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REPRODUCTIVE CYCLES AND ECOLOGICAL CONSIDERATIONS IN WOODY PLANTS

Riassunto — *Cicli riproduttivi e considerazioni ecologiche in specie arboree.* È una breve rassegna dei numerosi lavori riguardanti i cicli riproduttivi di specie legnose, nati per iniziativa di E. FRANCINI e di R. CORTI.

Dei molteplici aspetti (embriologici morfologici, strutturali, ecofisiologici, paleontologici, epiontologici) trattati in questi studi, vengono qui considerati quelli che, sulla base di valutazioni comparate, hanno consentito di trarre indicazioni sulla storia evolutiva delle specie studiate ed in particolare, sulle modalità del loro adattamento ecologico.

Per ogni specie si analizzano le sequenze stadiali dei processi riproduttivi e la ritmica del loro svolgimento; si mette in evidenza il possibile significato delle pause che interrompono il ciclo (se imputabili a cause organiche oppure a stasi imposte dal clima); si considera l'intervallo fra impollinazione e fecondazione sotto l'aspetto strutturale e fisiologico e in relazione al tipo di ciclo («annuale», «biennale», «triennale»); si rileva la misura della plasticità di una specie nei riguardi dell'adattamento all'ambiente.

Abstract — Research started by E. FRANCINI and R. CORTI on the reproductive cycles of some woody plants leads to comparative evaluations. The succession of the ontogenetic stages of the reproductive processes in different species belonging to the same genus is here considered. Some ecological conclusions about the adaptive features of the species considered can be inferred.

Key words — Reproductive cycles, woody plants, ecological implications.

On the occasion of the Meeting dedicated to G.B. AMICI it gives me great pleasure to accept the invitation to re-present the research carried out during the past fifty years on the reproductive cycles

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of woody species. One of the aims of this Meeting is to call in mind Tuscan contributions to the domain of plant embryology. The theme of the Meeting offers the opportunity of recalling the contributions of the Florentine School to the knowledge of the reproductive biology of woody species.

Many of studies initiated by Eleonora Francini and Roberto Corti were directed principally at the reproductive cycles of species of the genera *Pinus* and *Quercus*. These studies were further enlarged on by the contributions of colleagues and researchers from the Universities of Bari, Messina and Florence. However, the fundamental studies on the subject are those by Eleonora Francini and Roberto Corti which provided important knowledge to several branches of plant biology.

These studies reveal a particular methodology as regards research. They also show a particular care in the research planning stages of the various aspects associated with the life cycles of the species mentioned above. Those morphological, structural, ecophysiological, epiontological and paleontological aspects lead to a completeness of data, on a monographic level. At the same time, their keen and minute analytical investigation of events emerges, often offering the key to the interpretation of present or long distant events. Besides offering a vast range of information, these studies also present a valid basis for further research, for which new experimental methods and new study techniques are now available.

Embryological studies began by considering that historically ancient genera, rich in species and whose ontogenetic cycles are very long and peculiar, may lend themselves to comparative evaluations. These evaluations allow us to identify the line of their long evolutionary history and may, at the same time, reveal the ecological adaptation of the present species.

Research on reproductive cycles has been directed towards the careful analysis of the stadial sequences of the reproductive processes and of the meaning of short and long pauses that interrupt the cycle. These pauses may be due to organic factors or to periods of rest imposed by climatic factors. The structural and functional meaning of the time lapse between pollination and fertilization can explain the measure of plasticity and rigidity of a species with respect to the present environment.

This present examination of the contents of above-cited studies, considers only the ecological implications of reproductive cycles.

Reproductive cycles in genus Pinus

The succession of the ontogenetic stages of the reproductive processes of Pines is very similar to that of the typical cycles of Gymnosperms and Conifers, in particular. In fig. 1 (cfr. Francini-Corti,

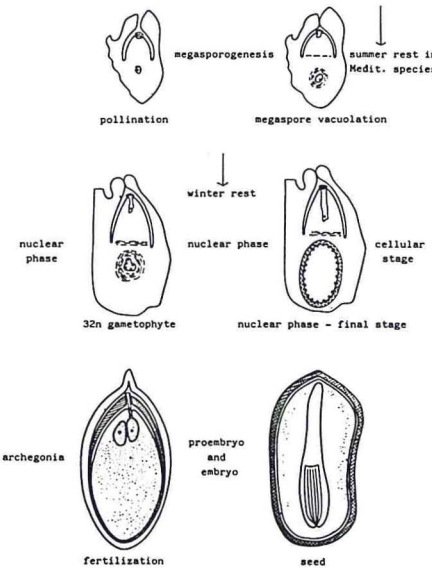

Fig. 1 — The most significant stages of the reproductive cycle in gen. *Pinus* (Francini-Corti, 1960; modif.).

