PHENOLOGICAL PHASES OF *QUERCUS SUBER* L. FLOWERING

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ABSTRACT

Importance of the definition of phenological phases of the male and female flowering is justified as a tool for the knowledge of the reproductive biology of cork oak. Importance is stressed on the role of reproductive biology on breeding and gene conservation programs of the species and for the realization of controlled crosses.

Morphological changes of the different stages of the phenological phases are described. Phases are nominated from **A** to **H** beginning on bud phase till end of stigmatic receptivity/emptying of the anthers. Full receptivity and maximum pollen shedding are defined as phase $\mathbf{F_2}$. Definition of $\mathbf{F_2}$ is a fundamental practical support for controlled pollination, with special reference for the establishment of time tables for pollen collecting and application.

Flowers of both sexes on various phases are described and illustrated by magnifying photographs. The occurrence of hermaphrodite flowers during spring flowering, with considerable significance, is mentioned and claims adequate research before controlled progenies shall be produced.

Studies conducting to time scales for the various phases are pointed as a essential step on the future research of cork oak while support for controlled pollination, contribution for the understanding of populations dynamics and for gene flow studies.

Further research needs on the reproductive system of *Quercus suber* are pointed. The importance of flowering phenology as a complementary tool on climatic studies is also discussed.

Key words: *Quercus suber*, cork oak, flowering, flowering phenological phases

Probably the greatest advances in tree-crop management in future years will result from further detailed analysis on the exact timing of floral initiation and of the complex developmental and physiological stages leading to anthesis.
SEDGLEY & GRIFFIN (1989)

INTRODUCTION

The mating pattern of a species influences the genetic differentiation of that species. An understanding of the flowering biology of a species is fundamental for studies of the mating pattern. Tree improvement programs mostly rely on seed production in seed orchards and crossing for assessments of genetic parameters. For both knowledge in flowering biology plays a crucial role.

Reproductive knowledge is a background of great importance for further management of the species in the fields of breeding and conservation of genetic resources (STERN & ROCHE 1974; NRC 1991, VARELA & ERIKSSON 1995). The breeding system of any species is strongly dependent on the floral structure, sexuality and phenology as well as on the dynamics of the population. In various species the primary observation on the flower architecture has shown enough to infer key features of the profile of the reproductive system such as obligatory selfing or outcrossing, propensity for dioecy, animal or wind pollination, etc. saving time on further studies (SEDGLEY & GRIFFIN 1989; DAFNI 1992).

Beyond usefulness on controlled mating, possibilities of gene flow between populations and interspecific hybridization may also have a first analysis through studies on flowering phenology (DUCOUSSO *et al.* 1993).

Quercus suber is a monoiceous species but hermaphrodite flowers may occur (MACHADO 1934, VARELA 1996). Main flowering season takes places during spring but other flushes may be seen around the year but great variability can be seen both at stand and tree level (VARELA 1994). The lack of a unique flowering season justifies the classification of sub-continuos flowering species (NATIVIDADE 1950; CORTI 1955). Complexity still happens on fruits maturation which can be of one year or of two years. Furthermore, all aspects of this variability may be seen on neighborhood trees but also within the same tree.

This complex reproductive behavior has been cause and consequence for the scarce knowledge still existing on the species. Recent research lines on the genetics of cork oak raised the need of studies on floral biology, special when controlled progenies have been claimed (VARELA 1994)

Studies initiated in 1993 revealed, at first, a high level of developmental diversity of cork oak turning definition of flowering phases into the main task of the observations being carried out. Therefore working on time scales, essential to plan the controlled crosses, immediately come up as impracticable while patterns of flowering phases were not established.

Being traits shaped by changes on morphology, proportions, color and other features flowering phases of cork oak reveal itself as observations not liable of being framed on metric measurements.

The tiny dimensions and subtlety of the changes turns assessment of the phases based on memorization difficult. Even written description was found to be insufficient support for accurate field observations whenever different phases are seen simultaneously. Therefore, standardization of the patterns of phenological phases turned out to be a fundamental tool for increase on efficiency and reliability of data collected through different teams, even for the same team along the years. Similar reasons can be found on chestnut research lines (BOUNOUS *et al.* 1994).

The size and color of male aments allow to allocate the time duration for maximum pollen shedding. Identical procedure for pistillate flowers was not possible before a clear understood of external morphology was achieved. Focused to build up patterns of the individual flowers, observations have not been compatible with fixing of time scales for the various trees as an all.

