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FLOWERING PHENOLOGY OF MEDITERRANEAN *QUERCUS* SPECIES IN DIFFERENT LOCATIONS (CÓRDOBA, SW IBERIAN PENINSULA)

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ABSTRACT. *Flowering phenology of Mediterranean Quercus species in different locations (Córdoba, SW Iberian Peninsula).* Periodical qualitative and quantitative checking of flowering phases was carried out over six growing seasons (1997-2002) for the three Mediterranean *Quercus* species found in Sierra Morena (Córdoba, SW Spain): *Q. ilex* L. ssp. *ballota* (Desf.) Samp., *Q. coccifera* L. and *Q. suber* L. A total of 60 individuals were selected. Additionally, 30 *Quercus ilex* ssp. *ballota* individuals were selected and studied in Sierras Subbéticas (Priego de Córdoba, SW Spain) in 1999 and 2000. Morphological changes occurring at different points in each phenological phase were charted. Among species differences were found for inflorescences/male and female flowers, in terms of the phenological flowering sequence. Male inflorescences displayed a more homogeneous development. All individuals and populations were proterandrous. Phenological trends and ranges were charted. Although trends varied with species and year, the overall phenological trend seemed to fit a sigmoid curve in all cases, increasing with phenological development. Shorter ranges were obtained in years with warmer springs, and longer ranges in colder years. Moreover, phenological range differed as a function of species and location. In general, *Q. ilex* ssp. *ballota* flowered earlier than the rest, *Q. suber* displaying the latest flowering period. Individuals located at lower altitudes and facing the sun flowered earlier, followed in most years by those located at higher altitudes. Thus, *Q. ilex* ssp. *ballota* flowered earlier in Sierra Morena than in the higher-altitude Sierras Subbéticas.

Key words. Flowering, *Quercus*, reproductive phenology, range, tendency.

RESUMEN. *Fenología floral de tres especies mediterráneas de Quercus en diferentes localidades (Córdoba, Suroeste Península Ibérica).* Se ha realizado un seguimiento periódico cuantitativo y cualitativo de las fenofases florales de tres especies mediterráneas de *Quercus* localizadas en Sierra Morena (Córdoba, suroeste de España) por un periodo total de seis años (1997-2002): *Q. ilex* L. ssp. *ballota* (Desf.) Samp., *Q. coccifera* L. y *Q. suber* L. Se seleccionaron un total de 60 individuos de las tres especies. Adicionalmente, un total de 30 individuos de *Quercus ilex* ssp. *ballota* fueron seleccionados y estudiados en las Sierras Subbéticas (Priego de Córdoba, suroeste de España) durante los años 1999 y 2000. Se estudiaron los cambios morfológicos ocurridos en cada fase fenológica. Se encontraron diferencias en el desarrollo fenológico entre inflorescencias/flores masculinas y femeninasen las diferentes especies estudiadas. Las inflorescencias masculinas mostraron un desarrollo más homogéneo. Todos los individuos y las poblaciones fueron proterandros. Las tendencias y amplitudes fenológicas fueron representadas gráficamente. Aunque las tendencias variaron en función de la especie y el año considerado, la tendencia general en todos los casos, se asemejó a una curva sigmoide aumentando su pendiente a medida que avanza su desarrollo fenológico. Las amplitudes fenológicas más cortas se obtuvieron los años con primaveras más cálidas, y las mayores en las más frías. Además, la amplitud fenológica fue diferente en función de la especie y la localización de los individuos. En general, *Q. ilex* ssp. *ballota* floreció antes que el resto, *Q. suber* presentó el periodo de floración más tardío. Los individuos localizados a menores altitudes y los dispuestos en dirección al sol florecieron antes, seguidos la mayoría de los años por aquéllos situados en altitudes mayores. De esta forma, *Q. ilex* ssp. *ballota* floreció antes en Sierra Morena que en las Sierras Subbéticas situadas a mayor altitud.

Palabras clave. Floración, *Quercus*, fenología reproductiva, amplitud, tendencia.

INTRODUCTION

Classical phenology is the art of subdividing the development of biological taxa into identificable sections along a time axis (Lieth 1997). These sections are termed phenophases, and are used to monitor the development of the life cycle of an organism. The occurrence of a phenophase is determined by the biotic characteristics of the plant species, and by local climate characteristics (Orshan, 1989). At the same time, climate variations influence flowering periods in many species (Zerboni *et al.* 1991, Puppi Branzi and Zanotti 1992). Nowadays, floral phenology includes the study of periodic events as influenced by the environment, especially temperature changes driven by weather and climate (Schwartz, 2003). Phenological behaviour varies from year to year, since weather conditions are not always the same; phenological observations must therefore be carried out over a number of years, in order to obtain a general overview. Floral phenological changes in anemophylous communities appear to fit a sigmoid pattern that may be approximated by a logistic equation (Latorre 1997). This pattern is associated with a progressive increase in temperatures that affects different phenophases in different ways (Pérez-Latorre and Cabezudo, 2002).

Phenology has recently emerged as an important focus of ecological research (Schwartz, 1999). Over recent years a wide range of applications have been developed. The forecasting of plant phenological phases is of great value in various areas of research – agriculture, public health, ecology, fitoclimatology, climate change – in which phenological data play a key role. At the same time, high levels of greenhouse gases detected in the air are evidently changing the earth's climate (Lieth, 1997); one of the main consequences will be a disturbance in the annual cycle of plants, and especially in the onset of the active period in spring (Myking and Heide 1995). Budburst could be brought forward in time, rendering buds more vulnerable to late spring frosts; alternatively, budburst could be delayed, thereby possibly not making full use of the available growing season (Myking and Heide 1995; Kramer 1997; Sparks *et al.* 2000). This could lead to changes in the geographical distribution of species and in forest composition (Kramer, 1997). Research into flowering phenology is a complementary tool in climate studies. Moreover, definition of the phenological phases of male and female flowering in dioecius species is essential in order to highlight the role of reproductive biology in breeding and gene-conservation programs (Varela and Valdiviesso 1996).

On the other hand, several studies have been focused on the characterization and comparison of the phenology of different plant communities and plant species in Mediterranean-type ecosystems (Pérez-Latorre and Cabezudo, 2002), as well as on the study of their phenomorphology and ecomorphological characters (Pérez-Latorre and Cabezudo, 2006). A study of Mediterranean vegetation based on growth forms and phenological phases can make a great contribution to existing classifications (ecological, physiognomic, phytosociological, etc. (Pérez-Latorre and Cabezudo, 2006)) and understanding phenological vegetative and reproductive behaviours and adaptations.

Field observations of floral development enable the major phases in the biological flowering process to be charted. A number of studies addressing *Quercus* floral biology focus on the morphology and diversity of the reproductive organs (Kaul 1985), the life cycle (Ducousso *et al.* 1993; Elena-Rosello *et al.* 1993; Oliveira *et al.* 1994), flowering (Varela and Valdiviesso 1996), and embryogenesis (Stairs 1964). The temporal distribution of phases discerned in the development of reproductive structures represents floral phenological development. Each of these stages is clearly differentiated and defined, both morphologically and physiologically, on the basis of inflorescence development from undifferentiated bud to catkin senescence or fruit formation (Varela and Valdiviesso 1996; Vázquez 1998). The ripening fruit is partially covered by the developing cupule (Kaul 1985), as although *Q. ilex* ssp. *ballota,* however in *Q. coccifera* a larger fraction of fruit was covered.