1960), the most important events of the cycle are indicated. The first event is pollination which gives way to the processes and without which the ovules degenerate (Francini-Corti, 1961). The vacuolation of the megaspore which follows, represents an important stage in those species in which a dry summer causes a stasis. The nuclear phase at the fifth conjugated division (32n) marks the stage in which a rest period is imposed by the cold winter in those species in temperate climates. The final stage of the nuclear phase is that in which the number of nuclei determines the size of the gametophyte. The number of nuclei seems to be constant in each of the different species. Then, the cellular stage of the endosperm, the fertilization and maturation of the seed are presented.

Using the same schematic drawing as in fig. 1, the sequences of the ontogenetic cycles of the pines studied are presented. The cycles are shown in parallel series to render the analogies and the differences more clearly visible and to facilitate the understanding of the meaning that can be attributed to them.

In fig. 2 three cycles of pines are compared; the second of these cycles is based on studies carried out on the North American and Central European species (FERGUSON, 1904). These studies examine species that live in wooded areas of the temperate zone. This second cycle can be considered representative of the majority of the pine species. The cycle of *Pinus heldreichii* (Monte Pollino) can be considered representative of the high mountain pine species; EMIG (1953) cites the same cycle for the Rocky Mountains climate. The cycle of *Pinus laricio* (Sila) is indicative of the response of a species to Mediterranean mountain climate.

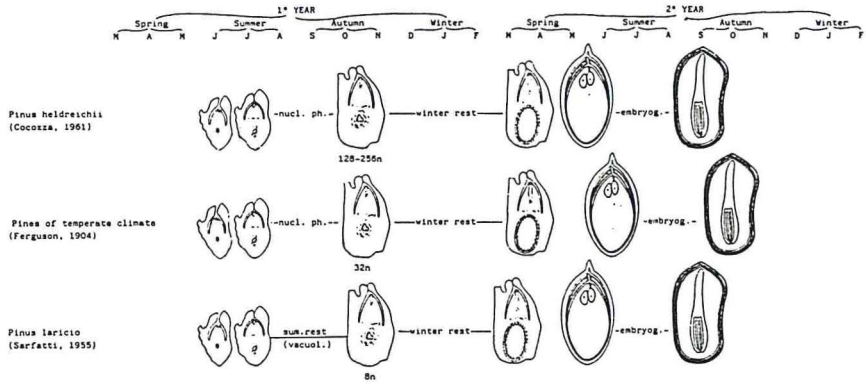

Fig. 2 — Reproductive cycles in gen. *Pinus*.

In the cycle of pines that grow in temperate climates we find a correspondence in two reproductive events: spring pollination and summer maturation of the embryo. This correspondence is common to the different woody species that live in the same temperate region. However, in the pine the sequence of the processes is not continuous; the long nuclear phase, which begins shortly after pollination, is interrupted after a certain number of coniugated divisions (after 7-8 divisions, i.e. 128-256n in mountain pines, after 5 divisions, i.e. 32n in typical temperate region pines, as in the greater part of the

species). In *Pinus laricio*, in addition to the winter rest, there is a summer rest which occurs at the megaspore stage. During the summer the megaspore undergoes vacuolation but not division. The winter pause delays the completion of the life cycle till the following year. Here the plasticity of the nuclear phase of the female gametophyte is evident. In *Pinus laricio* (a Mediterranean mountain pine) the dry summer causes a summer rest.

Fig. 3 presents the reproductive cycles of the Mediterranean pines studies by FRANCINI (1953, 1958). The samples were mostly gathered in the Jonic pine-forest (*Pinus halepensis* Miller) and along the Tyrrenian coast (*Pinus pinaster* Sol. and *Pinus pinea* L.).

