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Original article

Ecological aspects of the floral phenology of the cork-oak (*Q suber* L): why do annual and biennial biotypes appear?

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Summary — Phenological observations (periods of flowering and pollination, floral structures, etc) were made over a 3-year period in natural populations of *Q suber*. We demonstrated the existence of 2 different types of seed cycles in the cork-oak. The 'annual biotype', requires only 1 season to complete its reproductive cycle (*ie,* similar to that of the *Lepidobalanus* group), whereas the 'biennial biotype' requires 2 full years (similar to *Erythrobalanus*). The variability observed in the cork-oak, during the reproductive cycle, and the meaning of the existence of 2 different reproductive strategies in the same species, are discussed.

cork-oak / floral phenology / ecological variability / reproductive strategies / annual and biennial biotypes / *Quercus*

Résumé — Phénologie florale du chêne-liège (*Quercus suber* L) : aspects écologiques des biotypes annuel et biannuel. *Les observations phénologiques (époque de floraison et pollinisation, structures florales,* etc) *effectuées pendant 3 ans dans des populations naturelles de* Q suber, *ont montré une grande diversité morphologique et de comportement entre populations, mais aussi à l'intérieur de chaque population. Le chêne-liège présente 2 différents types de cycle reproductif; «biotype-annuel» qui a besoin d'une seule saison pour compléter la maturation de ses glands, et le «biotype-biannuel» qui a besoin de 2 ans. La variabilité phénologique observée chez le chêne-liège, ainsi que l'existence de 2 stratégies reproductives si différentes à l'intérieur d'une même espèce, sont discutées dans ce travail.*

***chêne-liège / phénologie florale / stratégies reproductives / variabilité écologique / biotypes annuel et biannuel /* Quercus**

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INTRODUCTION

The reproductive cycle and morphology of oak flower and seed development in *Quercus* have been reported for the different species (Corti, 1954, 1955, 1959; Turkel *et al,* 1955; Stairs, 1964; Kotov, 1969; Vogt, 1969; Jovanovic and Tucovic, 1975; Bonnet-Masimbert, 1978; Merkle *et al,* 1980). Although many dissimilarities are found between groups within the genus, the major difference of interest in this study is the time required for seed maturation. Seeds of the white oak group (*Lepidobalanus*) mature during a single growth season, while those of the red oaks (*Erythrobalanus*) require 2 seasons. The existence in cork-oak of the 2 different reproductive strategies, the 'annual' (similar to that of the *Lepidobalanus* group) and the 'biennial' (similar to *Erythrobalanus*) as well as the influence of climatic conditions on seed maturation were investigated in this study.

The phenology of cork-oak has been the subject of only a few studies. Important questions, such as the characteristics of the acorns produced at different times of the year, have been neglected by most authors. Knowledge of the complex phenology of cork-oaks is of interest to breeders for 2 reasons: 1) it provides more information on the genetic variability of the species; 2) such knowledge is of utmost importance for afforestation strategies, grafting, viability of seed orchards and propagation techniques in general.

MATERIALS AND METHODS

Observations were made on natural populations of *Q suber*, found together with holm-oaks, located in: S, Joaquin de Huelmos state (A), Salamanca province (UTM 30TL6960) at an altitude of 840 m. Here, the mesomediterranean cork-oak reaches its northern limit and it is mixed with *Q ilex* and *Q faginea*; north of Plasencia at the Umbría de Valcorchero (B) (UTM 30T QE4940) at an altitude of 642 m representing a community of subhumid thermo–mesomediterranean cork-oak. It is here where the mesomediterranean cork-oaks reach their optimum state; in proximity to the Gabriel y Galán reservoir (C), province of Cáceres (UTM 30T QE4757) at an altitude 411 m. This group represents a population which is geographically intermediate between (A) and (B). Only sporadic observations were made.

Meteorological data for localities A and B were obtained from the National Institute of Meteorologie, Moriscos and Plasencia stations, respectively (fig 1).

We monitored, for 3 consecutive years (1988, 1989, 1990), the different states of development of the male and female flowers and of the acorns present on each of the trees that we had previously selected and marked. The reproductive cycle in *Q suber* was followed placing particular emphasis on the time required for seed maturation from pollination to the fall of the acorns.

A total number of 91 individuals were observed: 47 growing in site A; 20 in site B and 24 in site C. The characters, recorded for each tree are shown in table I.

RESULTS

There was notable phenological variability among individuals within each of the studied populations, as well as between populations. The reproductive cycle (time required for seed maturation) is the character that shows the greatest among-population variation.