Quercus species, the most spread tree species of the Mediterranean forests, are dichogamous, and more particularly proterandrous, which enhances successful crossing between individuals of the same population and even between different species (Vázquez 1998). The reproductive biology in this group includes two different types of seed cycles: the “annual biotype”, that requires only one season to complete its reproductive cycle, and the “biennial biotype” which requires two full years. This complex reproductive behaviour may account to some extent for the lack of detailed knowledge of these species (Varela and Valdiviesso 1996). Moreover, there is a lack of information regarding *Quercus* behaviour across an altitudinal gradient of growth and over several years.

From an ecological standpoint, forest dynamics and structure depend on the reproductive phenology of woody species. In the «dehesas» – traditional, semi-natural, man-made systems found throughout the Iberian Peninsula and especially in south-western Spain – predominant evergreen *Quercus* are associated with cereal crops and grasslands that play a major role in avoiding soil erosion, increasing soil fertility and providing for genetic variability (Campos Palacín 1991; Joffre 1991). In the southern Spanish province of Córdoba, evergreen *Quercus* are also found in association with other wild species, as part of a predominant natural landscape (Pérez-Latorre *et al.*, 1993).

This study was carried out in the mountains of Córdoba, where *Quercus* is widespread: *Q. ilex* ssp. *ballota* (Desf.) Samp is the most abundant species, while *Q. coccifera* L. is marginally less common; *Q. suber* L. is abundant in wetter areas. These three evergreen species are typical of Mediterranean climate zones in the Mediterranean Basin. Both *Q. ilex* ssp. *ballota* and *Quercus suber* are of economic importance, since their acorns are a major food source for certain animal species vital to the region’s economy: pigs, bulls and deer. The economic value of *Quercus suber* is enhanced by cork production. This study charted floral phenology in all three *Quercus* species, which are the most abundant in the study area.

The purposes of the study were: (1) To standardize the external development of male and female flowers in the three *Quercus* species studied; (2) To determine the phenological behaviour at four different locations over six years; (3) To compare the phenological behaviour of *Q. ilex* ssp. *ballota* in two populations located at different altitudes.

MATERIALS AND METHODS

Study area

Locality A

The city of Cordoba (37º55'N, 4º45'W, 123 m above sea level) is located in the Southwest of the Iberian Peninsula in the fertile lowland of the river Guadalquivir, between Sierra Morena, in the North, and a flat expanse of arable land and Sierra Subbética, in the South. The climate is Mediterranean, with a touch of continentality; the average annual temperature is 18ºC, and average annual rainfall is 600 mm, based on 40-year data from the Spanish National Institute of Meteorology.

The study was run over six consecutive years (1997-2002) in the foothills of the Sierra Morena; vegetation is characteristically thermophilic, with a mixture of *Quercus ilex* ssp. *ballota*, *Quercus coccifera* and a fairly well-preserved population of *Quercus suber*.

Locality B

Additionally, *Quercus ilex* ssp. *ballota* was studied over a two-year period (1999-2000) in a mountainous area of Priego de Córdoba, a city in the province of Córdoba located in the Sierra Subbética Natural Park (37º26'N, 4º11'E, 900 m above sea level). The average annual temperature is 14.4ºC, and average annual rainfall is 765 mm, based on 40-year data from the Spanish National Institute of Meteorology. Due to its altitude, Priego de Córdoba is wetter and colder than Córdoba. The vegetation of the zone is thermophilic with a mixture of *Paeonia coracea*, *Paeonia broteroi, Pistacia lentiscus,* and *Quercus ilex* ssp. *ballota.*

Meteorological data were supplied by the Meteorological Network based in the city of Córdoba.

Methodology

Study plots

A total of 60 mature, well-developed individuals of the three *Quercus* species were selected in four different areas of the Sierra Morena, located at different heights and different orientations relative to the sun-facing:

Zone 1 (Medina Azahara): *Q. ilex* ssp. *ballota* grove located near Medina Azahara (Arab ruins), with the following coordinates: UTM 30S UG 3495. The area is 270 m above sea level, and sunny. Ten *Quercus ilex* ssp. *ballota* individuals were selected.

Zone 2 (El Cruce): *Q. ilex* ssp. *ballota* grove located half-way between Medina Azahara and Las Ermitas, with the following coordinates: UTM 30S UG 3998. This area is 440 m above sea level, and sunny. Ten *Quercus ilex* ssp. *ballota* and ten *Quercus coccifera* individuals were selected.

Zone 3 (Las Ermitas): *Q. suber* grove located between Las Ermitas and Lagar de la Cruz, with the following coordinates: UTM 30S UH 3800. This area is 520 m above sea level, shady. Ten *Quercus suber* individuals were selected.

Zone 4 (El Lagar): *Q. suber* grove - *Q. ilex* ssp. *ballota* grove located between Lagar de la Cruz and the crossroad with El Brillante, with the following coordinates: UTM 30S UH 3800. Height 550 m above sea level, sunny. Ten *Quercus suber* and ten *Quercus ilex* ssp. *ballota* were selected.

Q. coccifera are typical of degraded

soils, and the area in which they are found (Zone 2) displays strong housing pressure. For this reason, only a small population of well-preserved individuals was available for study.

Quercus suber is present in mountainous areas, in the highest and wettest zones; it was thus only present in Zones 3 and 4 of the study. *Q. ilex* ssp. *ballota* is more common over the whole area, as it is better adapted to local bioclimatic conditions; it was therefore present in more zones.

Additionally, 30 *Quercus ilex* ssp. *ballota* trees were selected in Priego de Córdoba (Sierras Subbéticas). These individuals were located in three different zones, with varying relative exposure to the sun: **Zone 1** (North-facing hillside); **Zone 2** (Watercourse); and **Zone 3** (South-facing hillside).

Phenology

For monitoring population phenology, several trees were selected for each *Quercus* species to reflect optimal development and normal seasonality. Each individual was assigned an identification number. Field work consisted in weekly visits to individual zones at the start of the flowering season, and twice-weekly visits during maximum flowering and the fruit-formation period. Samplings were carried out over six consecutive years in Sierra Morena and two consecutive years in Sierras Subbéticas, from January to July, when flower development and fruit formation take place. On each visit, branches and whole crown were observed, and the phenological phase noted.

Additionally, samples were taken from the first floral traces (first buds) right through to formed fruit, except for *Q. coccifera* whose fruits ripen in the next growing season. In 1997, sampling commenced on 12 February, thus, in some cases there is no information on the initial phenological phases. Samples taken in the field and labelled were later analysed in the laboratory. Buds, flowers and fruits were observed with a magnifying glass; morphological data were recorded; the longitudinal size of buds, flowers and catkins was measured. For these measurements, an average of 30 elements was used. Finally, a phenological herbarium was developed using the field samples collected, for reference purposes.

A series of floral phases was established, each phase being designated by a letter. Capital letters were used for male flower phases, and lower-case letters for females. Description of phenological phases was based on previous studies of *Quercus suber* (Varela and Valdiviesso 1996) in Portugal and *Quercus ilex* ssp. *ballota* (Vázquez 1998) in Extremadura (NW Spain), in order to provide a standardized sequence of reproductive phases for the three species studied here.