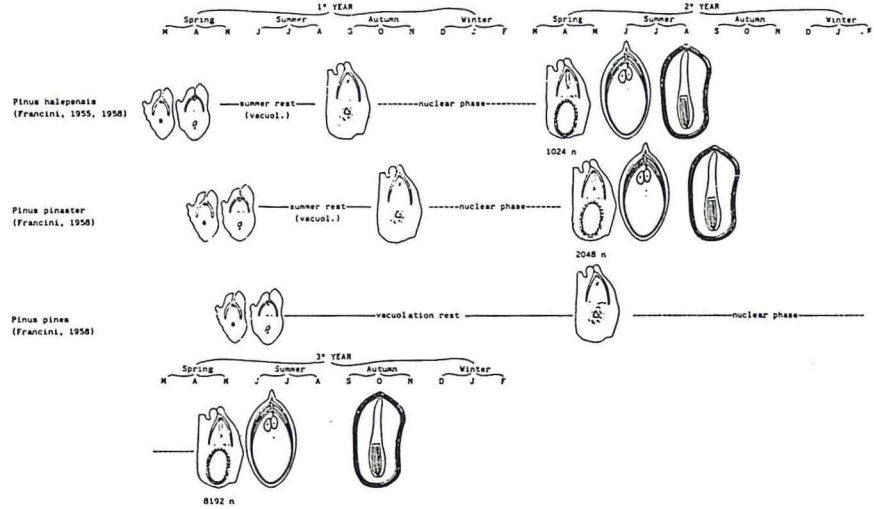

Fig. 3 — Reproductive cycles in gen. *Pinus*.

The cycle of *Pinus halepensis* is indicative of a species with typical mediterranean characteristics. The cycle presents one single interruption at the beginning of summer, during the uninucleate gametophyte stage. In autumn the conjugated divisions begin and then the slow, laborious process of the construction of the nuclear gametophyte takes place during the mild winter which allows the activity to proceed uninterrupted, so that in the summer of the following year the cycle reaches completion.

The cycle of *Pinus pinaster* is characterized, as in the above men-

tioned one, by a long summer rest during the uninucleate gametophyte stage. This pause therefore shifts the nuclear phase to the autumn-winter period. Like the Aleppo pine, the cluster pine presents a cycle which is typical of the Mediterranean species. A characteristcs which differentiates the two species is the period of pollination: earlier (i.e. March) in the Aleppo pine, later (i.e. the second half of April) in the cluster pine. This seems to be a consequence of an eastern Mediterranean climate with a longer dry season, in the first case, and of a western Mediterranean one (with oceanic influences), in the second.

The cycle of *Pinus pinea* is conditioned by the late pollination which halts the development of the uninucleate gametophyte before the summer. The long interruption of the cycle at this stage (i.e. 11 months) is followed by the nuclear phase which begins in the spring of the following year; it consists of 13 conjugated divisions and takes a year to reach completion. The cellular phase of the gametophyte, fertilization and the development of the embryo follow rapidly. Because of the two long rest (i.e. the rest at the megaspore stage and at the nuclear phase), the reproductive cycle of *Pinus pinea* requires three years to reach completion. The cycle of *Pinus pinea* though concording with that of preceding species in employing the mild winter period for the development of the nuclear phase of the gametophyte, does not present a summer rest as the Mediterranean species does (FRANCINI-CORTI, 1969, 1970).

Pines seem to have adapted to the conditions of a seasonal climate, modifying their reproductive cycle. The nuclear phase represents a plastic phase; the shorter the season suitable to the course of the reproductive processes is, then the shorter this phase is. In temperate climate with mild winters and dry summers, the greater part of the development of the nuclear phase takes place in winter; this also shows the particular need for water during this vescicular phase. The summer represents a period of inactivity. During this phase, only the vacuolation of the megaspore takes place. The latter prepares a utricle which requires water; this is the critical stage, from an ecological point of view (FRANCINI, 1958). The vacuolation phase of the megaspore is a very long process in the Mediterranean species. This marks an important stage of the cycle also because during the long vacuolation process the proliferation of the spongy tissue, which becomes multilayered, takes place. The proportion of

this tissue in the different species varies in relation to the dimensions the nuclear gametophyte reaches (FRANCINI, 1954). Said tissue shows an intense secretory activity from which the development of the endosperm and embryo benefit.

