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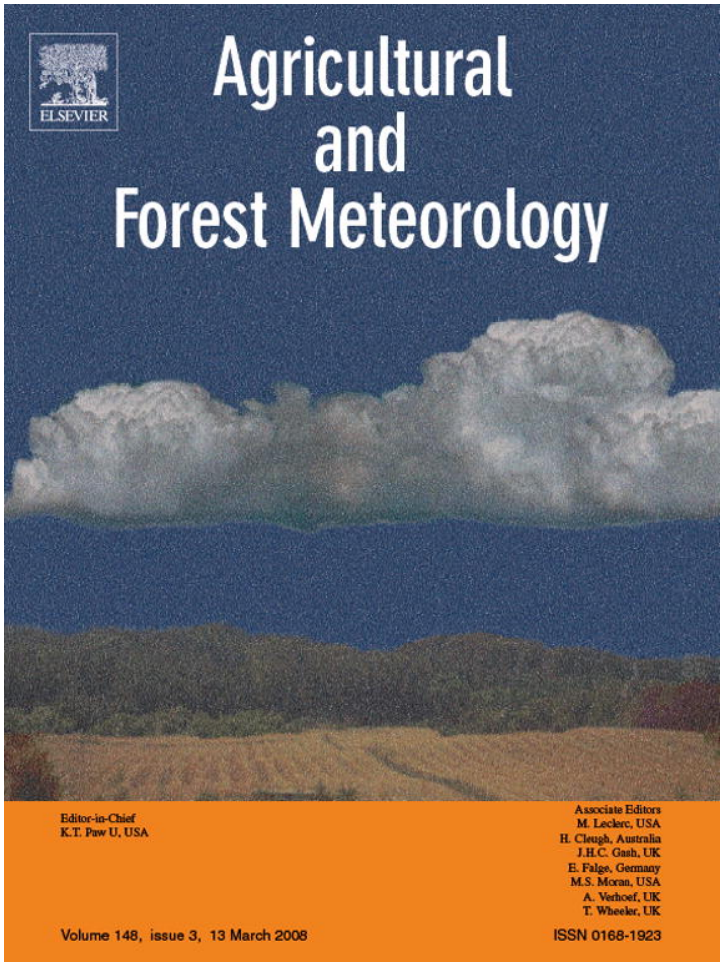

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Regional phenological models for forecasting the start and peak of the *Quercus* pollen season in Spain

H. García-Mozo [a,*], *I. Chuine* [b], *M.J. Aira* [c], *J. Belmonte* [d], *D. Bermejo* [e], *C. Díaz de la Guardia* [f], *B. Elvira* [g], *M. Gutiérrez* [h], *J. Rodríguez-Rajo* [c], *L. Ruiz* [i], *M.M. Trigo* [j], *R. Tormo* [k], *R. Valencia* [l], *C. Galán* [a]

[a] *Departamento de Botánica, Ecología y Fisiología Vegetal, Universidad de Cordoba, Spain*
[b] *Centre Ecologie Fonctionnelle Evolutive CNRS Montpellier, France*
[c] *Departamento de Biología Vegetal y Ciencias del Suelo, Universidad de Vigo, 32004 Ourense, Spain*
[d] *Unidad de Botánica, Facultad de Ciencias, Universidad Autónoma de Barcelona, 08193 Bellaterra, Barcelona, Spain*
[e] *Colegio de Farmacéuticos de Zaragoza, Spain*
[f] *Departamento de Biología Vegetal, Facultad de Ciencias, Universidad de Granada, 18001 Granada, Spain*
[g] *Dpto. Química de Medio Ambiente, Aerobiología y Toxicología Ambiental, Universidad Politécnica de Cartagena, Spain*
[h] *Departamento de Biología Vegetal II, Universidad Complutense de Madrid, 28040 Madrid, Spain*
[i] *Departamento de Biología Animal, Vegetal y Ecología, Universidad de Jaén, 23071 Jaén, Spain*
[j] *Departamento de Biología Vegetal, Facultad de Ciencias, Universidad de Málaga, 29080 Málaga, Spain*
[k] *Escuela Universitaria de Ingeniería Técnica Agrícola, Universidad de Extremadura, Badajoz, Spain*
[l] *Departamento de Biología Vegetal, Facultad de Biología, Universidad de León, 24071 León, Spain*