Reproductive phenophases were used as a tool to study *Quercus* phenological behaviour in the study areas. For quantitative characterization of floral phenophases, a number from 1 to 8 was assigned to each phase. A tree was assigned to a given phase when at least 50% of the crown was in that phase (Varela and Valdiviesso 1996). Phenophases per individual were recorded in Microsoft Excel files, and the average daily values of phenological phases were calculated for each population at different sampling dates. Floral phenological tendency and range were charted, and results for years and populations were compared.

RESULTS

Phenological phases

Male and female floral development followed different patterns, and morphological changes were evident both between and within the two types of inflorescence as a function of developmental stage. A total of eight phenological phases were described for male and female flowering, covering the full morphological development for each species (fig. 1).

Male flowering

Male flowers occurred in catkins emerging in reproductive buds at the top of the previous season's branches and at the base of current-season branches. Anthers did not burst simultaneously. Eight different phenophases were defined for the three *Quercus* species studied.

A-Closed bud: this corresponds morphologically to the swollen bud, of 1-2 mm. Brownish-grey closed buds could not be differentiated from vegetative buds. This phase is simultaneous with the development of the first vegetative buds.

B-Bud development: in this phase, the bud was larger, up to 2-4 mm. Bud development commenced. A varying number of meristematic structures were seen to be developing at the same points.

C-Catkin development: erect catkins. A short, bare pedicel; the remainder of the catkin could be discerned. *Quercus ilex* ssp. *ballota* and *Quercus coccifera* showed yellow catkins and *Quercus suber* showed purple catkins. Flowers could still be distinguished due to tight clustering. Catkin size was no larger than 1 cm.

D-Catkin elongation: growth of the inflorescence axis. Catkins were up to 2 cm in length. Erect catkins and closed flowers were distinguishable along the axis.

E-Start of flowering: pendant yellow catkins. Catkin growth ceased. Flowers in anthesis; anthers mostly closed, although up to 20% of flowers were releasing pollen.

F-Full flowering: most flowers (20-80%) shedding pollen. Some flowers were starting to wither following pollen release.

G-Senescence: over 50% of flowers had stopped releasing pollen; catkins had turned brown to drying-out of most anthers.

H-Catkin fall: flowering completely over, only dried-out catkins left on branches, now starting to fall.

Female flowering

Female *Quercus* flowers are arranged in spikes on the axils of new-growth leaves. Spike axis growth lasts over several days, giving rise to continuous flower formation. Eight different phenophases were defined for the three *Quercus* species (fig. 1).

a-Closed bud: whitish, pilose reproductive axillary buds, about 1-2 mm long, only visible through a magnifying glass.

b-Inflorescence development: first spikes occurred on axils of new leaves. Closed flowers were visible as small pilose swellings 1 mm in length, only visible through a magnifying glass.

c-Flower differentiation: female flowers displayed erect greenish styles. Pilose bracts, visible at the flower base, flowers up to 2 mm in length.

d-Full flowering and receptivity: fully-formed female flowers distinguishable inside the inflorescence. Over 50% of flowers in the spike displayed shiny, yellowish-white, viscous stigmas. Full receptivity.

e-Stigma oxidization: Increased flowers size. Stigmas turned dull brown by oxidization. Flowers had not yet lost receptivity.

f-Loss of receptivity: considerable increase in flower size. Future pericarp of the fruit visible above developing cupule. The bracts of the incipient cupule were of membranous consistency. Stigmas, which were black and hard, had lost their receptivity.

g-Fruit formation: fruit now formed. Woody consistency of the cupular bracts, all

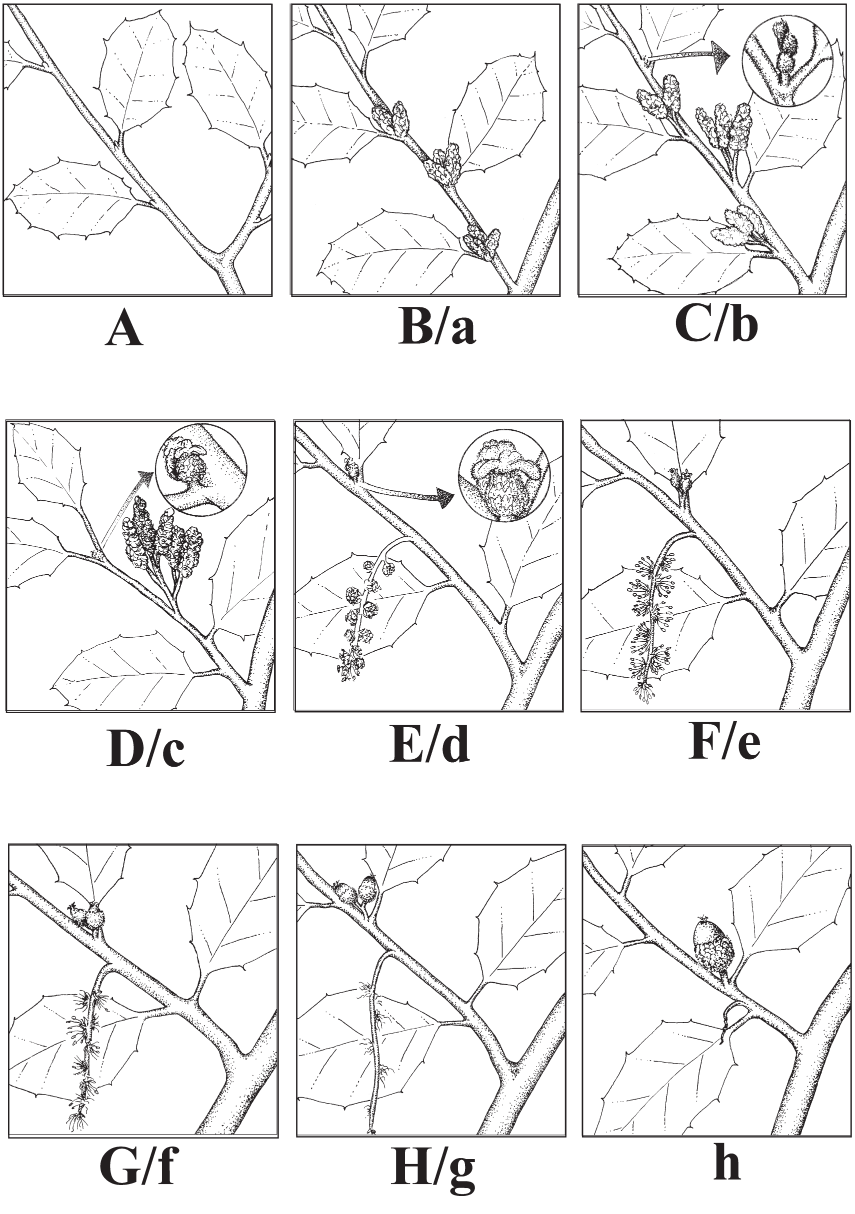


Figure 1. Flower development. Male and female floral phenophases in Quercus: **A**. Closed bud, **B**. Bud development, **C**. Catkin development, **D**. Catkin elongation, **E**. Start of flowering, **F**. Full flowering, **G**. Senescence, **H**. Catkin fall , **a**. Closed bud, **b**. Inflorescence development, **c**. Flower differentiation, **d**. Full flowering and receptivity, **e**. Stigma oxidization , **f**. Loss of receptivity, **g**. Fruit formation, **h**. Fruit development. *Fenofases florales masculinas y femeninas en Quercus. **A**. Yema cerrada, **B**. Desarrollo de la yema, **C**. Desarrollo del amento, **D**. Elongación del amento, **E**. Inicio de la floración, **F**. Plena floración, **G**. Senescencia, **H**. Caída de amentos, **a**. Yema cerrada, **b**. Desarrollo de la inflorescencia, **c**. Diferenciación de la flor, **d**. Plena floración y receptividad, **e**. Oxidación del estigma, **f**. Pérdida de la receptividad, **g**. Formación del fruto, **h**. Desarrollo del fruto.*

studied species displayed characteristic cupular shape.

h-Fruit development: Fruit developed.