Within-population variation

Considerable phenological variability among individuals of the same population was observed in sexual behavior, despite the fact that oaks are monoecious (both male and female flowers appear on the same tree). The investment of resources in

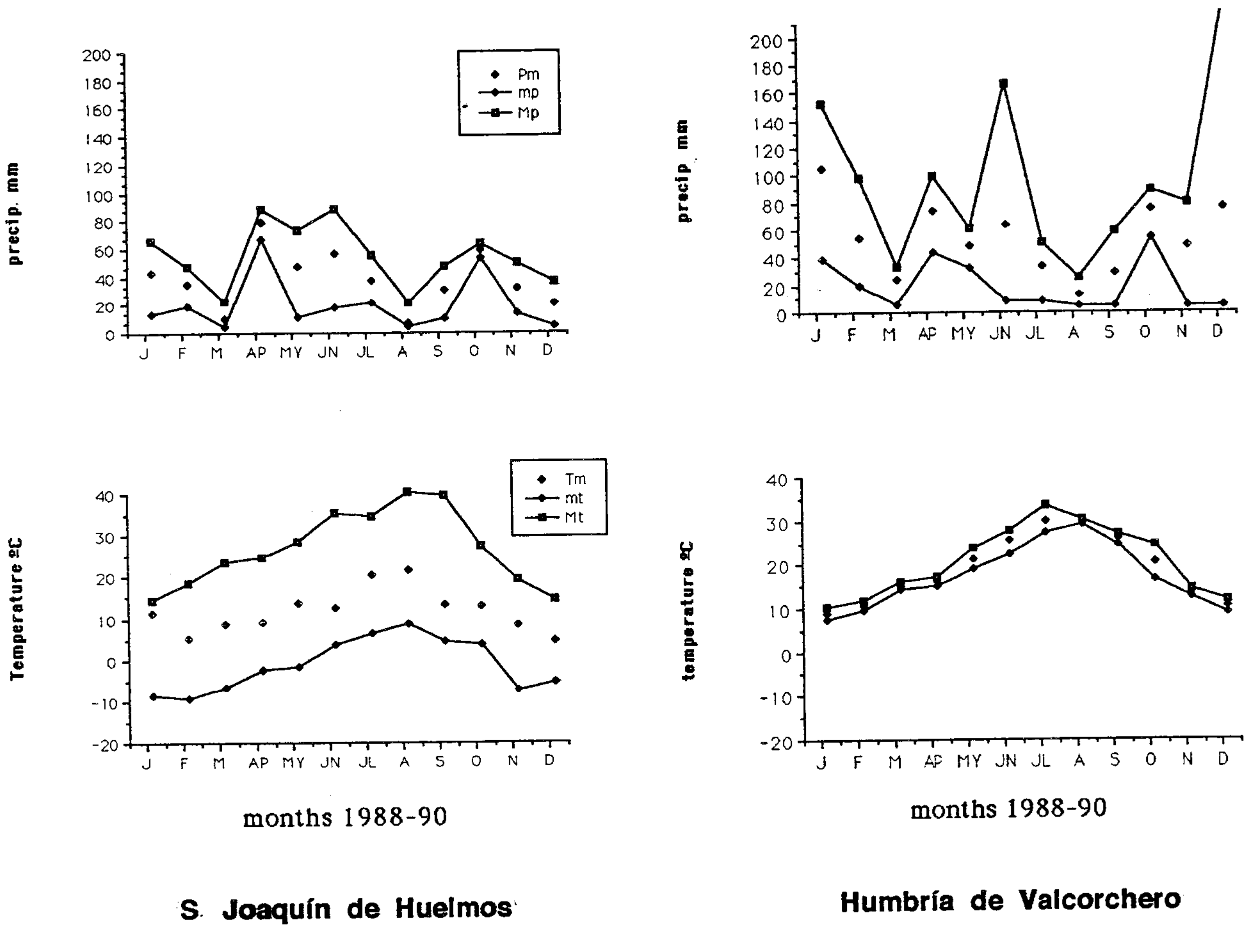

Fig 1. Diagrams of precipitation and temperature averages for the years 1988, 1989, 1990. Data from the meteorological stations at Moriscos (population S Joaquín de Huelmos) and Plasencia (population Valcorchero). *Tm* (median values of temperature/mo), *Pm* (median values of precipitation/mo), *M* and *m* (maximal and minimal temperature or precipitation/mo).