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ABSTRACT

The study sought to achieve the broadest possible spatial and temporal predictions by examining genetic variations in the timing of flowering between populations of the Iberian *Quercus* species using pollen data from 15 sites in Spain. The specific objective of the study was to develop and fit regional phenological model to predict the flowering start and flowering peak of *Quercus* species in the Iberian Peninsula by ascertaining whether potentially significant genetic variations in the timing of flowering required different phenological models or if, on the contrary, regional models for several localities can explain the variability detected in *Quercus* phenology in Spain. Model estimates did not vary greatly as a function of environment within similar climate areas where the same species grew; thus, model estimates of the temperature response of individuals growing in similar climate areas did not differ significantly. The percentage of variance explained by models was greater in models fitted with local data (75–97%). Nevertheless, acceptable results were also obtained using regional models (55–85%). The lowest value was found for the Simplifed Model including all Spanish sites together (51%).

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* *Corresponding author at*: Departamento de Botánica, Ecología y Fisiología Vegetal, Campus de Rabanales, Universidad de Cordoba, Spain. Tel.: +34 957 218 719; fax: +34 957 218 599.
E-mail address: bv2gamoh@uco.es (H. García-Mozo).
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1. Introduction

In view of the major impact of climate change on ecosystems, many studies have sought to model the response of plant phenology to climate (Schwartz, 2003). Most such studies have highlighted a strong relationship between temperature and plant phenology, especially in woody plants. A number of authors have used these models to predict the consequences of increasing temperatures on the phenology of temperate-zone trees, in order to determine whether species would break bud or flower later or earlier (Walther et al., 2002; Galán et al., 2005). The reproductive phenology of temperate tree species is commonly assumed to be strongly related to temperature and also locally adapted to different climate ranges. However, recent research suggests that local adaptation is not as great as expected, due to high levels of gene flow, marked year-on-year climate variations and the plasticity of phenology. Studies have shown that phenological models can be established for tree populations including individuals scattered over wide regional areas. Chuine et al. (2000) reported a common response to temperature in natural populations of *Alnus glutinosa*, *Ulmus minor* and *Carpinus betulus* distributed throughout central Europe.

The present study aimed to develop a temperature-based model to explain and forecast the main *Quercus* reproductive phenological phases in the Iberian Peninsula: flowering start and flowering peak. The prior hypothesis took into account the anemophilous nature of these species, which prompts a high potential gene flow due to wide pollen dispersal (up to hundreds of kilometres) (Faegri and Iversen, 1989); moreover, the marked ability of Iberian *Quercus* species to adapt to different climate ranges has been amply demonstrated, especially in the evergreen *Quercus ilex* subsp. *ballota* Desf. (Samp) (Faust, 1989; Larcher, 1995). Therefore, the selective force attributed to climate-related variables such as temperature is partially reduced in these species. It was hypothesized that the balance between factors contributing to local adaptation would not lead to significant genetic variations in phenology between close populations.

The study sought to achieve the broadest possible spatial and temporal predictions by examining genetic variations in the timing of flowering between populations of the Iberian *Quercus* species using pollen data from 15 sites in Spain. The main objective of the present work is to develop a temperature-based model to forecast the start and peak of *Quercus* flowering in the Iberian Peninsula. The influence of genetic patterns in the phonological response is also studied in order to use the minimum number of validated models to predict *Quercus* reproductive phenology in the Iberian Peninsula to optimise real application. The possible impact of global warming on *Quercus* phenology is also discussed taking into account the great ecological and economical importance of this genus in the Mediterranean area.