This task, is expected to be taken in coming studies, now that phases have been perceived. Thus the purpose of this paper is to describe the external development of the floral structures of the male and female flowers, with major emphasis for the crucial phase of the reproductive process, the pollination phase – pollen shedding and receptivity of the female flower.

MATERIAL AND METHODS

Observations where carried out on 3 permanent plots located in Azeitão (Quinta da Serra) and two in Alcobaça (Mata Nacional do Vimeiro). The three populations exhibit considerable environmental variation, both of ecological and anthropogenic origin as patent on Table 1. Sites differ on climate and soils and trees are submitted to different management methods.

Quinta da Serra – It is a uneven stand of natural origin, irregular spaced. It is submitted to sustained agroforestry management. Climate is of Mediterranean type with mild winters and considerable summer drought. The plot may be considered as representing the average ecological requirements of the species in Portugal. This plots includes 24 trees.

Mata Nacional do Vimeiro, Alcobaça – It is a region of average climate for cork oak in Portugal. Climate is mild, both in winter and summer. Soils are fertile and the species exhibits excellent vigor. MN Vimeiro is a state experimental unit without any kind of economical management. In this state forest two plots were chosen, Alcobaça I and Alcobaça II. Alcobaça I – It is an uneven stand of irregular spacing. Plot size – 20 trees. Alcobaça II – It is a plot of even aged trees in regular spacing managed under a coppice regime. Plot size – 20 trees. In all the cases trees have been randomly chosen among the existing.

During 1993 observations were focused on descriptive recording of the flowers' morphological development.

Observations carried along 1994 had an increasing on the number of flowers, frequency and details of the flower developmental sequence was also supported by photographic registrations of the various phases.

Table 1 Characterization of the plots. P — precipitation in mm; M °C – mean temperature of the hottest month; N °C – mean temperature of the coldest month.

Plot	Latitude (N)	Longitude (W)	Precipitation (mm) total	Precipitation (mm) summer	M °C	N °C	Emberger coefficient Q_2	Management
Quinta da Serra	38°29'	9°00'	764	34.2	29.0	5.6	110	intensive agroforestry
Alcobaça I MN. Vimeiro	39°29'	9°00'	945	53.0	25.8	4.8	156	uneven stand, irregular spacing
Alcobaça II	39°29'	9°00'	945	53.0	25.8	4.8	156	coppice regime