There was generally some overlap between full receptivity in a single female and the start of male flowering. However, not all members of a given population flowered simultaneously. Phenophases did not always coincide: thus, when one individual was at the start of the flowering period, another was at the end of that period. All selected individuals displayed fertile male and female flowers simultaneously.

Inter-species differences were found for catkins and spikes in terms of the phenological flowering sequence, although male inflorescences displayed a more homogeneous development. Spikes had far fewer flowers, and displayed a gradient of growth from base to tip; basal flowers were usually at a more advanced phenological stage. Three or more different phenological stages were sometimes apparent within the same inflorescence.

Although phenological development was similar in the three evergreen species studied, several floral morphological differences were observed. Catkin length varied considerably: catkins in *Q. ilex ssp. ballota* were up to 10-12 cm long, compared to 15-17 cm in *Q. suber* and 4-7 cm in *Q. coccifera*. On spikes, the number of flowers per inflorescence ranged between 1 and 9. Female flowers in anthesis were partially embedded in the developing cupule. The ripening fruit was partially covered by the cupule; in *Q. coccifera* a larger fraction of fruit was covered.

Inflorescences and fruits occurred on new branches in all selected *Q. ilex* ssp. *ballota* and *Q. suber* individuals, in *Q. coccifera* inflorescences and fruits were observed both on new branches and on previous-year branches, since fruit requires two years to ripen.

The *Q. ilex* ssp. *ballota* flowering process in Priego de Córdoba was similar to that observed for the same species in Sierra Morena in 1997; however, in 2000 most individuals in Zone 1 (north-facing hillside) produced only vegetative buds.

Phenological tendency

Sierra Morena

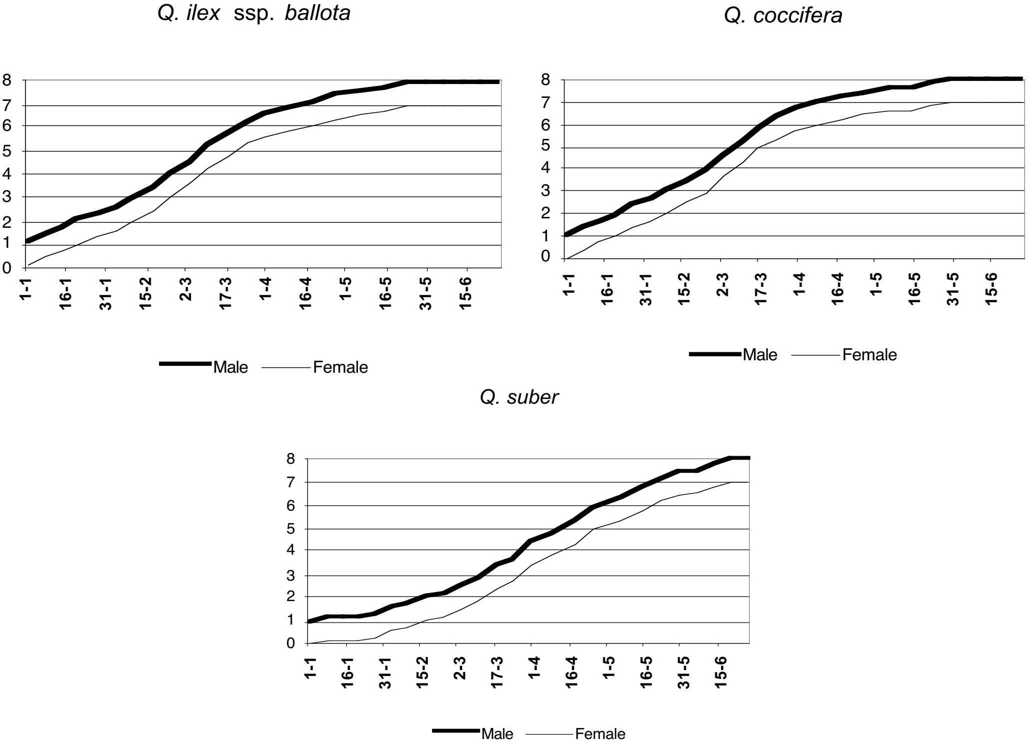
Figure 2 shows average phenological-tendency curves, reflecting average numerical values assigned to the various phenological stages (male and female) described above for each of the three *Quercus* species studied (*Q. ilex* ssp. *ballota, Q. coccifera* and *Q. suber*) from 1997 to 2002. The Y-axis represents phenological values and the X-axis the sampling date for each study year. The phenological tendency was studied from January to June for *Q. ilex* ssp. *ballota* and *Q. coccifera*, and from February to early July for *Q.suber*, except in 1997, when samplings of all species began in February. Phase number 8 corresponds to the end of male and female phenological sampling, and covers the period to the last sampling day.

Although the tendency varied among species and years, the general phenological tendency seemed to fit a sigmoid curve in all cases, rising with time; the slope depended on the consecutive start of the various phenophases. Slow development in the initial phases was followed by fast changes during the flowering period. Moreover, phase to phase transition was not gradual in some cases, probably due to meteorological changes or sampling frequency; as a result, the curve has a staggered appearance (fig. 2).

Sierras Subbéticas

Figure 2 shows phenological tendency curves reflecting the average numerical

Sierra Morena



Sierras Subbéticas

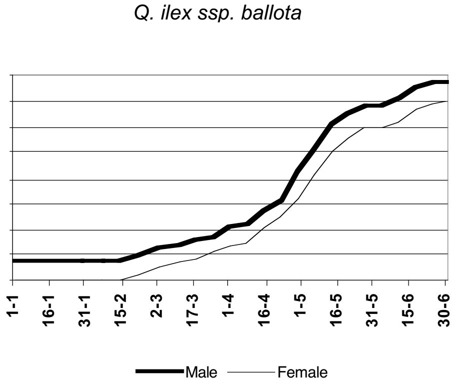


Figure 2. Average phenological tendency curves of the three *Quercus* studied species in Sierra Morena and *Q. ilex* ssp. *ballota* in Sierras Subbéticas. Y-axis: 1. Phenophase A; 2. Phenophase B/a; 3. Phenophase C/b; 4. Phenophase D/c; 5. Phenophase E/d; 6. Phenophase F/e; 7. Phenophase G/f; 8. Phenophase H/g. X-axis: Date. *Curvas de la tendencia fenológica media de las tres especies de Quercus estudiadas en Sierra Morena y Q. ilex ssp. ballota en las Sierras Subbéticas. Eje-Y: 1. Fenofase A; 2. Fenofase B/a; 3. Fenofase C/b; 4. Fenofase D/c; 5. Fenofase E/d; 6. Fenofase F/e; 7. Fenofase G/f; 8. Fenofase H/g. Eje-X: Fecha.*