2. Materials and methods

2.1. Studied areas

The 15 sampling-sites displayed different climate, topographic and vegetation characteristics; the main features are summarised in Table 1. North-western Spain has a mild, rainy climate, influenced by the Atlantic Ocean. The predominant form of vegetation is deciduous woodland, with a large population of *Quercus robur* L. Three of the provinces: Vigo, Lugo and Santiago, are located in the Euro-Siberian region, with similar weather and vegetation conditions, and low altitude. *Q. robur* L. (the first to flower) is the most common *Quercus* species in local forests. The remaining sampling-sites are located in the Mediterranean Region, although Ourense and Leon display a marked Euro-Siberian influence. The sampling site located in the Northeast of the Iberian Peninsula, Barcelona, is surrounded by a typically Mediterranean landscape, with abundant holm oaks (*Quercus humilis* Miller, *Quercus ilex* subsp. *ilex* L., and *Quercus suber* L. Kermes oak (*Quercus coccifera* L.) woodland is found on the most impoverished soils. *Q. humilis* is the first to flower and, together with *Q. ilex* subsp. *ilex*, it is the main source of the *Quercus* pollen peak in this area. The Central area has a dry, continental climate with significant inter-seasonal variations in both temperature and rainfall. In the countryside around Madrid and Zaragoza, the dominant *Quercus* species is the holm-oak *Q. ilex* subsp *ballota,* which appears in areas of oak-grass savannahs used for livestock farming and known as *dehesas*, but also in the Mediterranean forest of the surrounding mountains. The landscape of León is characterised by mid-altitude holm-oak woodland, although higher woodland populated by *Q. pyrenaica* and *Q. faginea* Lam. is also found. These two species flower with less intensity one month later than the holm-oak. The Southern region includes five of the sampling-sites: Córdoba, Priego, Jaén, Granada, Málaga and Cartagena. This region has a warmer, drier Mediterranean climate, with more moderate conditions in the coastal areas of Málaga and Cartagena. Typical vegetation includes *dehesas* of holm-oak (first flowering), cork-oaks (last flowering) in the most humid areas with acid soils, and kermes-oak (second flowering) in impoverished soil areas.

2.2. Phenological data

Airborne *Quercus* pollen data were drawn from 15 localities in Spain (Fig. 1); time series varied between sites, from 7 to 24 years (Table 1). The last year analysed was 2005. Main biogeographical characteristics of the sampling-sites are shown in Table 1. Pollen data were collected using Hirst volumetric traps (Hirst, 1952), following the standard methodology laid down by the Spanish Aerobiology Network (REA) (Galán et al., 2007). The *Quercus* pollen-season start-date, indicating the start of flowering, was defined as the first day on which one pollen grain/m^3 was recorded and the five following days recorded one or more pollen grains/m^3 (García-Mozo et al., 2000). The peak date was defined as the day on which maximum pollen counts were recorded, i.e. the date when most plants in a given population were in full bloom. Phenological models were developed to predict both dates.

2.3. Temperature data

Mean daily temperatures were recorded at local weather stations at each sampling-site; all stations belonged to the Spanish Meteorological Institute (INM).

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Table 1 – Biogeographical characteristics of the study sites

Regions			Sampling periods	Alt.	Coord.	T°	R_f	*Quercus* species	Start species	Peak species
South	South-western	Córdoba	(1982–2005) 24 years	123	37°50′N, 4°45′W	18.0	674	*Quercus ilex* subsp. ballota, *Quercus coccifera*, *Quercus suber*, *Quercus faginea*	*Q. ilex* subsp. ballota	*Q. ilex* subsp. ballota
	South-eastern	Badajoz	(1993–2005) 13 years	186	38°53′ N, 6°58W	16.8	497	*Q. ilex* subsp. ballota, *Q. suber*, *Q. coccifera*	*Q. ilex* subsp. ballota	*Q. ilex* subsp. ballota
		Priego	(1994–2004) 11 years	650	37°26′N, 4°11′W	14.4	650	*Q. ilex* subsp. ballota, *Q. coccifera*	*Q. ilex* subsp. ballota	*Q. ilex* subsp. ballota
		Jaén	(1996–2005) 10 years	550	36°46′N, 3°47′W	17.0	582	*Q. ilex* subsp. ballota, *Q. coccifera*, *Q. faginea*	*Q. ilex* subsp. ballota	*Q. ilex* subsp. ballota
	South coast	Granada	(1992–2005) 14 years	685	37°11′N, 3°35′W	15.5	462	*Q. ilex* subsp. ballota, *Q. coccifera*, *Q.suber*	*Q. ilex* subsp. ballota	*Q. ilex* subsp. ballota
		Málaga	(1992–2005) 14 years	5	36°47′N, 4°19′W	18.0	575	*Q. ilex* subsp. ballota, *Q. coccifera*, *Q.suber*	*Q. ilex* subsp. ballota	*Q. ilex* subsp. ballota
		Cartagena	(1993–2004) 12 years	10	37°36′ N, 0°59′ W	17.0	300	*Q. ilex* subsp. ballota, *Q. coccifera*	*Q. ilex* subsp. ballota	*Q. ilex* subsp. ballota
Centre	Centre	Madrid	(1993–2005) 13 years	600	40°27′N, 3°45′W	14.0	440	*Q. ilex* subsp. ballota, *Q. pyrenaica*, *Q. coccifera*, *Q. faginea*	*Q. ilex* subsp. ballota	*Q. ilex* subsp. ballota
		Zaragoza	(1994–2005) 12 years	200	41°39′N, 2°48′E	15	314	*Q. ilex* subsp ballota, *Q. coccifera*, *Q. faginea*, *Q. pubescens*	*Q. ilex* subsp ballota	*Q. ilex* subsp ballota
		León	(1994–2005) 12 years	830	42°34′N, 5°35′W	11.0	535	*Q. ilex* subsp ballota, *Q. pyrenaica*, *Q. faginea*	*Q. ilex* subsp. ballota	*Q. ilex* subsp. ballota
West	North Western	Ourense	(1993–2005) 13 years	130	42°21′N, 7°51′W	13.8	802	*Q. robur*, *Q. pyrenaica*, *Q. suber*, *Q. ilex* subsp ballota	*Q. robur*	*Q. robur*
		Vigo	(1995–2005) 11 years	50	42°14′N, 8°43′W	15	1338	*Q. robur*, *Q. pyrenaica*, *Q. suber*	*Q. robur*	*Q. robur*
		Santiago	(1993–2005) 13 years	270	42°53′N, 8°32′W	12.8	1545	*Q. robur*, *Q. pyrenaica*	*Q. robur*	*Q. robur*
		Lugo	(1999–2005) 7 years	454	42°0′N, 7°53′W	11	963	*Q. robur*, *Q. pyrenaica*	*Q. robur*	*Q. robur*
East	North eastern	Barcelona	(1994–2005) 12 years	90	41°24′N, 2°9′E	16.4	593	*Q. ilex* subsp. ilex, *Q. humilis*, *Q. coccifera*, *Q. suber*	*Q. humilis*	*Q. humilis*, *Q. ilex subsp. ilex*