Table I. List of the phenological characters recorded for each tree.

1. Presence (a) or absence (b) of new female flowers (N) (of the current year) or old (O) ones (previous year)
    - 1a)–1. Receptive female flowers (N): the stigmata are visible, greenish–yellow in color and have a humid appearance
    - 1a)–2. Non receptive female flowers (N): the stigmata have changed color and become brownish–black
    - 1a)–3. Female flowers (O) on a branch of the previous year

2. Presence (a) or absence (b) of (male) catkins
    - 2a)–1. Buds and or catkin primordia (non-dehiscent anthers)
    - 2a)–2. Rape-pollen (dehiscent anthers)
    - 2a)–3. Already disseminated pollen (reddish–brown catkins)

3. Presence (a) or absence (b) of acorns
    - 3a)–1. A small amount
    - 3a)–2. A large amount

the male and female reproductive structures and in the vegetative function varied widely allowing us to distinguish between 4 different types of trees (table II): 1) male trees, which produce few female flowers and never produce acorns; 2) female trees, which produce few male flowers or the catkins are aborted before production of pollen, c) vegetative trees, which have no male or female inflorescences and whose leaf biomass is greater and 4) androgynous trees, which produce both kinds of inflorescences and whose acorn yield is high.

Table II. Frequencies (%) of male, female, vegetative and androgynous trees in the natural populations (A, B and C) of *Q suber*.

Site	*Male*	*Female*	*Vegetative*	*Androgynous*
C	22.2	44.4	–	33.3
B	11.1	44.4	12.5	30.0
A	6.3	36.1	38.2	19.1

Among-population variation

We showed the existence of 2 types of reproductive behavior cycles in the examined populations: trees with a short cycle and those with a long cycle, corresponding to the populations located at sites B and A, respectively; both types of trees were found at site C.

Long cycle (data obained from S joaquin de Huelmos)

The male flowers (catkins)

The period of male flowering extends from the end of March to the end of July (the anthers are dehiscent and the majority of pollen from a single tree is shed). The greatest percentage of trees with mature male flowers was observed in June (fig 2).

Pistillate flowers

Their development takes place during June–July and each individual shows 1-month with respect to male flowers (fig 2). The female primordia appears in the apex

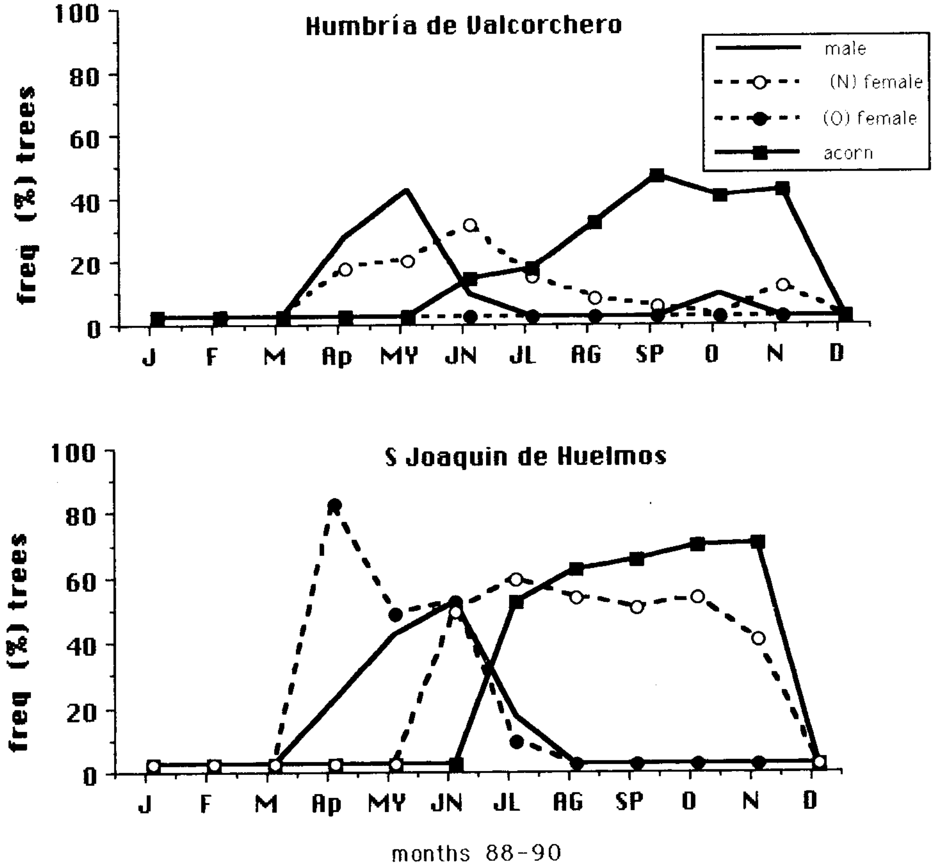

Fig 2. Percentages of trees (averages for the year 1988, 1989, 1990) with male flowers, old (O) and new (N) female flowers and with acorns; data obtained from Umbría de Valcorchero (CC) and S Joaquín de Huelmos (SA).

