this paper, research was focussed more closely on the role of the different variables, with the ultimate aim of developing a model for forecasting holm-oak yield. For this purpose pollen dynamics, *in-situ* phenological data and weather parameters were measured. Weather conditions govern the pollen season, particularly in terms of timing and intensity, but their effect varies depending on the type of population and on its topographical location and the climate area. *In-situ* phenological observations of floral development contribute to a better understanding of aerobiological data, as well as to a more efficient localization of major pollen sources [40]. In this paper, by studying both types of data, it was apparent that most of the airborne pollen came from the holm-oak population under study, which would explain why total annual airborne pollen governed the final harvest. This hypothesis is supported by the fact that, because of the physical characteristics of *Quercus* pollen grains, their pollen dispersal capacity is relatively limited [21, 41, 42].

A strong positive correlation was observed between annual airborne pollen counts and annual acorn harvest size. The close match lends support to the wind pollination hypothesis advanced by many authors for other oak species [10, 11, 12, 14, 15].

Weather-related parameters prior to pollination govern the timing and the intensity of holm-oak pollination [43]. Here it was observed that January rainfall and April relative humidity were the major factors influencing PIs. Whereas January rainfall exerted a positive influence, April relative humidity prompted a decrease in pollen dispersal due to the harmomegathy property of pollen grains that cumulate water and increase the size and weight, prompting their fall, and thus impairing the capacity for effective pollinization. Moreover, our results indicate that variations in crop yield were partially in response to changes in weather conditions. The variable most affecting AP – apart from PI – was September rainfall. Other authors have reported that summer drought leads to young-acorn abortion and consequently to low fruit production [35, 36]. April relative humidity and May minimum temperature exerted a negative influence, probably due to reduced pollination success and the death of young fruits at high temperatures.

The results obtained in the presented study provide only a partial answer to a question crucial for 'dehesa' ecological systems: whether acorn production is pollen- or resource-limited. Marked increases in acorn production were recorded in association with high airborne pollen levels, but also in association with favourable resources (mostly water availability). Notably, the flat area of the study site recorded higher acorn production due to greater water availability.

These results indicate that an acorn-production forecasting model can be constructed using PI as the main influencing variable, but also using a number of other weather parameters as indicated above. The reliability of the model was externally validated using data not included in its construction; validation yielded acceptable results, with a minimum error of estimation. This model could thus be very useful for planning cropping and pig feeding strategies in the study area. Further research could extend the model to other parts of Spain in order to optimize 'dehesa'-based agricultural policy.

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