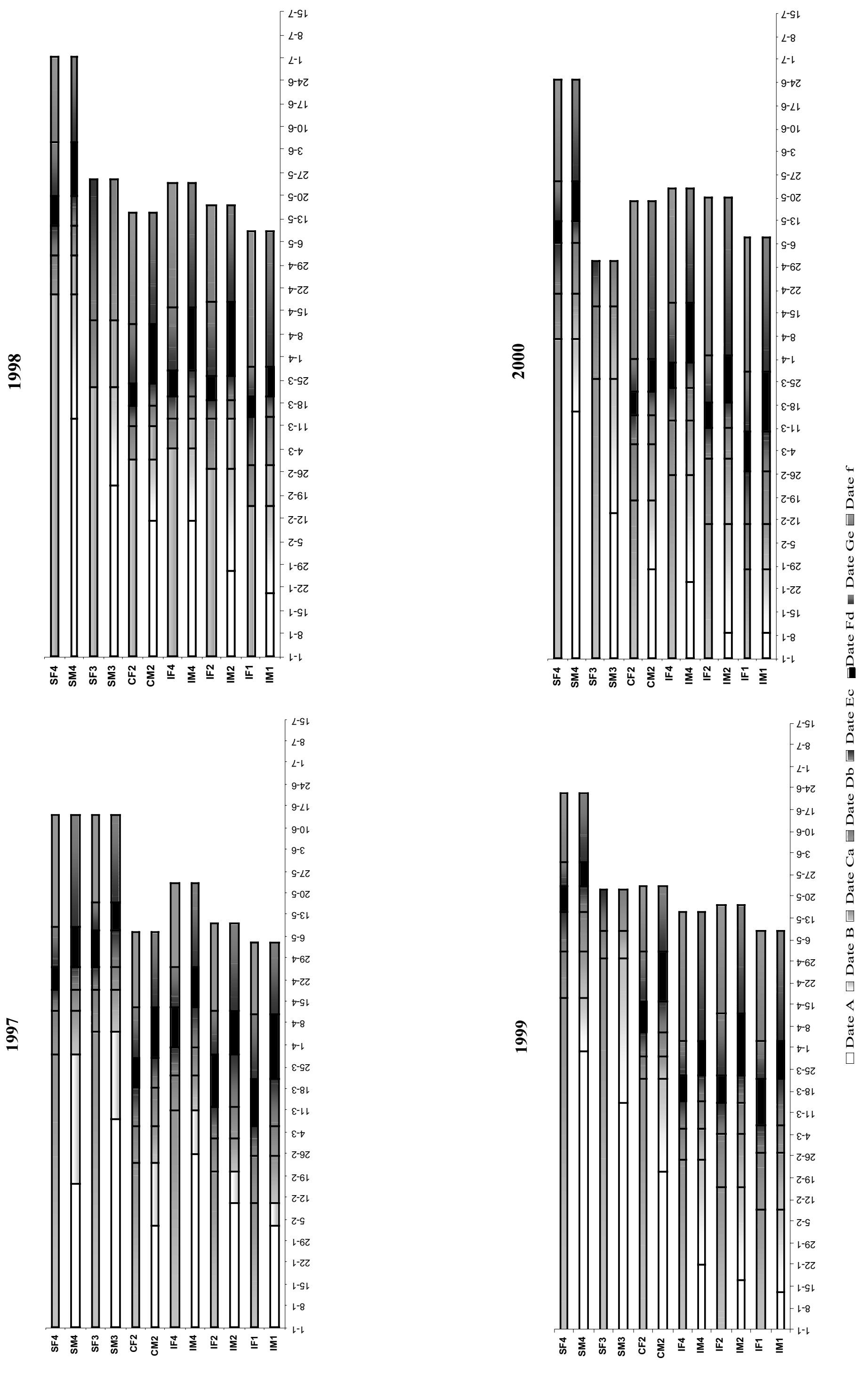

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Figure 3A.

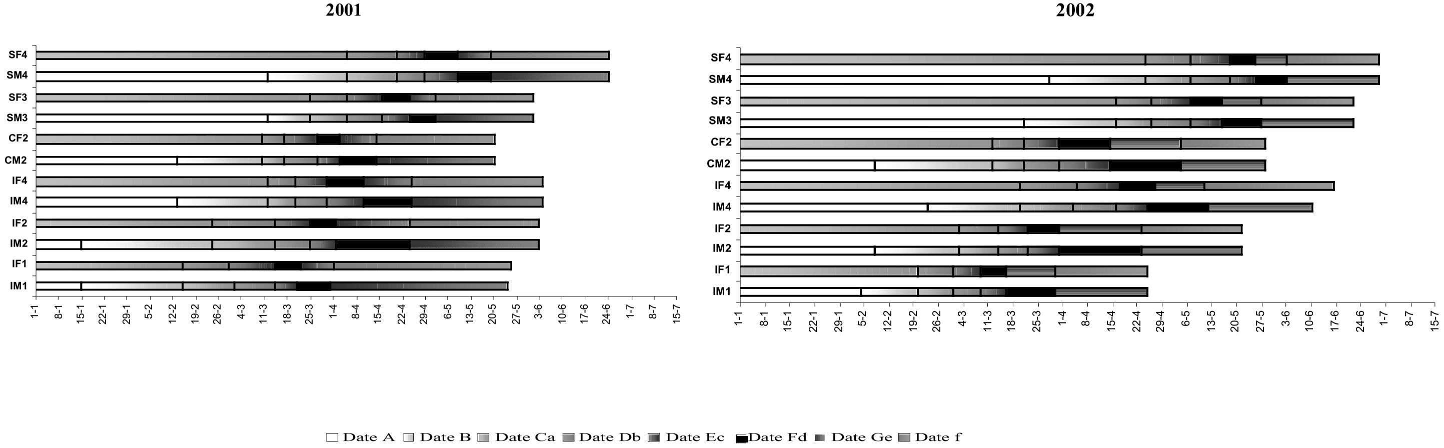

Figure 3A (continuación). Phenological range of: *Quercus ilex* ssp. *ballota* male (IM) and female (IF) flowering from zone 1, 2 and 4; C: *Quercus coccifera* male (CM) and female (CF) flowering from zone 2; S: *Quercus suber* male (SM) and female (CF) flowering from zone 3 and 4. Phenological range variability of the three Quercus selected species in Sierra Morena during the studied period (1997-2002). Male phenophases: A: Number of days from 1st January in which the whole trees are in A phase to the beginning of B. B: Number of days from B phase to C. C: Number of days from C phase to D. D Number of days from D phase to E. E: Number of days from E phase to F. F: Number of days from F phase to G. G: Number of days from G phase to H. Female phenophases: a: Number of days from 1st January in which the whole trees are in a phase to the beginning of b. b: Number of days from b phase to c. c: Number of days from c phase to d. d: Number of days from d phase to e. e: Number of days from e phase to f. f: Number of days from f phase to g. *Variabilidad de la amplitud fenológica de las tres especies de Quercus seleccionadas en Sierra Morena durante el periodo de estudio (1997-2002). Fenofases masculinas: A: Número de días desde el 1 de enero en que los árboles están en fase A hasta el inicio de la B. B: Número de días de la fase B a la C. C: Número de días de la fase C a la D. D Número de días de la fase D a la E. E: Número de días de la fase E a la D. F: Número de días de la fase F a la G. G: Número de días de la fase G a la H. Fenofases femeninas: a: Número de días desde el 1 de enero en que los árboles están en fase a hasta el inicio de la b. b: Número de días de la fase b a la c. c: Número de días de la fase c a la d. d Número de días de la fase d a la e. e: Número de días de la fase e a la d. f: Número de días de la fase f a la g.*