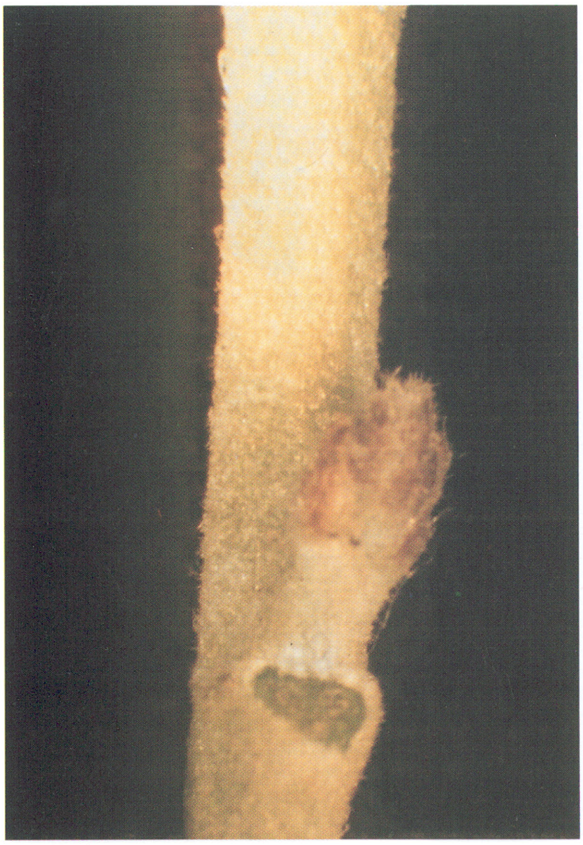

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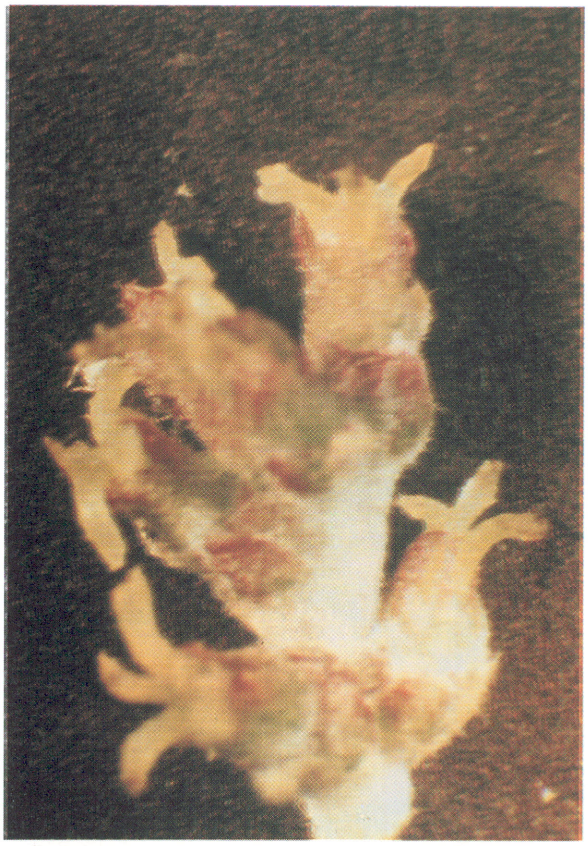
Figure 1 Female flowering in phase **Df** – Appearance of the reproductive axilar buds with green scales. The scar of the leaf can be seen. Magnification – 14.3 ×.

⇧

Figure 2 Female flowering in phases **Ef** (right side) and **F** (left side) – Development proceeds by elongation of the spike axe and emergency of the first pair of flowers. Onset of stigmas can occur in this early stage. Magnification – 23.2 ×.

⇦

Figure 3 Female flowering in phase **Ff** – Flowers show distinct, erect, divergent yellow stigmas with curved pinkish/brownish tips. The ax of the spike is visible and the elongation could eventually go on. Magnification – 13.7 ×.



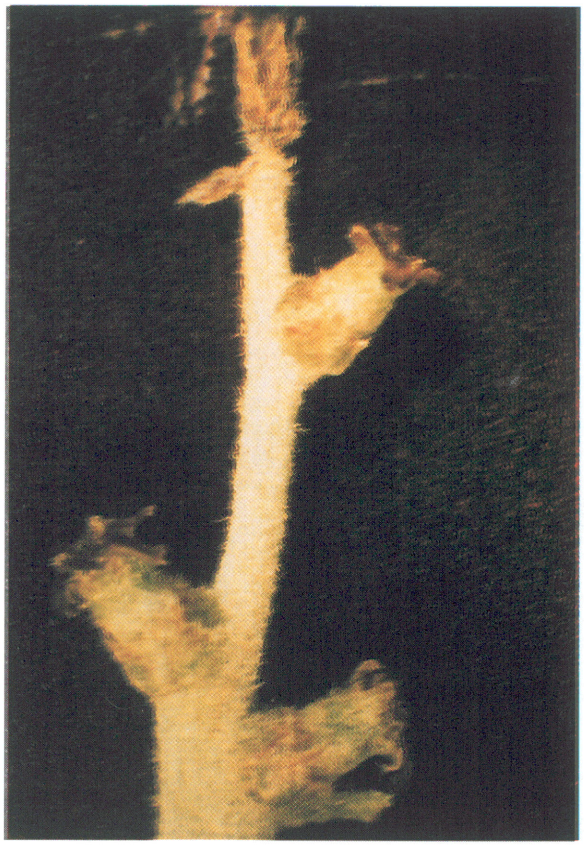


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Figure 4 Full receptivity, phase $\mathbf{Ff_2}$ – flowers show plump stigmas in clear divergent position, with shining yellow and viscous pattern. In this case all flowers are in full receptivity phase but to considered a spike in phase $\mathbf{Ff_2}$ it is enough that more then 50% show the pattern. Magnification– 12.5 ×.

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Figure 5 Female flowering in phase **Gf** – Receptivity is loss, stigma become tarnished yellowish brown. Magnification – 8.4 ×.

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Figure 6 Female flowering – **Hf** – All the stigmas lost the receptivity exhibiting a dark brown colour. The involucre, now individualised from the rest of the structures, is clearly visible. Magnification – 20 ×.