The fixed points of the reproductive biology of pines, are: earlier or later spring pollination, end of spring or beginning of summer fertilization and a rapid development of the proembryo and of the embryo in the summer.

REPRODUCTIVE CYCLES IN SPECIES OF GENUS JUNIPERUS

The Italian species of the sect. *Oxycedrus* have been studied by CIAMPI (1958a, 1958b).

Fig. 4 shows the cycles of *Juniperus oxycedrys* L., *Juniperus oxycedrus* subs. *macrocarpa* (Sibth et Sm.) Ball and the cycle of *Juniperus communis* L. s.l..

Juniperus oxycedrus and its subspecies show the two-year type reproductive cycle. The organization of the ovules takes place in autumn but pollination occurs in the middle of winter. At the end of the winter the meiotic process, the organization of the megaspore, the nuclear and the cellular phase of the gametophyte, follow quite

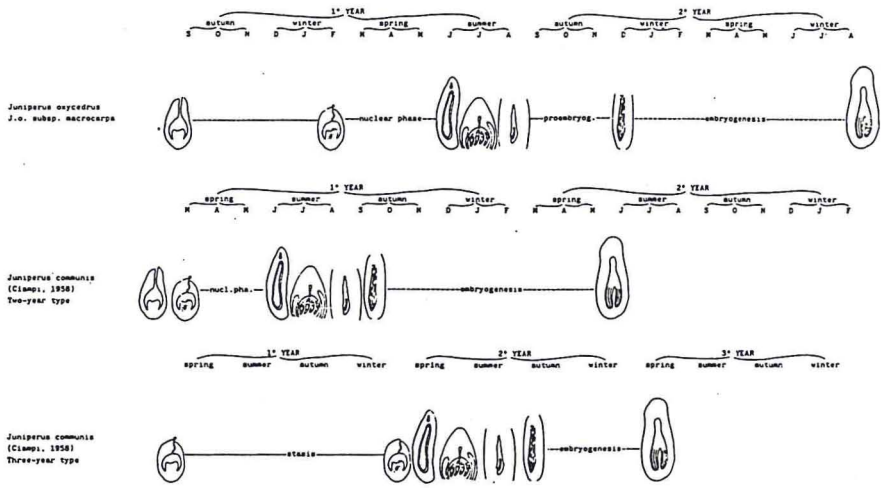

Fig. 4 — Reproductive cycles in gen. *Juniperus*.

rapidly. Fertilization takes place in the middle of summer. The post-fertilization processes are extremely slow; from the end of the summer to the beginning of the winter the zygote goes through an organizing period while awaiting the onset of climatic conditions which are favourable to the development of the embryo. In winter an embryonal mass appears, but only a year later the morphologically mature embryo is present.

The anthesis and therefore the pollination which occurs in winter reveal the Mediterranean characteristics (i.e. of a mild winter climate) of the species. The rest period at the zigote stage at the begining of the summer can be considered the answer to the dry period of the Mediterranean climate ([1]). The long period that precedes the embryogeny indicate that the biochemical processes, which in the *Pinus* are connected with the formation of the spongy tissue, are displaced, at least partially, to the post-fertilization stage in *Juniperus*.

The study of the reproductive processes in *Juniperus communis* s.l. has led to the recognition of two types of cycles: one two year type and one three year type cycle. In the former type, which is found in biotypes that live in Mediterranean climates, the chronological order of the succession of the diverse stages is the same as in the two preceding junipers, but the organization of the ovules takes place in spring. Biotypes of *Juniperus* that live in temperate climates or in mountain places present a three year type cycles. As happens in all the woody species that live in same regions, pollination takes place in spring but the development of the ovule is suspended before megasporogenesis occurs and awaits the following summer. The stage which goes from the differentiation of the mother cell to fertilization, takes place without any interruptions. In this species it is the rhythm of the sequences of the nuclear phase that is adjusted to the lenght of the propitious period, accelerating the succession of the divisions.