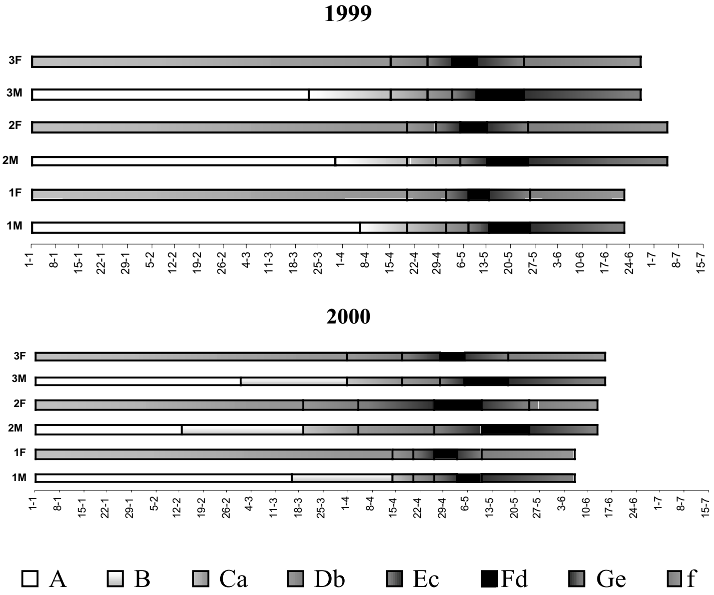

Figure 3B. Phenological range of *Quercus ilex* ssp. *ballota* male (M) and female (F) flowering from zone 1, 2 and 3. Phenological range variability of the three *Quercus ilex ssp ballota* selected zones in Sierras Subbéticas during the studied period (1999-2000). Male phenophases: A: Number of days from 1st January in which the whole trees are in A phase to the beginning of B. B: Number of days from B phase to C. C: Number of days from C phase to D. D Number of days from D phase to E. E: Number of days from E phase to F. F: Number of days from F phase to G. G: Number of days from G phase to H. Female phenophases: a: Number of days from 1st January in which the whole trees are in a phase to the beginning of b. b: Number of days from b phase to c. c: Number of days from c phase to d. d: Number of days from d phase to e. e: Number of days from e phase to f. f: Number of days from f phase to g. *Variabilidad de la amplitud fenológica de las tres zonas selccionadas de Quercus ilex ssp ballota en las Sierras Subbéticas durante el periodo de estudio (1999-2000). Fenofases masculinas: A: Número de días desde el 1 de enero en que los árboles están en fase A hasta el inicio de la B. B: Número de días de la fase B a la C. C: Número de días de la fase C a la D. D Número de días de la fase D a la E. E: Número de días de la fase E a la D. F: Número de días de la fase F a la G. G: Número de días de la fase G a la H. Fenofases femeninas: a: Número de días desde el 1 de enero en que los árboles están en fase a hasta el inicio de la b. b: Número de días de la fase b a la c. c: Número de días de la fase c a la d. d Número de días de la fase d a la e. e: Número de días de la fase e a la d. f: Número de días de la fase f a la g.*

values given to the various phenological stages (male and female) of *Q. ilex* ssp. *ballota* for the three study zones in Priego de Córdoba over both study years (1999-2000). The general phenological tendency appeared to fit a sigmoid curve. However, the phenological tendency during 2000 in Zone 1 (north-facing hillside), displayed a sharper slope; phase to phase transition was more abrupt due to the lack of data, since only two trees in that zone flowered in 2000 – the other trees in Zone 1 produced only vegetative buds.

Phenological range

Sierra Morena: Inter-species and Inter-annual variability

Figure 3 A shows bar charts for temporal distribution range of male and female phenological phases in the Sierra Morena

SPECIES	*Zone*	*1997*	*1998*	*1999*	*2000*	*2001*	*2002*
	(1)	125	130	130	129	145	116
Q. ilex ssp. *ballota*	(2)	131	138	138	141	155	142
	(4)	144	145	136	144	156	163
Q. coccifera	(2)	128	136	144	140	141	149
Q. suber	(3)	166	146*	143*	122*	153	174
	(4)	166	183	174	177	176	181

Table 1. Flower development total length for each one of the species during the studied period (1997-2002) in Sierra Morena (number of days from the beginning to the end,). (*): Data up to D/c phenophase. *Amplitud total del desarrollo floral para cada una de las especies durante el periodo de estudio (1997-2002) en Sierra Morena (número de días desde el comienzo hasta el final). (*): Datos hasta la fenofase D/c.*

area (zones 1, 2 and 4), based on the development of the buds/flowers pool. Phenological range is the number of days that a concrete phenophase lasts. This figure shows the inter-species and inter-annual male and female floral phenological range for *Quercus* over the study period (1997-2002).

The Y axis represents species by sex and zone, while the X axis represents sampling dates from 1 January to the last day of sampling.

Inter-species and inter-annual differences in phenological range were observed for every phenophase. In all three species, the longest phenophase every year was bud development in both sexes. Once flowering was over, the male senescence phenophase and the female loss-of-receptivity phase were the longest. In most years, full flowering was shorter in females than in males.

The flowering period in *Q. ilex* ssp. *ballota* and *Q. coccifera* was earlier (second fortnight in April) than that of *Q. suber* (late April-May) (fig. 3A).

Although double flowering was not a general finding in the study area, some *Q. ilex* ssp. *ballota* and *Q. suber* trees displayed a second (male or female) flowering period at the start of autumn in both 1999 and 2001. This second flowering was probably due to mild temperatures and higher rainfall, following a stress period caused by harsh summer conditions. However, double-flowering was not completed, and stopped in phenophase D/c.

Some differences were apparent between members of the same species, as a function of location. Comparison of the temporal distribution of phenophases between *Q. coccifera* and *Q. ilex* ssp. *ballota* in Zone 2, where both species are abundant, revealed that flowering periods occasionally overlapped, but on other occasions were separated by an interval of up to 10 days. In 1999, *Q. coccifera* flowered 24 days later than *Q. ilex* ssp. *ballota* in the same zone, probably due to poor rainfall over the previous months, which may have had a more negative impact on *Q. coccifera* as a shrub.