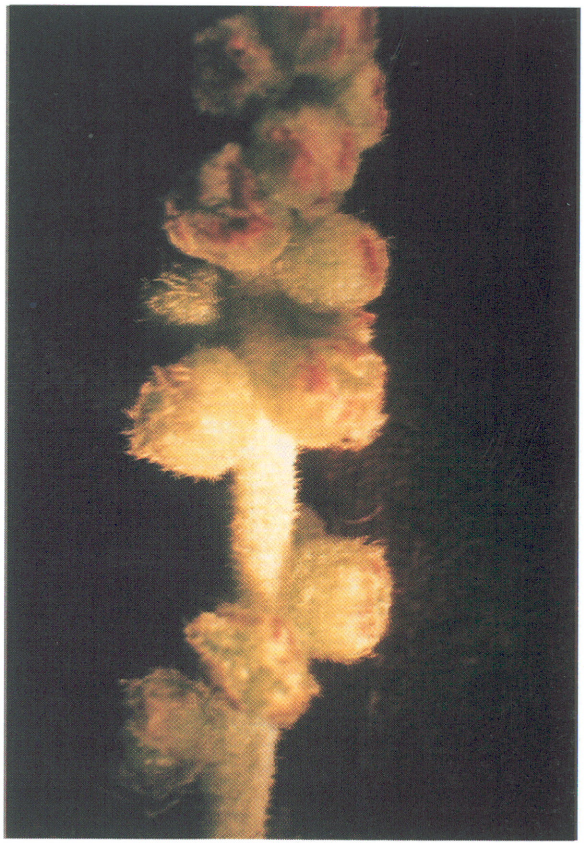

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Figure 7 Em – Anthers became individualised with green yellowish colour. Photo shows an entire male catkin in phase **Em**. Magnification – 9 ×.

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Figure 8 Detail of anthers in phase **Em**. Magnification – 8.9 ×.

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Figure 9 Catkin in phases **Em** and **Fm** Pollen shedding begins in less than 50% of the flowers of the catkin. Magnification – 9.2 ×.

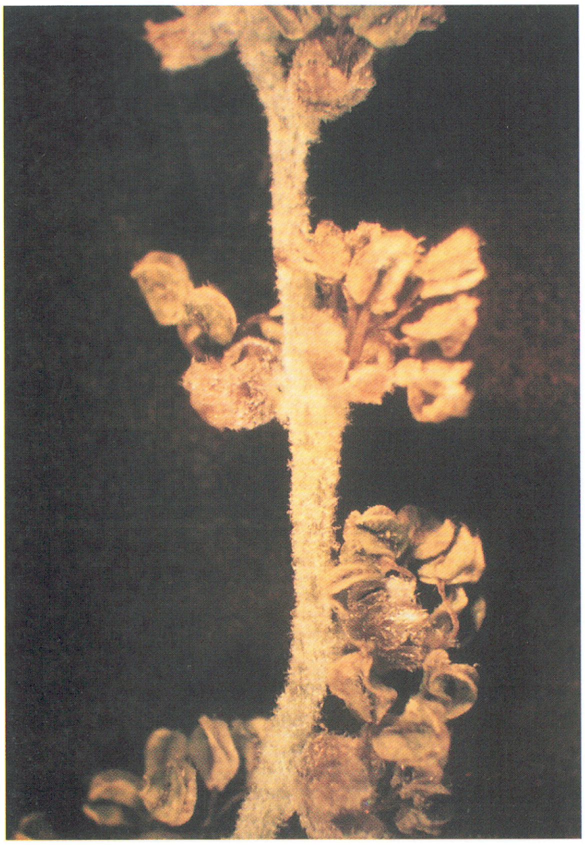

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Figure 10 Phase **Fm$_2$** – Full anthesis: Pollen shedding is occurring at least in 50% of the catkin flowers. During this phase some anthers of the catkin may release all the pollen loosing the yellowish feature. Magnification – 9.2 ×.

⇧

Figure 11 Detail of an anther in phase **Fm$_2$** – Full anthesis. Magnification – 22.7 ×.

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Figure 12 Gm – Great majority of the anthers are brownish, in consequence of the pollen emptying and drying. Magnification – 9.2 ×.

Trees have been regularly observed since end of March with labeling of several branches for continuos observations, in order to cover the phenological sequence. Flowers in identical stage were collected and photographed using a magnifying glass WILD 420 equipped with a camera WILD makroskop M 420 and a film Fuji RAP, 100 ASA).