Also in *Juniperus* the nuclear phase is the most sensitive to the diversity of the climatic conditions. In *Juniperus communis* it lasts slightly more than one month in high mountain biotypes, and two

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([1]) A rest period at the zygote stage has been also observed in two tipical Mediterranean species: *Pistacia lentiscus* L. studied by SCARAMUZZI (1960) and *Arbutus unedo* L., studied by PACINI (1969) and VILLA (1981). In *Pistacia* the rest period is about three months long; in *Arbutus* is about six months; in this last case the reproductive cycle can be considered two-year type.

or three months in the species that live in mild climates. The possibility of delaying the initiation of the cycle after the pollination, and that of moulding the nuclear phase according to the specific conditions, are mechanisms presumably at the basis of the capacity of adaptation of *Juniperus communis* to the most varied environmental conditions and can explain the extremely vast distribution of this species.

Reproductive cycles in the species of genus Quercus

Also the reproductive cycles in genus *Quercus* show peculiar aspects in which the mode of adaptation of the species to the seasonal climate of the present distribution zones, can be traced. At the same time, the species seem to preserve signs of the original endogenous rhythm which interferes with the seasonal rhythm. Also in genus *Quercus* pollination occurs at a very early stage in the development of the reproductive organs, and for the completion of these, sometimes, quite a long period is necessary.

The studies on the reproductive cycles of the Italian species of genus *Quercus* dwell on the morphogenetical aspects and on the ecological implications of the development of the female flower. In fact, a peculiar characteristic of the flower is its incompletness at the moment of anthesis and of pollination; it consists of a simple perianth and of the sole stigmatic apparatus. An important point of the reproductive cycle of genus *Quercus* is in the rhythm of the organization of the ovary and of the ovules.

Following pollination, thanks to the impulse generated by the pollen, the appearence of the ovule primordia occurs. From the primordia stage to the ovules completion 2-3 months pass in some species, in others more than a year. In the former case the ripening of acorns occurs in the same year as pollination; if the processes are too slow, an interruption is necessary which delay the completion of the cycle to the following year.

The one year or two year type maturation of acorns, nevertheless, is constant only in some species; in others, the one year and two year type cycle occurs side by side. In this last case there is no concordance between biological and climatic events and the interpretation of the relationships between organic pauses and rest periods caused by climate, is more difficult.

Beginning with fig. 5 (cfr. FRANCINI-CORTI, 1960) which represents the most important moments of the cycle, the succession of the events of the reproductive cycles of the species studied are show. The first event is pollination which finds the female flower incomplete with only the stygmas. In the second drawing the female flower is almost complete; thanks to the growth of the base of the stigmatic apparatus, the stylus is produced. This is a complex structure that acquires,

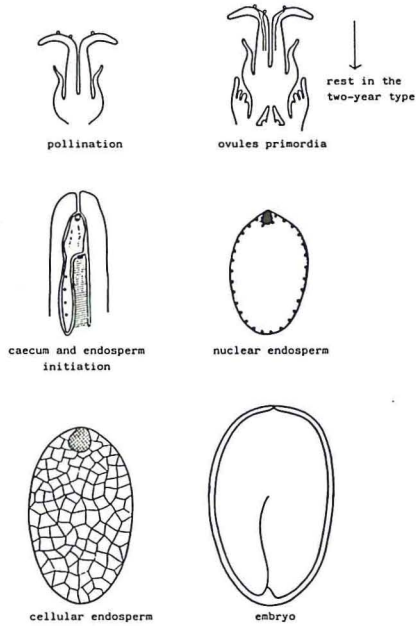

Fig. 5 — The most significant stages of the reproductive cycle in gen. *Quercus* (FRANCINI-CORTI, 1960; modif.).

in the two year maturation species, the function of a resting place for the pollen tube (CORTI, 1959). In the ovary cavity the ovule primordia have appared. This stage, characterized by the presence of the ovule primordia is an important phase in the reproductive cycle of the species of genus *Quercus* because it marks a stage of organic rest in the species having a two year type maturation of the acorn. The third and fourth drawing indicate the particular aspect that the embryo-sac assumes immediately after fertilization, when the so-called «caecum» is produced. Inside the caecum the fusion nucleus migrates and the first divisions of the nuclear endosperm take place.

The cellular stage of the endosperm and some of the first postfertilization stages are represented in the fifth drawing. In the last drawing, we have the embryo, i.e. the completion of the embryogenetic processes.