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Fig. 1 – Location of the study sites in Spain.

2.4. *Phenological models*

The phenological models reported here were based on the Unified Model for budburst of trees described by Chuine et al. (2000). A modified general model was created in order to fit parameters to both start and peak dates.Unified Start Peak (UnSP) models used 14 parameters, and were based on mean temperature data from 1 September.Variables for UnSP models:

- t_s, start-date
- t_p, peak date
- t_0, 1 September
- t_1, start-date of accumulation
- S_f, (t) state of forcing at day t
- R_f, t rate of forcing at day t
- R_c = chilling rate function
- F^* = critical value of S_f
- T_b = base temperature
- x_t, mean daily temperature
- UnSP Model (a_{start}, b_{start}, c_{start}, d_{start}, e_{start}, a_{peak}, b_{peak}, c_{peak}, d_{peak}, e_{peak}, c_{01}, c_{02}, C_{crit}, t_c)

The state of forcing (S_f) is described as a daily sum of rates of forcing, with t as the start-date of accumulation, ts as the date of flowering start, t_p as the peak date and x_t as the mean daily temperature.

$$S_f = \sum_{t_1}^{t_s,t_p} R_f(x_t) = F* \quad (1)$$

$$R_f(x_t) = \frac{1}{1 + e^{d(x+e)}} \quad (2)$$

(define the response to forcing temperature)

The state of chilling S_c is described as a daily sum of rates of chilling, with t_0 the starting date of dormancy, t_1 as the date of quiescence

$$S_c = \sum_{t_0}^{t_1} R_c(x_t) \quad (3)$$

$$(t_c) \quad R_c(x_t) = 1/(1 + e^{a(x-c)^2 + b(x-c)}) \quad (4)$$

(define the response to chilling temperature)

C_{crit} function describes the response of bud growth to temperature, indicating the relationship between the state of forcing and the state of chilling.

$$(C_{crit}) \; F* = c_{01}\, e^{c_{02} C_{crit}} \quad \text{(state of forcing needed to burst)} \quad (5)$$

First, a separate model was fitted for each sampling-site; second, a simplified model was developed for all sites taken together; finally, different regional models were tested. For

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this latter purpose, data from several sampling stations were pooled, following grouping by proximity, by species spectrum and by climate characteristics. Data from groups of sites were called populations, and the resulting models were termed regional models. Models were fitted using the least-squares method and the Metropolis simulated-annealing algorithm (Chuine et al., 1998). After complete fitting, models were also fitted by extracting data for some years. Predicted results were validated by comparing real and expected data.

2.5. Stability of model estimates across environments

Quercus flowering start and peak dates were used to test the hypothesis that estimates obtained using phenological models fitted using data from neighbouring populations sharing *Quercus* species spectra and climate characteristics would not differ significantly.