For the definition of the phenological phases of cork oak flowering we benefited from previous experience on *Castanea saliva* and *Juglans regia* (VALDIVIESSO 1991; VALDIVIESSO *et al.* 1993).

All these species are monoiceous with unisexual flowers. Staminate inflorescences are of ament type. Pistillate flowers also have morphological common aspects, flowers are apetal with well developed stigmas but incipient style.

In what concerns flower parallels on development behavior are specially evident among male catkins on the three species. On female flowers similarities are more evident among *Juglans regia* and *Quercus suber*.

RESULTS

Phenological evolution of flowers within inflorescence shows differences between catkins and spikes. Evidence comes up in spikes where outphazing from basal to tip flowers can be of 3 or more different phenological stages. In spite of also showing differences within flowers, male inflorescence have a more homogeneous development.

Flowers of different plots showed similar morphologic patterns of phenology. Yet dates of occurrence differed, Quinta da Serra was the earliest, followed by Alcobaça I and lately Alcobaça II (coppice regime). However observations of one year are insufficient for the establishment of patterns. To establish phenological differences among these or any other populations there is the need to have time scales. This job is now facilitated after the definition of phenological phases.

The problem of annual/biennial (NATIVIDADE 1950; CORTI 1954) fructification can get new insights from our kind of studies. *Quercus suber* is commonly referred on bibliography as a species with several seasons of flowering. The occurrence of female flowering without the presence of male and vice versa was reported (NATIVIDADE 1950; ROSSELLO *et al.* 1993). It has even been considered as an important factor for significant seed productions (ROSSELLO *et al* 1993) although the biological development of such kind of flowering is not explained. Cork oak reproductive behavior is very complex and still needs long detailed research.

Female flowering

Female flowers occurs in inflorescence of spike type on the axis of the new leaves. The female flower is surrounded by an involucre. The ovary is inferior, consisting of three carpels with two ovules each. Usually only one ripens as the seed (NATIVIDADE 1950).

The female inflorescence is a spike and occurs in the axils of the new leaves, therefore in mixed buds.

The elongation of the spikes axes proceeds during some days given origin to a continuos process of flowers formation. Normally the inflorescence shows a gradient of growth from the base to the tip. Thus, basal flowers are usually more advanced in phenological stage.

Female flowers are of small size, around 3 mm of length, without any kind of conspiscuosness. Observations showed a range from 1 to 12 flowers per spike corresponding to a mean number of 2.3 (VARELA 1994).

Phenological phases of female flowering

The present work adopts the patterns of phenological sequence in use for nut fruits trees, in Estação Nacional de Fruticultura Vieira Natividade (ENFVN), namely *Juglans regia,* and *Castanea saliva* (VALDIVIESSO 1991; VALDIVIESSO *et al.* 1993).

The evolution of the female flowering its macroscopically revealed through a sequence of phenological stages, denominate by capital letters from "**A**" to "**H**", and characterized as follows:

Af – Brownish mixed bud completely enclosed on protective scales.

Bf – Swelling and elongation of the bud with opening of the scales.

Cf – Emergency of the first leaves.

Df – Appearance of the reproductive axillar buds with green scales (Fig. 1).

Ef – Elongation of the spike axe and emergency of the first pair of flowers. Onset of stigmas can occur in this early stage (Fig. 2).

Ff – Flowers show distinct, erect, yellow stigmas with curved pinkish/brownish tips. Axis elongation proceeds (Fig. 3).

Ff_2 – Full receptivity. More then 50% of the flowers of the spike show plump stigmas in clear divergent position, with shining yellow and viscous pattern (Fig. 4).

Gf – Receptivity loss in some stigma which become tarnished yellowish brown (Fig. 5).

Hf – All the stigmas lost the receptivity exhibiting a dark brown color (Fig. 6).

Male flowering

Male flowers, organized in catkins, occur in reproductive buds of the previous season growth, occasionally in the base of shoots of the current year.

The staminate inflorescence consist of several flowers grouped in catkins. In full development the catkin attains an average length of 5 cm ranging from 3 to 6 cm. The individual catkin comprise 15 to 25 flowers radially seat around the axis of the hanging catkin. Each flower is formed by 4 to 6 tepals with equal or double number of anthers (NATIVIDADE 1950).

Anthers are supported by filaments of 2 to 5 mm, comprising two lobes separated by a notorious sulcus. They bear the pollen sacs. Anthers of a flower do not burst simultaneously. The flowers of a catkin do not bloom at the same time. The blooming comes up usually from the basal toward the distal portion on the catkin. Therefore, the pollen shedding per catkin extends for few days, though the duration is influenced by weather.