Species having a one year type cycle (fig. 6)

The cycle of *Quercus ilex* L. has been studied by CORTI (1959). This species shows quite rapid cycle from the moment of pollination (in May) to that of fertilization (in July). The completion of the embryo and the acorn ripening take place during the summer. This continuous cycle, which does not present an appreciable rest period, can be considered the answer to a Mediterranean climate with a dry period which is no too long. The species, in fact, is represented on a small scale in the eastern Mediterranean areas where the dry period is rather long.

Studies extended to trees of different latitudes and altitudes show that, in this species, the cycle is rather rigid and that the ecological plasticity of *Quercus ilex* mountain biotypes, cannot be attributed to a plasticity of reproductive cycle but probably to the action of polygenes (CORTI, 1958a, 1959).

The cycle of *Quercus pedunculata* Ehrh, is a one year type too. Observations undertaken by CORTI (1968) in the Selva Pisana have consented the comparison of moments of the reproductive cycle of

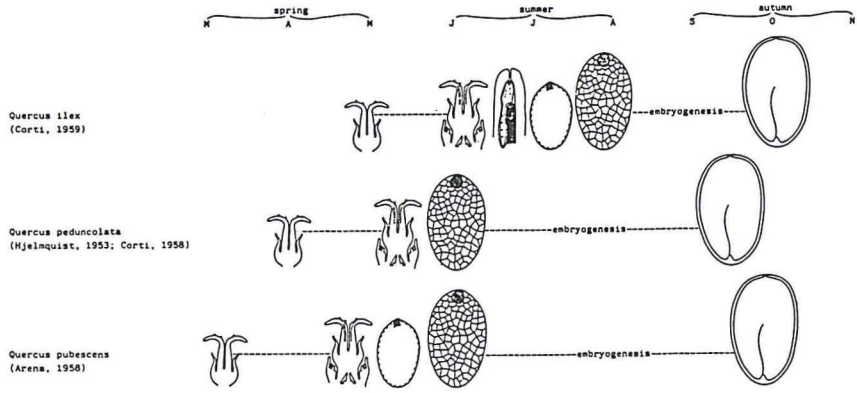

Fig. 6 — Reproductive cycles in gen. *Quercus*.

Quercus pedunculata in that area, with the cycle of the same species studied in southern Sweden by HJELMQUIST (1953). The Tuscan trees show an anticipation of the onset of the cycle due to early flowering, but the course of the cycle remains the same. In Tuscany, flowering and consequent pollination occur in mid April; at the end of May zygote and nuclear endosperm are present. The time lapse between pollination and fertilization is about 45 days. The embryogeny occurs during the summer; the acorns are morphologically mature at the end of the season.

The cycle of *Quercus pubescens* Willd. was studied by ARENA (1958). The flowering and pollination occur in mid-March, fertilization at the end of May; embryogeny is completed at the end of June. Pollination and fertilization are separated by a time lapse of about two months; the ripening of the acorns takes about six months (from May to October). The early flowering and the continuous succession of processes, indicate that *Quercus pubescens* has adapted to a climate with an early spring which enables a rapid completion of the most delicate phases of the cycle.

The three species examined present a one-year reproductive cycle which is continual. It can be considered a rapid cycle if we think of the laborious morphogenetic processes required for the construction of the ovary, between pollination and fertilization. The cycle of *Quercus ilex* has many features in common with that of the broadleaf-deciduous species which are typical of temperate climates. In the latter the rapid cycle is established presumably because of a distinct winter season which shortens the vegetative period (SCHARFETTER, 1953; CORTI, 1959). None of the three cycle examined have an organic rest period; the impulse that derives from the pollen induces a morphogenetic activity which leads, after a short time, to the completion of the flower. Pollination and fertilization are separated by a lapse of time which varies from one month and a half to about two months; the maturation of the acorns takes place during the summer.