Models were fitted:

(1) using data for each separate site, local model (LM)
(2) using pooled data for all sites, simplified model (SM)
(3) using data for a group of sites, regional model (RM)

The F value, which measures the distance between individual distributions, was calculated as

$$F = \frac{[(SS_1 - SS_2)/(df_2 - df_1)]}{[SS_2/(df_{TOT} - \Delta df_2)]} \quad (7)$$

where SS_1 and SS_2 are the residual sum of squares of models, df_2 and df_1 the degree of freedom of models, and df_{TOT} is the total degree of freedom. Model estimates were deemed to vary with environment if the F value was significantly higher than the critical value of F (df_2–df_1, df_{TOT}–df_2).

2.6. Measurement of local variations

SMs and RMs were tested against LMs for the sites concerned. The percentage variation between populations was defined as

$$100\left[\frac{(SS_1 - SS_2)}{(SS_{TOT})}\right] \quad (8)$$

where SS_{TOT} is total variance. The population effect was significant if this value was significantly higher than the critical value of F (df_2–df_1, df_{TOT}–df_2).

3. Results

3.1. Responses of flower buds to temperature

As a graphic example of the temperature requirement, Fig. 2 shows the state of forcing (Fig. 2a), the state of chilling (Fig. 2b) and the negative relationship between the two (Fig. 2c) for the SMod developed for all Spanish sites together. This phenological model assumes that flower bud dormancy is broken by chilling temperatures and that bud development is regulated by forcing temperature over a given threshold.

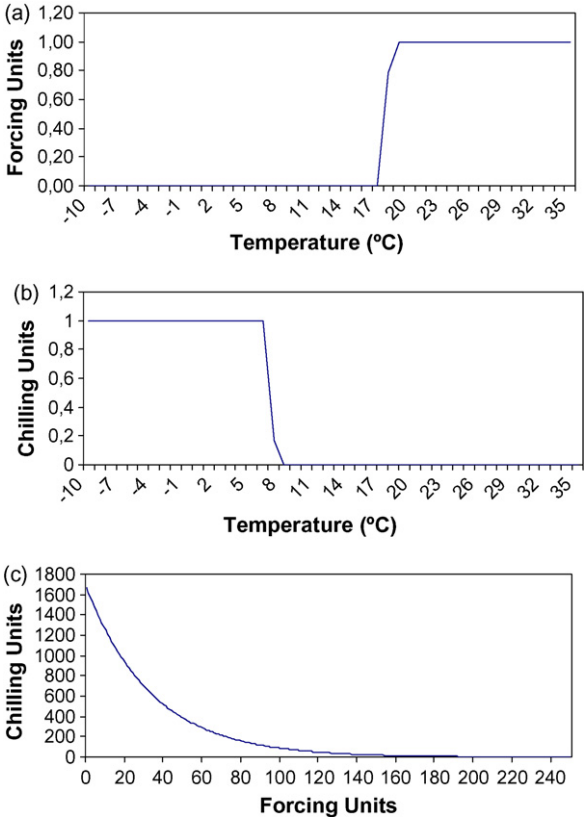

Fig. 2 – Country model for the start and peak flowering dates in Spain. (a) Relationship between temperature and heat units calculated with the country model. (b) Relationship between temperature and chilling units. (c) Relationship between heat units and chilling requirements.

Firstly, models were fitted at a local scale. Table 2 shows the parameter estimates for each model and the variance in flowering dates (R^2) explained by each variable. Analysis shows that reaching a minimum state of chilling was not always reached before cumulating forcing temperatures. The t_c data (from 1 September) indicate the average date when chilling requirements were fulfilled. At some sites, dates close to 1 September confirm this. This lack of chilling requirement was especially apparent on the Mediterranean coast localities as Cartagena and Barcelona.

Although the results shown in Table 2 suggest that chilling temperatures were not always accumulated to break dormancy in Mediterranean species, the greater the chilling temperatures recorded, the lower the forcing temperatures required to reach budburst, as shown in Fig. 2c for the SM.

The percentage of variance explained by models was greater in models fitted with local data (75–97%). Nevertheless, acceptable results were also obtained using regional models (55–85%). The lowest value was found for the SM including all Spanish sites together (51%).