Male phenological development in *Q. suber* was anomalous in 1998, 1999 and 2000 in zone 3, where none of the selected trees completed the reproductive cycle. Catkins which were already formed and had differentiated flowers, withered and the flowers failed to open out (fig.3A). Temporal distribution of phenophases in this species was normal from the start of elongation to the catkin stage, at which point catkins

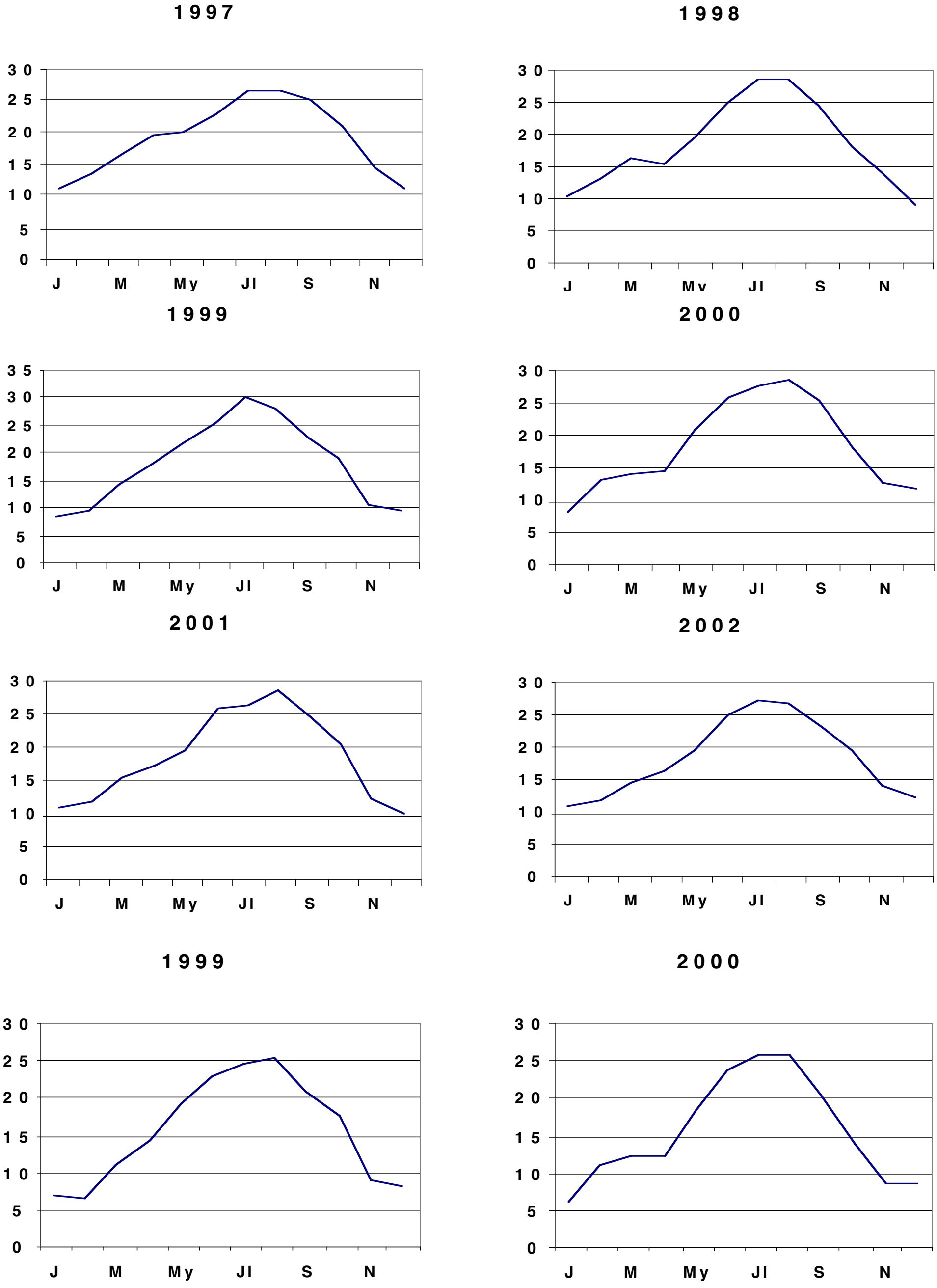

Figure 4. Monthly average temperature for the studied years: 1997-2002 in Sierra Morena; 1999-2000 in Sierras Subbéticas. *Distribución mensual de las temperaturas medias para cada uno de los años de estudio: 1997-2002 en Sierra Morena; 1999-2000 en Sierras Subbéticas.*

	YEAR	
ZONE	*1999*	*2000*
North hillside	174	158
Watercourse	187	165
South hillside	179	167

Table 2. Flower development total length of *Q. ilex* ssp. ballota for each one of the sampling zones during the studied period (1999-2000) in Sierras Subbéticas. *Amplitud total del desarrollo floral de Q. ilex ssp. ballota para cada una de las zonas de muestreo durante el periodo de estudio (1999-2000) en las Sierras Subbéticas.*

development ceased and catkins assumed a senescent appearance. The length of phase D in those years coincided with occurrence of catkin senescence.

In early spring of 1998, 1999 and 2000 years, sharp falls in temperature were recorded (fig. 4). In Córdoba, unusually low temperatures coincided with development of male phenophase D. In March 1998, minimum temperatures fell to as low as 2.8º and 1.8ºC, and a mean temperature of around 10ºC were recorded. Early-spring weather conditions were similar in 1999 and 2000. Zone 3 trees are located in a shady zone and therefore low temperatures caused more devastating damage to developing plant structures. Table 2 shows the total range of the flowering period for each *Quercus* species in the different sampling zones indicated for all six study years, expressed as number of days from 1 January to the end of the flowering period. Values for phenological range differed for each sampling zone and study year. Shorter ranges were obtained in years with warmer springs and longer ranges in colder years. Phenological range in *Q. ilex* ssp. *ballota* from zone 1 was shorter because it is a sunny zone located at a lower altitude; in most years, trees in zone 4, at a higher altitude, showed a longer range. Over the two last years, *Q. suber* showed a greater total phenological range in zone 4 than in the lower-altitude zone 3 (tab.1).

Sierra Morena: Inter-zone intra-species variability

Within the same species those individuals located at lower altitudes flowered before those located at higher altitudes. *Q. ilex* ssp. *ballota* from zone 1 (270 m) flowered first, followed by trees in zone 2 (440 m) and finally those in zone 4 (550 m). With regard to *Q. suber*, trees in zone 3 (520 m) flowered first, followed by trees in zone 4 (550 m), with the exception of 1997. Results for 1998, 1999 and 2000, when flowering development was truncated, were not taken into account. Zone 3 is a shady area comprising large trees set close together; sunlight therefore does not reach the whole crown of each tree. As a result, flowering was delayed in 1997 even though trees were located at a lower altitude than those of zone 4. Nevertheless, at the end of 2000, trees were heavily pruned, and consequently flowering took place earlier in both 2001 and 2002 (fig. 3A).

Sierras Subbéticas: Inter-zone variability

Figure 3B shows bar charts for the temporal distribution range of male and female phenological phases based buds/ flower pool development in Sierras Subbéticas. In general, the phenophase range differed as a function of the holm-oak zone in Priego de Córdoba. In 1999, trees located on the south-facing hillside flowered first, followed by those in the Watercourse and finally those on the north-facing hillside, although with only a few days' difference. By contrast, in 2000 the first trees to flower were those on the north-facing hillside followed, those in the Watercourse and finally those in south-facing areas. This result is probably due to the lack of the data for 2000, when only two trees flowered. The previous year, these trees were severely damaged by lack of rainfall at the start of autumn, by plant lice and/or by pruning, with the result that in spring 2000 only vegetative buds were produced.

The results obtained in 1999 show that the first trees to flower were those facing south, followed by the trees in the Watercourse and finally north-facing trees. In individual trees, the south-facing part of the crown also flowered first.

Sierras Subbéticas: Inter-annual variability

The flowering period commenced earlier in 2000 than in 1999 (fig. 3B). The total floral phenological range in the various sampling areas in Priego de Córdoba was shorter in 2000 than in 1999, when higher spring temperatures were recorded (fig. 4). The total range of the flowering period was lowest on the north-facing hillside in both years.