Species having a two-year type cycle

The cycle of *Quercus trojana* Webb. studied by BIANCO (1961) is shown in fig. 7. The essential features of the reproductive cycle of this species are: flowering, pollination, ovary and ovule primordia

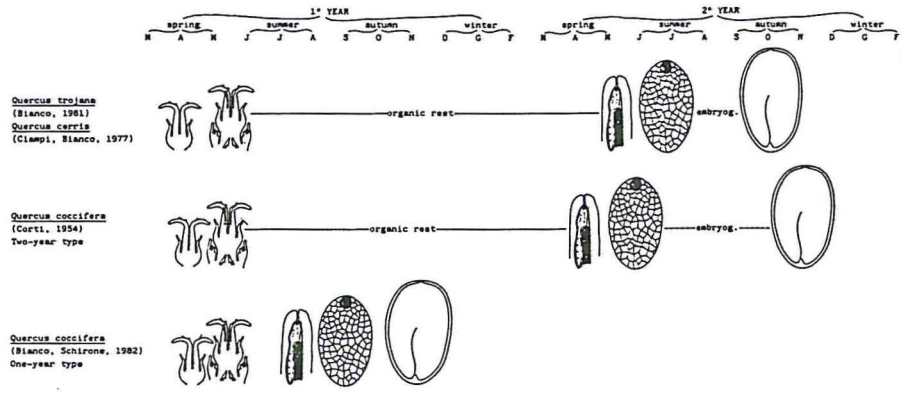

Fig. 7 — Reproductive cycles in gen. *Quercus*.

development during spring. In June the cycle is interrupted; the ovule development is resumed in the spring of the following year, after a lapse of about 11 months. Then the cycle continues without pauses until the acorns reach maturation in October.

This species has a two-year type reproduction cycle with a period of inactivity at the beginning of the summer of the first year in relation to the period of summer drought, which is very marked in the eastern Mediterranean climate.

The cycle of *Quercus cerris* L. was studied by CIAMPI and BIANCO (1977) in Tuscany and in Apulia.

The reproductive cycle of *Quercus cerris* is characterized by a time lapse between pollination and fertilization which is prolunged for more than a year. But in *Quercus cerris* the long period of inactivity is not completely explicable on the basis of climatic factors. During this period (end of May, beginning of June) the climatic conditions are still favourable to the development of the ontogenetic processes.

The period of inactivity which occurs in oak trees at the primordia stage of the ovules, and which can determine the type of the reproductive cycle (one-year or two-year type), seems to have originate with the setting into motion of an endogenous mechanism at a precise moment during development. This mechanism can occur even when the climatic conditions seem to be favourable to the continuation of the cycle. At the same time, it allows the preservation of the potentialities which induce the resumption and the continuation of the ontogenentic processes.

Species having a mixed cycle

The cycle of *Quercus coccifera* L. (fig. 7).

CORTI (1954) described a two-year cycle for *Quercus coccifera*. In the same species biotypes having a one-year type cycle with spring flowering, a one year type cycle with autumnal flowering and a two-year type delayed cycle have been reported (BIANCO and SCHIRONE, 1982).

The two-year type cycle begins in late spring. A period of inactivity at the ovule primordia stage, begins towards the end of May; it terminates at the end of March of the following year. Fertilization, endosperm development and embryonic processes end in October.

In *Quercus coccifera* (Apulia), flowering occurs several times during the year and it has been ascertained that often it marks the beginning of reproductive cycles which take place side by side with the two-year cycle.

The one-year cycle with flowering and pollination in spring, is continuous and does not have an organic pause. In the one-year type cycle with flowering and pollination in autumn, fertilization occurs slightly later; in spring, the ripening of the acorns is simultaneous with those of the two-year type cycle. There is a period of inactivity in the two-year type delayed cycle which terminates in autumn instead of March.

The cycle of *Quercus suber* L. (fig. 8).

This cycle was studied by CORTI (1955) on samples from several localities. The cork-trees populations oftentimes show a two-year type cycle. Flowering occurs at the beginning of May; rest begins at the primordia stage of the ovules in June and continues until April of the following year. In the biotype which has a one-year type cycle, ovule development resumes after just one month of inactivity. It has been reported that also a so-called late one-year cycle exists. In this type, acorn maturation occurs in the middle of winter; the inactivity which precedes ovule development continues for about two months.

The cycle of *Quercus aegilops* L. (fig. 8).