3.2. Stability of model estimates across environments

Model parameters were fitted to data for populations at various levels (local, sub-regional, regional and peninsular), to

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Table 2 – Estimates of the different models

Type of model	Region/ locality	Model code	R^2	SS_{res}	a_{start}	b_{start}	c_{start}	d_{start}	e_{start}	c_{01}	c_{02}	C_{crit}	t_c	a_{peak}	b_{peak}	c_{peak}	d_{peak}	e_{peak}
SM	Spain	SM	**0.51**	−102374.30	0.49	15.00	−23.72	−0.33	−17.96	1668.15	−0.03	151.78	296.19	0.00	0.10	−33.13	−0.27	−19.91
RM	South	RMS	**0.55**	−39984.16	0.01	0.06	−12.38	−0.27	−19.97	2636.08	−0.07	27.94	280.39	0.02	−0.14	−7.25	−0.50	−19.69
	South-Eastern	RMSE	**0.72**	−6330.27	1.73	−28.46	0.68	−0.86	−11.77	458.72	−0.02	63.14	220.85	2.30	−24.52	−3.92	−32.07	−13.01
	Central South	RMCS	**0.72**	−9460.58	0.13	3.35	−22.35	−0.83	−17.46	152.41	−0.02	64.49	224.48	1.31	−10.96	−6.55	−0.38	−19.61
	South Coast	RMSCs	**0.69**	−8814.65	1.47	−22.21	−9.57	−0.95	−1.99	200.24	0.00	1.22	198.58	7.53	−6.05	−19.58	−39.12	8.43
	Centre	RMC	**0.68**	−11940.17	1.25	−29.97	−0.91	−30.54	−12.71	2728.64	−0.49	201.08	251.52	0.01	0.23	−25.30	−36.44	−17.34
	NorthWest	RMNW	**0.57**	−17264.00	0.01	−1.50	1.01	−23.14	−14.89	309.19	−0.50	194.48	236.59	0.00	0.09	−38.93	−35.08	−16.17
	NorthEast	RMNE	**0.85**	−3811.85	0.00	15.00	−12.52	−12.81	−19.77	2186.43	−0.48	3.49	241.71	9.63	−4.87	−10.66	−40.00	−16.42
LM	Cordoba	LM1	**0.76**	−3889.01	0.36	−12.00	5.73	−29.65	−15.84	221.46	−0.22	186.72	259.63	0.03	0.62	−23.14	−11.61	−9.75
	Priego	LM2	**0.87**	−871.14	1.50	3.20	−13.12	−22.82	−13.73	336.34	−0.15	11.08	211.56	5.23	9.47	−12.87	−17.64	−15.87
	Jaen	LM3	**0.87**	−471.70	0.08	−29.47	9.34	−7.66	−8.69	100.44	0.00	149.56	261.39	0.62	−16.52	3.52	−40.00	−10.57
	Granada	LM4	**0.77**	−2862.88	1.57	−14.10	−15.15	−40.00	−0.44	203.05	0.00	1.37	44.79	1.76	−20.04	−6.16	−40.00	−4.04
	Malaga	LM5	**0.86**	−1627.59	10.00	−22.85	−22.37	−22.75	−3.66	201.93	−0.01	1.50	48.54	1.33	−0.19	−19.92	−0.34	3.02
	Cartagena	LM6	**0.75**	−3153.46	0.64	−20.17	−11.97	−0.37	−12.80	1599.21	−0.22	5.24	10.77	2.52	−21.63	−21.02	−40.00	−14.43
	Badajoz	LM7	**0.85**	−2512.53	1.62	−25.48	−7.23	−18.55	−15.88	546.37	−0.03	62.05	263.96	0.89	−13.09	−9.40	−5.04	−19.88
	Madrid	LM8	**0.77**	−3400.86	0.62	−20.57	8.93	4.32	7.45	2566.83	−0.44	198.60	247.20	0.73	15.00	−17.78	−26.95	−19.93
	Leon	LM9	**0.84**	−1498.21	1.69	−0.50	−4.76	−10.23	−12.12	77.24	−0.40	2.01	133.53	8.84	−9.81	−3.74	−17.34	−14.87
	Zaragoza	LM10	**0.86**	−1495.68	0.25	7.14	−38.79	−1.55	−16.33	567.65	−0.04	51.28	296.93	2.69	−29.21	−12.68	−9.60	−15.86
	Barcelona	LM11	**0.85**	−3811.85	0.00	15.00	−12.52	−12.81	−19.77	2186.43	−0.48	3.49	241.71	9.63	−4.87	−10.66	−40.00	−16.42
	Ourense	LM12	**0.79**	−1172.23	1.49	−11.41	−16.30	0.05	−20.00	127.25	−0.01	1.24	22.11	0.00	−30.00	−10.07	0.01	−12.21
	Vigo	LM13	**0.85**	−2168.00	0.00	−22.49	−7.73	−40.00	−4.25	314.11	−0.01	44.82	72.68	3.81	−29.48	−11.59	−13.99	1.76
	Santiago	LM14	**0.78**	−1848.00	6.26	−21.57	−6.25	−2.37	−16.33	322.58	−0.16	16.48	225.90	1.24	2.45	−9.03	−18.98	−14.71
	Lugo	LM15	**0.97**	−253.66	9.45	−28.77	−11.78	−31.79	5.73	200.17	0.00	2.65	175.96	3.18	0.24	−16.70	−28.59	−3.07