Phenological evolution of male flowering

The evolution of the male flowering is macroscopically revealed through a sequence of phenological sequences, characterized by:

Am – Round and brownish bud completely enclosed on protective scales.

Bm – Swelling and elongation of the bud with opening of the scales.

Cm – Emergency of the catkin with round shape due to the tight clustering of the flowers.

Dm – Elongation of the catkin.

Dm_2 – Half of the flowers are individualized and the catkin becomes pendent. The process goes from the base to the tip.

Em – Anthers became individualized with green yellowish color (Fig. 7 and 8).

Fm – Pollen shedding begins in less than half of the flowers of the catkin (Fig. 8 and 9).

Fm_2 – Full anthesis: Pollen shedding is occurring approximately in half of the catkin flowers. Some anthers may eventually became empty loosing the yellowish feature (Fig. 10 and 11).

Gm – Due to drying the great majority of the anthers are brownish, in consequence of the pollen emptying (Fig. 12).

Hm – All the anthers are dark brown and the catkin fall is eminent.

DISCUSSION AND PERSPECTIVES

The field observations on the flower development led to the description of the most important stages of the process of flowering. Emphasis was focused on F_2 stage for flowers of both sexes, corresponding to pollen shedding and stigmatic receptivity.

Definition of phenological phases is not a goal per se, rather a tool for several fields of research which are foreseen to happen in cork oak in a near future.

Artificial crosses

Isolation of female flowers and emasculation

Female flowers shall be isolated in phase **Df**. This early stage is advisable rather than phase **Ef** to ensure there is no pollen deposition from unwanted sources. Due to the tiny dimensions of the pistillate flowers it is possible that on phase **Ef** some flowers have already stigmas in early receptivity which can host the pollen until full receptivity. Therefore, safety points to phase **Df**.

Simultaneously the branches must be emasculated. It is supposed to be a unique operation on the beginning of the process because male flowering is usually more precocious than female and no second flush of male flowering has ever been reported.

Hermaphrodite flowers

Hermaphrodite flowers, occurring in inflorescence of an appearance close to normal pistillate spikes, were observed during this study with considerable significance. Former references already point this phenomenon but only for summer/autumn flowering.

The occurrence of this type of flowers during spring, the elected season for controlled crosses, is a key feature on controlled crosses of the species which can not be neglected.

Minutious observations to eliminate the hermaphrodite flowers should be performed to avoid selfing and gneitogamy. As hermaphrodite flowers occur on spikes among the female flowers the elimination means opening of the bags during the critical period which may lead to pollen contamination.

Besides being time consuming, this procedure still carries contingency. Difficulties may arise on the detection of these kind of flowers due to their small size.

Certainty of the crosses can only be attained by means of studies using genetic markers on embryos or progenies. Therefore, controlled crosses on cork oak is a field where investigation claims support of genetic markers.

If detection of self progenies becomes feasible through biomarkers, emasculation may even become unnecessary reducing the costs on controlled crosses.

Pollen collection

Branches for pollen collection shall be picked when catkins are in phase **Dm_2**. The aim of such methodology is to avoid risks of pollen mixtures. On this stage there are any anther realizing pollen, therefore contamination does not occur.

Although the use of fresh pollen is preferred to preserved for biological reasons (SEDGLEY & GRIFFIN 1989) particularly because of the financial load storage means, artificial pollination are often required.

Therefore, procedures to avoid contamination shall be used even if the pollen is to be used immediately, without storage. The branches shall be picked is this early stage and transported to laboratory where the maturation is to be completed. Phase $\mathbf{Dm_2}$ eliminates risks of contamination.

Yet, the operation of pollen collection must still having into account the phenological stage of the surrounding trees. A tree in maximum pollen shedding phase easily leads to external contamination of the immature catkins. Special procedures must be developed for these situations.

During maturation at laboratory conditions of total isolation among the branches of the various trees under processing must be assured. People and tools used for pollen extraction must be carefully cleaned. Isolated devices are needed because pollen is easily carried by air movements even on a laboratory atmosphere (SEDGLEY & GRIFFIN 1989).

After these procedures the pollen, carefully labeled, may be used directly or stored.

Processes for pollen storage, the longevity and manipulation of fresh pollen for *Quercus suber* are still unknown, therefore needing appropriate studies.