This cycle was studied by SCARAMUZZI (1960) at Tricase (Lecce). The trees growing in this locality are attributed to the *macrolepis* subspecies, which is the most widespread in the eastern region; it presents mixed byotypes. The majority of these presents a two-year

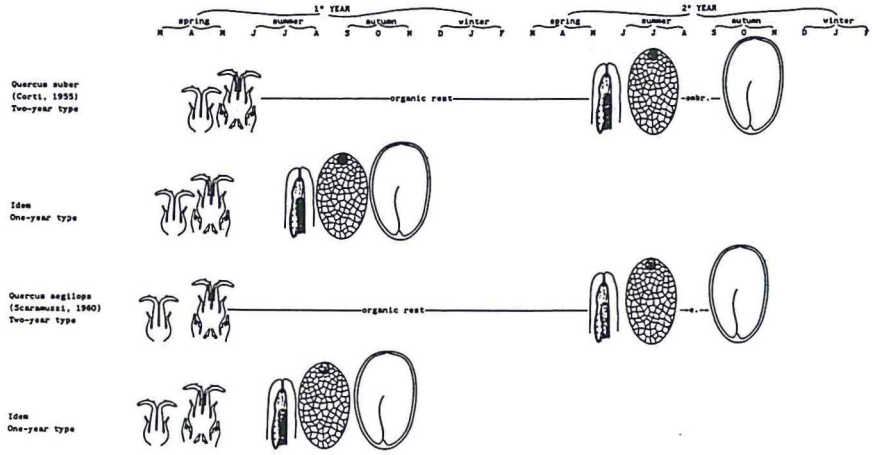

Fig. 8 — Reproductive cycles in gen. *Quercus*.

type cycle; in these the pause at the ovule primordia stage lasts 11 months. In the one-year biotype the period of organic inactivity is non-existant: the cycle is continuous and reaches completion during the same year as pollination.

In the genus *Quercus* the meaning of the one-year or two-year ripening of the fruits in the species which have a constant cycle, becomes clear when concordances occur between the rhythm of the biological events and the climatic rhythm. In these cases one can deduce that one-year type cycle species as well as the two-year type cycle species represent the conclusion of diversified processes of evolution. The former type, by shortening the stages of the cycle, makes the development of the reproductive processes continuous; the latter, by introducing a period of inactivity, leads to the two-year type cycle. This pause always occurs when the ovules are at the primordia stage during which, presumably, the impulse derived from the pollen exhaustes itself (Corti, 1955; Francini-Corti, 1960). The resumption of ovule development in the spring of the following year, enables certain species and certain biotypes to accomplish their reproductive processes even in climates with short vegetative periods.

The interpretation of mixed cycles and their multiple range of variability is more difficult. The species which have mixed cycles generally grow in relatively low latitudes where the climate has not as defined a winter period as that of the higher latitudes. It is

thought, for example, that *Quercus suber* evolved in a Mediterranean climate with oceanic influences. This climate is particularly conservative as regards primitive characteristics and favours the survival of long cycles. The differentiation of biotypes with one-year as well as two-year maturation acorns has allowed a vast distribution from the shores of the Atlantic Ocean to the Italian peninsula and to Tunisia (CORTI, 1955; FRANCINI-CORTI, 1960).

Quercus aegilops, a European east mediterranean species, presents cycles like that of *Quercus suber*, but even less variable. The species shows some primitive characteristics in the western part of its Mediterranean area. Because of the more continental climate with its longer dry summer period, the two-year biotype was favoured (FRANCINI-CORTI, 1960) in the eastern area.

In *Quercus coccifera* (Apulia), flowering and the other stages of the reproductive cycle seems controlled by endogenous rhythm and therefore are not related to seasonal cycles. The phenomena observed in *Quercus coccifera* (Apulia) may be interpreted as the reappearance of ancestral characteristics in a Region of genetic instability. This Region is the meeting-place of the eastern and western biotypes and, from a climatic point of view, is favourable to the development of these cycles (BIANCO and SCHIRONE, 1982).

The interpretation of the biological meaning of different cycles in relation to the origin of the species and the history of its evolution, seems to convalidate the hypothesis advanced by SCHARFETTER (1953) suggesting a tropical origin of the genus. In genus *Quercus* it is very likely that the species which have a slower organization of the ovules correspond to an ancestral development model, which is associated with a uniform climate and controlled by an endogenous rhythm which does not disappear even when the species grows in a temperate climate.

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