df_{tot}: total degrees of freedom; SS_{res}: residual sum of squares; C_{crit}: response of bud growth to temperature; c_{01} and c_{02}: parameters of C_{crit} function; t_c: date from 1 September when the chilling requirements were fulfilled; *a*, *b*, *c*, *d*: model parameters estimates for the start and peak. Bold values indicate significant probability (<0.01).

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ascertain whether any significant variation existed in the response of phenology to environment, and whether it would thus be necessary to build different phenological models. Regional-model results supported the hypothesis that model estimates do not greatly vary with environment within a similar climate area and over a similar *Quercus* species spectrum. It was therefore concluded that model estimates of the response to temperature in individuals growing in similar climate areas are not significantly different, and thus that regionally simplified phenological models are sufficient to provide a general idea of *Quercus* phenological behaviour across the Iberian Peninsula.

3.3. *Measurement of local variations*

F-test results for comparison of variance in models for different groups of sites are shown in Table 3. Statistically significant differences (bold face) indicate variance (variability) between groups. The results suggested that regional models were effective and that a comparison between

Table 3 – Measure of the genetic variation between populations

		SS	df	MS	*F*	*p*	R^2
LM1 + LM2+···+LM15/SM	SM	108028.89	14	7716.35	**2.02**	**0.00**	**0.34**
	Site effect	71338.30	196	363.97			
	Residual	31036.00	172	180.44			
	Total	210403.18	382	550.79			
RMS + RMC + RMNW + RMNE/SM	SM	108028.89	14	7716.35	**3.12**	**0.00**	**0.14**
	Site effect	29374.30	42	699.39			
	Residual	73000.00	326	223.93			
	Total	210403.18	382	550.79			
LM1 + LM2 + ···LM7/RMS	RMS	48078.02	14	3434.14	**6.12**	**0.00**	**0.38**
	Site effect	33582.50	84	399.79			
	Residual	6401.50	98	65.32			
	Total	88062.02	196	449.30			
LM8 + LM9 + LM10/RMC	RMC	25339.78	14	1809.98	0.99	0.51	0.15
	Site effect	5545.42	28	198.05			
	Residual	6394.75	32	199.84			
	Total	37279.95	74	503.78			
LM12 + ··· + LM15/RMNW	RMW	22915.59	14	1636.83	1.66	0.07	0.29
	Site effect	11822.11	42	281.48			
	Residual	5441.89	32	170.06			
	Total	40179.59	88	456.59			
RMCS + RMSE + RMSCs/RMS	RMS	48077.85	14	3434.13	**3.44**	**0.00**	**0.17**
	Site effect	15378.66	28	549.24			
	Residual	24605.50	154	159.78			
	Total	88062.02	196	449.30			
LM1 + LM7/RMCS	RMCS	23864.30	14	1704.59	1.57	0.12	0.09
	Site effect	3059.04	14	218.50			
	Residual	6401.54	46	139.16			
	Total	33324.88	74	450.34			
LM5 + LM6/RMSCs	RMSCs	19599.40	14	1399.96	1.45	0.21	0.14
	Site effect	4033.60	14	288.11			
	Residual	4781.05	24	199.21			
	Total	28414.06	52	546.42			
LM2 + LM3 + LM4/RMSE	RMSE	16380.32	14	1170.02	0.51	0.96	0.09
	Site effect	2124.55	28	75.88			
	Residual	4205.72	28	150.20			
	Total	22710.59	70	324.44			

Variances explained by the country, region and local areas. SS: sum of squares; df: degree of freedom; MS: minimum square (sum of squares/degree of freedom); *F*: Fisher–Snedecor statistic; *p*: probability; R^2: explained variance. Bold values indicate significant variance between groups.