of the young shoots. The majority of receptive female flowers can be observed during June and early July. Flowers with pollen on their brown stigmata begin to appear during the last days of June. The young ovary of the pollinated flowers is covered by a husk and enters a 'period of dormancy' (Corti, 1955). Flowers remain in this state until the following spring-summer (O flowers).

Fruit maturation (from pollination to seed maturation)

Maturation takes place during the month of June, when the female flowers are receptive, the pollen grains are shed and they germinate on the receptive stigmata. After pollination, a period of dormancy begins which lasts until the next spring–summer (May–June), *ie*, 10–11 months. The embryo requires 4–6 more months to mature.

The greatest percentage of trees with fruit was observed in November (fig 2).

Acorns drop takes place in October and November. Very few old flowers remain on trees with a large number of new female flowers. This observation could explain the *veceria* (*ie* an exceptional yield that occurs periodically–every 2, 3, 4 or more year– which is characteristic of cork-oaks) (Montoya Oliver, 1988).

Vegetative growth

The first leaf primordia can be observed at the end of May when the old leaves fall. By the end of June, very few dry leaves remain in the tree and the new ones are already fully developed.

Short cycle (diffuse flowering) (data obtained from Umbria de Valcorchero)

Male flowers (catkins)

Male flowers are formed in these populations during the months of April, May and June. The greatest percentage of trees with mature flowers was observed in May (fig 2).

Pistillate flowers

Their development is initiated in April, May and June, and extends almost uninterrupted until August (diffuse flowering or subcontinuous) (fig 2).

Maturation of the embryo

The embryo matures simultaneously with female flowering; maturation begins in June-July (with the earliest flowers appearing in April) and extends throughout the summer. In this population, the seed maturation process is continuous; the seed is fertilized and continues to develop to maturity during the summer of the year in which pollination took place. Fertilization occurs after 1–2 months of dormancy and maturation, and the seed drops 3-5 months later (fig 2).

The different stages of the reproductive cycles of *Q suber* are summarized in figure 3.

DISCUSSION AND CONCLUSION

The current study clearly shows the existence of 2 well-differentiated reproductive strategies in the same species. These strategies manifest themselves in the maturation of the acorn and, more specifically, the time required from pollination to the fall of the rape-fruit. They are: 1) the biotype of annual maturation of the acorn (short cycle) and 2) the biotype of biennal maturation (long cycle).

The only distinctive and easily observable differentiating character between the biennial and annual types is the shoot on which the fruit develops; fruit developing on the current year's shoot indicates the annual strategy while fruit developing on the shoot of the previous year indicates a biennial strategy. As this is the only observable difference, we have to inquire as to its value and significance for the species. What are their respective adaptive advantages? How can we explain the existence of 2 different reproductive strategies in the same species?

One of the primary causes appears to lie in the physiological plasticity of the species, which enables it to adapt to variable and unpredictable climatic conditions, characteristic of the mediterranean climate.

The S Joaquin de Helmos population is at a marginal site in terms of the distribution of the species; the summer droughts are long, winters are quite long an bitter with late frosts in the spring. The driest season is the summer, so that the most favorable time for flowering is the end of spring and early summer when the possibility of frosts has been reduced.