The establishment of the time tables for pollen collecting on the several mates is also necessary on the planning of the controlled mating.

Application of the pollen

Pollen must be injected while female flowers are in phase $\mathbf{Ff_2}$. As in a spike flowers are usually not all in the same phase average duration of Ff_2 is a basic step for realization of controlled pollination. Time tables for the average duration of phase Ff_2 are necessary to plan the applications.

Pollen collection is a time consuming and rather expensive operation even if to be used in fresh condition. Artificial pollination is also time consuming requiring several applications of pollen to raise the success of the fertilization. Therefore maximization of the use of fresh pollen is not attained if there is no knowledge of phenologic rhythms of the partners.

The number of days of assynchronization acceptable for controlled crosses based on fresh pollen must be appraised taking into consideration the longevity of the pollen and the behavior of the chosen mates.

The time length for pollen application must be monitored through observations on other female spikes situated on branches close to the ones used for controlled crosses.

The knowledge of the reproductive biology of cork oak points that trees tend to keep their relative behavior, *i.e.*, precocity or lateness on flowering are characteristics rather stable from year to year, for both male and female flowering (VARELA & SÁ 1995).

As cork oak is a species with reproductive behavior of great variability these trends still need more years of observations to be confirmed. The support it means on the realization of controlled pollination justifies such studies.

If artificial pollination is to performed with stored pollen than the most important information is the average duration of the female receptivity.

Therefore, for rationalization of the all process knowledge of phenologic rhythms and average duration of the female receptivity are the basic information for realization of controlled mating

Populations dynamics

The phenological behavior of the individuals within a population is a base to understand the reproductive dynamics. Asynchrony on the fertile phases means limited chances of crossing and consequently a genetic split of the population into sub-groups intrafertile because of phenological coincidence.

As a rule trees are not uniform in one phase. The criterion to define the phase for a tree shall be reported to the development of 50% of the flowers (IPGRI 1994)

As the flowering phases last for some days there are possibilities of crosses since the onset till the end of the fertile phases. Therefore, to understand the population dynamics, and to make empirical evaluations of the population effective size observations shall be focused on the number of flowering trees which are synchronized on phases $\mathbf{Ff}$, $\mathbf{Ff_2}$, $\mathbf{Gf}$ and $\mathbf{Fm}$, $\mathbf{Fm_2}$ $\mathbf{Gm}$.

Gene flow

Gene exchange among populations through pollen flow can also have appraisal through the knowledge of the phenological phases of the populations in consideration.

The probabilities of gene flow among neighborhood populations are closely dependent on the synchronization of the various individuals in respect to phases $\mathbf{Ff}$, $\mathbf{Ff_2}$, $\mathbf{Gf}$ and $\mathbf{Fm}$, $\mathbf{Fm_2}$ $\mathbf{Gm}$.

Changes of pollen transferring are high if the phenology of these phases is harmonized, but they are very unlike if the trees are clearly outphazed.

Therefore, the simple recording of flowering phenomenon among neighborhood populations is insufficient to deduce gene flow.

Inter specific hybridization

The chances of interspecific hybridization are the result of species compatibility, distance and synchronization of anthesis and gynesis (ELENA ROSSELLO *et al.* 1992, BOUNOUS *et al* 1994, WILSON 1994).

Phenological distances may act as key impediment on interspecific hybridization overwhelming the condition of compatibility.

Compatible species which phases $\mathbf{Ff_2}$ and $\mathbf{Fm_2}$ differing of several weeks is a efficient way of preventing hybridization. It is the case of *Quercus suber* and *Quercus ilex* which populations often grow in mixed stands in Portugal. However, the flowering behavior of the two species in close populations, therefore in the same ecogeographic conditions, is usually marked by great differences in time (VARELA 1995).

Usually *Q. ilex* ends flowering some weeks before *Q. suber* begins. In a few cases it is possible to observe the latest trees of *Q. ilex* in phase **Hm** while the earliest *Q. suber* are in phase **Dm**. As female flowers are usually of late emergency the probability of hybridization between the two species must be regarded as low.

Without knowledge of flowering phases the simple observation of flowering could lead to wrong interpretations of the possibilities for hybridization.

Climatic studies

Time tables of phenological phases in a population can provide complementary information for climatic studies (BETTENCOURT 1982). This may be enhanced if clones of a given individual are studied during several years spread on different sites.

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