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populations was feasible at that level. Models fitted with local and sub-regional data did not provide greater accuracy in explaining variations in flowering-times between populations. The proposed division into four main regions: North-West (Ourense, Vigo, Santiago and Lugo), North-East (Barcelona), Central (Madrid, Zaragoza and Leon) and South (Cordoba, Badajoz, Priego, Jaen, Granada, Malaga and Cartagena) would appear to be sufficient for effective forecasting of *Quercus* flowering start-date and peak-date in the Iberian Peninsula.

4. Discussion

This analysis covered a wide geographical area with different climate features. In view of the large number of records studied, the results may be considered representative for the whole of Spain. The response of spring species, such us *Quercus*, to temperature was clear. Throughout Europe, earlier flowering species have been shown to be more sensitive, and therefore better indicators of changes in temperature than later-flowering species. Menzel et al. (2006) recommended further research to determine the response to temperature in warmer countries such us Spain. The present study modelled the temperature response of flowering start and flowering peak in major tree species. Model estimates for different populations proved stable across environments. Although a strong response of flowering start-date to temperature has already been reported in earlier studies (García-Mozo et al., 2002, 2006), the factors controlling peak flowering date, when most individuals are spreading pollen, hitherto remained somewhat unclear; the present results confirm that temperature also plays a key role in determining this date.

R^2 statistic was significant in most of the model runs, and highly significant in some cases. The percentages of variance explained by local models were on average greater than those explained by regional and national models. Nevertheless, acceptable results were also found obtained using regional models. This suggests that regional models may be sufficiently effective, and thus that local models are not necessary. This would facilitate forecasting by the Spanish Aerobiology Network (REA, http://www.uco.es/rea/). Improved knowledge of the influence of climate on pollen seasons is also valuable from a medical standpoint, in that climate-related changes in pollen seasons will affect the presence of airborne allergens (Beggs, 2004). The present results bear out World Health Organization conclusions: ''an earlier start and peak of the pollen season is being more pronounced in species that start flowering earlier in the year, and that duration of season is extended in spring and summer flowering species '' (Huynen and Menne, 2003).

There was no significant difference in the *Quercus* flowering response to temperature in similar bioclimatic areas. Model estimates did not vary greatly as a function of environment within similar climate areas where the same species grew; thus, model estimates of the temperature response of individuals growing in similar climate areas did not differ significantly. Similar findings are reported for flowering start-date in other early-flowering spring species in Northern Europe (Chuine et al., 2000).

Due to their economic importance for domestic animal production in Spain, *Quercus* species have been subject to marked human selection, particularly in southern Spain (Blondel and Aronson, 1995), where semi-natural ecosystems called ''dehesas'' feed high-quality-meat pigs, lambs and cows, and are thus a key factor in the agricultural economy. Local adaptations of tree phenology due to this selection would prove a serious constraint to the prediction of phenological behavior. However, it has been shown that a common phenological model can be used over a wide geographical area where species do not differ.

Climate change has already modified the phenology of numerous plant species over recent years (Parmesan and Yohe, 2003; Galán et al., 2005) and models suggest that these changes will increase in magnitude (Osborne et al., 2000; García-Mozo et al., 2006). One of the most widely expected consequences of climate change will be an increase in minimum temperatures, especially in winter and early spring (Ahmad, 2001); it is during this period that the reproductive structures of early-spring-flowering species are developed, while late-spring-flowering species are still in the undifferentiated-bud phase (Galán et al., 2001a, b).

The response of trees will depend largely on the species, the latitude and the intensity of change (Taiz and Zeiger, 1998). There is evidence of an advance in flowering dates of wild plants across Europe, apparent in almost 80% of species. The mean advance of spring flowering dates has been calculated at 2.5 days per decade (Menzel et al., 2006). *Quercus* phenology has been reported as a good indicator of future climate change, due to its dependence on temperature and its geographical distribution over the high-risk warming area of the Mediterranean basin (García-Mozo et al., 2002, 2006). In this area, late spring temperatures are not expected to increase as much as winter and early spring temperatures. Therefore, the present study offers a means of predicting the impact of climate change by modelling future climate scenarios in order to determine the expected advance of flowering (start and peak). The regional models obtained here will be very useful for application of the Regional Climate Models proposed by the Intergovernmental Panel on Climate Change. These scenarios forecast future climates under different CO_2 scenarios and can be used in impact, vulnerability and adaptation studies.

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