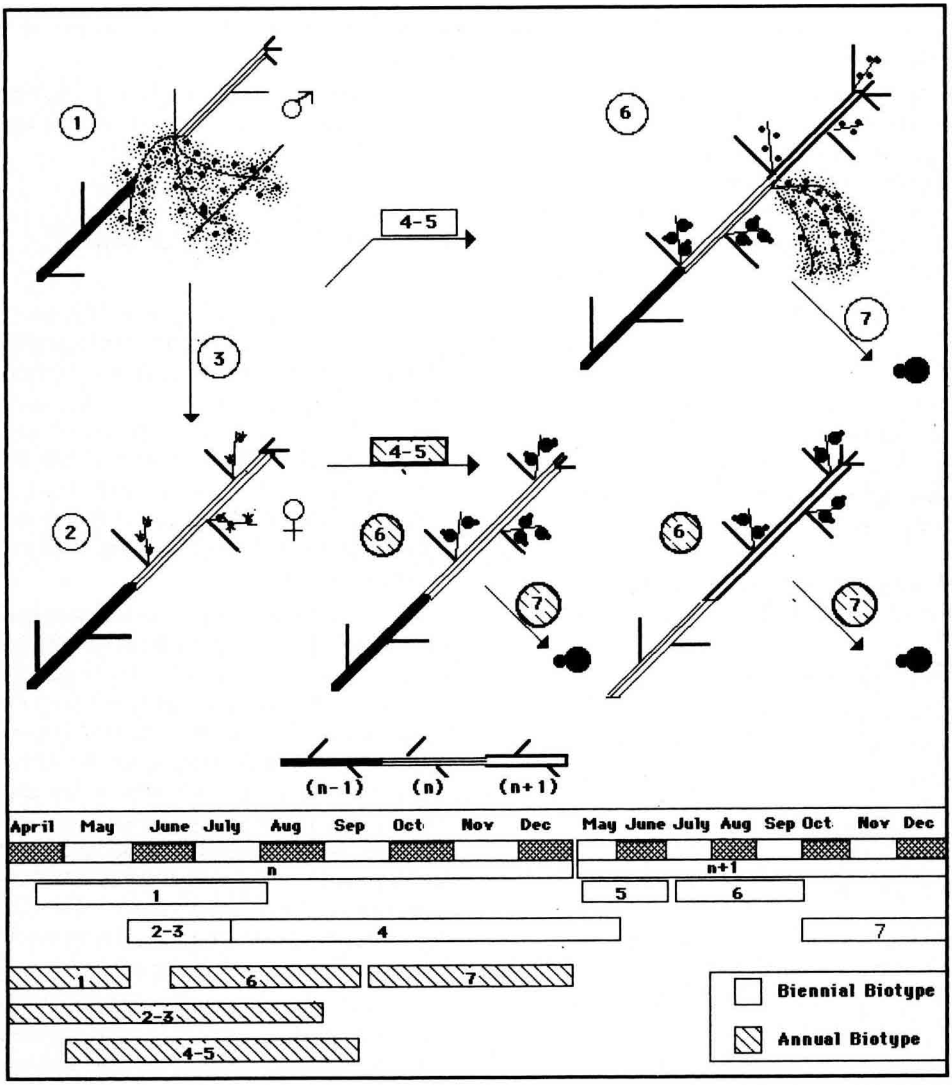

Fig 3. The reproductive cycles in cork-oak *(Q suber)*: 1) male flowers on the previous year shoots (*n*–1); 2) female flowers in the axils of the new leaves of the year (*n*); 3) pollination; 4) the period of dormancy; 5) fertilization; 6) development of the acorn; 7) acorns drop; (n–1), (n), (n+1) are 3 consecutive years.

The long period of dormancy and the timing of reactivation of development also appear to be optimal for the climatic conditions. If fertilization occurs after a short period of dormancy (or immediately after pollination), the beginning of the development of the young acorn will coincide with the prolonged summer drought. To avoid this, the species has resorted to an extension of the period of dormancy so that the fertilization and development periods coincide with the end of the unfavorable season, in these trees, annual flowering coincides with the fertilization of the flowers of the previous year.

In Umbria de Valcorchero the cork-oak may be exposed to climatic conditions more favorable to its development. At this site, we observed that flowering (male as well as female) occurred earlier than in the other population. As summers are very hot and dry at this location flowering and acorn-development must be avoided during this season. We also noted that flowering and fruit maturation were extended for longer periods, in this population.

In both cases studied, we found that 'self-induced' flowering (Corti, 1955) and reactivation of development were influenced by microclimatic conditions. Although a general interpretation at the species level would require a more extensive study, it seems, from our results, reasonable to consider the annual and biennial biotypes as 2 ecological strategy types resulting from species adaptation to a Mediterranean climate. The annual biotype maintains the characteristics of the primitive type (slow type)–with a reduction of the period of dormancy–adapted to areas with subhumid Mediterranean climates which have less contrast between seasons. The biennial biotype is, on the contrary, the response of the species to harsh climatic conditions; it is able to colonize those environments in which the annual form is unable to adapt.

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