Although double flowering was not a general finding in the study area, some *Q. ilex* ssp. *ballota* trees displayed a second (male o female) flowering period at the start of autumn in 1999.

Table 2 shows the total range of the flowering period for *Q. ilex* ssp. *ballota* in each sampling zone, for both years, expressed as number of days from 1 January to the end of the flowering period.

Sierra Morena vs. Sierras Subbéticas

Comparison of *Q. ilex* ssp. *ballota* floral phenological behaviour in the two main sampling zones in the province of Córdoba in 1999 and 2000 (fig. 3), disclosed that the flowering period in all three study zones in Córdoba lasted from 1 March to 1 April, while in Priego de Córdoba flowering took place in May. The temporal distribution range for floral phenophases in the three Córdoba zones in 2000 ran from 1 March to the second fortnight in April, while in Priego de Córdoba it ran from late April to late May.

The start of the *Q. ilex* ssp. *ballota* flowering period took place later in the higher-altitude Sierras Subbéticas than in Sierra Morena. Phenological ranges in Priego de Córdoba were greater due to the lower temperatures recorded there (fig.4).

DISCUSSION

Quercus species are monoecious; male and female flowers are produced by the same individual with certain temporal and spatial variations. Vázquez (1998) defines the presence of protogynous or protandrous individuals as reproducing strategies, but in the present study areas, over six years, only protandrous individuals were found. Maturation of male flowers takes place during catkin elongation, since pollen maturation takes place in that phase (Sharp and Chisman 1961; Stairs 1964; Wolgast and Stout 1977). Data for total crown morphology at a given date in all three species showed that the predominant male phenophase tended to overlap with a different female phenophase.

The catkin elongation phase usually overlapped with the female flower differentiation stage, while full flowering and receptivity in the female overlapped with the start of flowering in the male, coinciding with the start of pollen release. Moreover, not all trees in a given population developed at the same speed. Similar findings have been reported for other species, in which the flowering process was not simultaneous between trees or even on a single tree. Oaks are characterized by a high between-individual variability that can be attributed to a variety of physical factors of pollen dispersion and to oaks flowering traits (Streiff et al, 1999). This could be a reproductive strategy for enhancing crosses between species and individuals (Vázquez 1998); intra-species variation may thus be related to environmental diversity (Latorre and Bianchi 1998; Grime 1979; Aseyev *et al.*, 2005). Moreover, reproductive success and seed formation at a global woodland level is largely determined by the difference in the start of flowering within a mass of trees (Vázquez 1998) and heterogeneity of pollen dispersal (Streiff *et al.*, 1999). This heterogeneity, joined to long-distance gene flow and variability of mating success all contribute to maintain high levels of diversity in oaks stand (Streiff *et al.*, 1999).

Flowers of different *Quercus* species and populations displayed parallel morphological patterns of phenological development, but the temporal distribution of phenophases differed both between species and between trees of the same species in different sampling zones. Trees in the five selected areas are exposed to different bioclimatic conditions, depending on facing distribution and altitude; as a result, the flowering period started later in zones at a higher altitude. This was particularly evident when comparing the temporal distribution of phenophases of *Q. ilex* ssp. *ballota* in Córdoba and Priego de Córdoba, where flowering started later and the total phenological range was greater. At the same time, phenological development was also determined by relative position; trees facing south flowered before those facing north. At individual level, the south-facing part of the crown also flowered earlier (Vázquez 1998). Thus, viewing the population as a whole, those individuals whose crowns faced south flowered earlier.

Moreover, *Q. ilex* ssp. *ballota* in zone 4 flowered later than *Q. coccifera* in all years except 1999, when it flowered earlier. This may have been due to insufficient rainfall prior to the flowering period, which would have a more negative impact on *Q. coccifera* as a shrub not reaching underground water; even though studies in other species suggest that flowering is more strongly influenced by temperature than by rainfall (Spano *et al.* 1999; Garau *et al.* 2000; Reeves and Coupland 2000).

Q. suber is commonly referred to in the bibliography as a species with several flowering seasons (Elena-Rosello *et al.* 1993; Varela and Valdiviesso 1996; Díaz-Fernández *et al.*, 2004). The presence of inflorescences and fruits on new branches indicates an annual reproductive strategy, while their presence on previous-year branches suggests a biennial one. Here, *Q. suber* displayed an annual reproductive pattern over the study period. On the other hand, Díaz-Fernández *et al.* (2004) reported a relationship between phenology and acorn maturation as influenced by environmental conditions, which determine the annual or biennial pattern. Although double flowering was not a general finding in the study area, some *Q. ilex* ssp. *ballota* and *Q. suber* trees displayed a second (male o female) flowering period at the start of autumn in both 1999 and 2001. This second flowering was probably due to mild temperatures and higher rainfall, following a stress period caused by harsh summer conditions. However, double-flowering was not completed, and stopped in phenophase D/c. Double flowering has been reported in the Iberian Peninsula by Curras and Laguna (1985, 1986) in Valencia and Vázquez (1998) in Badajoz, in both *Q. ilex* ssp. *ballota* and *Q.* suber.

Weather conditions prior to flowering and vegetative growth are decisive factors in plant development and it has been observed in *Quercus* pollen season (García-Mozo *et al.*, 2002; García-Mozo *et al.*, 2006). Prolonged dry periods may weaken trees, causing loss of leaves and reducing vegetative growth and thus the possibility of vegetative and floral bud formation

(Cabezudo *et al.* 1993; Pérez-Latorre *et al.* 1996). Moreover, a competitive role exists between reproductive and vegetative phenophases to acquire plant resources (Pérez-Latorre and Cabezudo, 2002). In Priego de Córdoba, trees on the north-facing hillside in 2000 showed signs of damage, and only two produced floral buds, the others produced vegetative buds, probably as a result of dry conditions at the start of the previous autumn.

Reproductive processes taking place in spring in these species are closely related to population dynamics and structure (Vázquez 1998). Most studies in temperate-zone trees species assume that temperature regulates phenological development induced by a chilling period, depending on the species and geographical areas, that induces budburst followed by a period with forcing temperatures (also variable) that releases dormancy and thus triggers the onset of growth (Aron 1982; Hari and Häkkinen 1991; Frenguelli *et al.* 1992; Kramer 1997; Wielgolaski 1999; Chuine 2000; Fulton *et al.* 2001; Galán *et al.* 2001). Once buds have begun to develop, floral structures are exposed to the weather conditions which determine the whole of the phenological process. The catkin elongation phenophase is highly sensitive to sharp change in humidity (Sharp and Chisman 1961). Moreover, adverse temperature conditions recorded during that phase in *Quercus gambelii* Nutt. (Neilson and Wullstein 1980) and *Q. suber* (García-Mozo *et al.* 2001) are reported to have a negative effect on the reproductive cycle of the tree, interrupting catkin development, probably due to a sharp drop in minimum temperatures, as occurred here in *Q. suber* in Sierra Morena over three consecutive years (1998, 1999 and 2000) when frosts were recorded in early spring.

The length of each floral phenophase differed between species, zones, years and sexes. Trees located in sunny areas displayed a shorter total phenological range. Moreover, shorter ranges were recorded in years with warmer springs; temperature and solar radiation have been shown to influence the flowering process in these *Quercus* species (Vázquez 1998). In general, female phases displayed a shorter range. Moreover, slow development in the initial phases was followed by fast changes during the flowering period, with a subsequent slowing down in the final phases.

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