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An integrated study of bud development and phenology enhances our understanding of coexistence and reproduction in two Mediterranean *Quercus* species

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Abstract. Vegetative growth is a two-phase process involving slow cell division followed by potentially rapid cell expansion. In seasonal climates, trees adjust these developmental sequences to exploit favourable growth periods optimally. However, elucidating the precise mechanistic links between environmental drivers and developmental processes in trees remains challenging.

Detailed analyses of apical bud organogenesis, and phenology, are used to study the coexistence of the evergreen *Quercus ilex* L. subsp. *ballota* (Desf.) Samp. and the deciduous *Q. faginea* Lam. at a Mediterranean site where both co-occur. Phenological and organogenetic patterns proved similarly highly synchronised in both species, but bud burst was later in *Q. ilex* than in *Q. faginea*. Nevertheless, in both species, organogenesis commenced in early spring (bud swelling or bud burst) and had finished by mid-September, with bud development completed by November. Winter buds contained fully preformed embryonic shoots with well-developed male inflorescences and initiated female inflorescence meristems.

The results suggest that organogenesis and shoot extension may compete for resources during summer, potentially explaining the alternating pattern of years of vigorous primary growth observed in *Q. ilex* but not in *Q. faginea*. Moreover, the unexpectedly early initiation of female inflorescence meristems in both species – relative to key phases of bud and fruit development – suggests that the advanced stages of fruit development described in mast years may overlap with the initiation of inflorescence meristems and the formation of new buds. This could explain the occurrence of smaller buds and reduced flowering in the year following mast events – a pattern not observed in years of normal fruiting.

1 Introduction

Earth's vegetation is classified into biomes primarily shaped by climate (Walter, 1977). Within each biome, species exhibit structural and physiological adaptations to their native environments, which may constrain their success elsewhere. Climate change threatens to disrupt these equilibria, particularly in vulnerable regions such as the Mediterranean basin, a recognised biodiversity hotspot (Lionello and Scarascia, 2018).

The Mediterranean climate is characterised by two stress periods (winter frost and summer drought) and two favourable seasons for plant growth (spring and autumn) (Gil-Pelegrín et al., 2017; Mitrakos, 1980). Trees must adjust their phenological sequences to maximise the use of these favourable periods (Misson et al., 2011). However, phenological cycles cannot be perfectly aligned with these brief periods, and trees are unable to develop all organs simultaneously. This results in resource competition among meristems under limiting conditions (Polák et al., 2006). These com-

plex constraints give rise to trade-offs (Bazzaz et al., 1987; Begon et al., 2003; Obeso, 2002; Silvertown and Lovett Doust, 1993; Stearns, 1989) and necessitate prioritisation in resource allocation (Génard et al., 2008; Le Roncé et al., 2020; Suzuki, 2001; Wiley and Helliker, 2012).

Phenology plays a central role in integrating developmental processes (Delpierre et al., 2017; Vitasse et al., 2009), enabling, in response to environmental cues, growth during favourable periods and dormancy during adverse ones. However, identifying mechanistic links between environmental drivers and developmental responses remains a key challenge (Laube et al., 2014; Misson et al., 2011).

Summer water availability is widely regarded as the critical factor for the survival of *Quercus* species in the Mediterranean (Limousin et al., 2009; Montserrat-Martí et al., 2009; Rambal et al., 2003). Physiologically, the evergreen habit is advantageous, allowing year-round carbon assimilation and greater resilience to climatic and edaphic stress, whereas the deciduous habit mitigates winter stress (Escudero et al., 2017; Gil-Pelegrín et al., 2017). However, from a phenomorphological perspective, neither habit is particularly optimal, as Mediterranean *Quercus* are physiologically active plants in summer (Orshan, 1989), developing certain organs during the dry summer (Alla et al., 2012; Montserrat-Martí et al., 2009). To cope with water scarcity, deep roots facilitate subsoil water uptake (Orshan et al., 1989). In addition, summer-active meristems are protected by bud scales (buds), scaly cupules (immature acorns in July and August), or bark (cambium), or are buffered by access to the soil moisture (fine roots), thereby reducing the risk of desiccation (Alla et al., 2013). As a result, summer growth in *Quercus* species is restricted to well-protected organs that maintain meristem and primordia turgor, enabling extension growth (Hsiao and Xu, 2000; Palacio et al., 2008). In contrast, the growth of unprotected organs, such as additional growth units (lammas shoots), is limited (Montserrat-Martí et al., 2009) and more frequent in wet summers (Hover et al., 2017). In the Mediterranean climate, the effective coordination of vegetative and reproductive growth requires precise timing and resource allocation among organs. However, significant knowledge gaps persist, particularly regarding organogenesis (Puntieri et al., 2002; Sabatier et al., 2003) and the adjustment of organ-specific growth under variable climatic conditions. Fundamental to understanding these adjustments is the nature of growth itself, as a plant's response to climate is intrinsically linked to the mechanisms of growth. The primary growth of plants is the consequence of two general and well-coordinated morphogenetic events: organogenesis and extension. The initiation of new organs (organogenesis) is the product of undifferentiated cells conforming the apical meristem (Barthélémy and Caraglio, 2007). New cell production involves two stages: (a) cell division, which is comparatively slow and highly sensitive to low temperatures (Francis and Barlow, 1988; Körner, 2021, 1991); and (b) cell expansion, including vacuolation, which can increase cell volume 10- to 20-fold (Taiz, 1992), and may proceed under colder conditions. Consequently, cell division is usually the growth-limiting step, giving rise to a spectrum of climate-driven growth strategies. At one extreme is "continuous" growth, where cell division and expansion follow successively to produce most of the annual biomass. At the other, under short or suboptimal growing seasons, these stages may occur separately, leading to "stored" growth. Many species, including *Quercus* spp., follow an intermediate strategy, with part of the meristematic growth stored and protected in overwintering buds.

This study investigates the influence of summer drought on development in the evergreen *Quercus ilex* subsp. *ballota* (Qi) and the deciduous *Q. faginea* (Qf), with a focus on their seasonal adjustments in organ growth. To this end, we integrate two key and complementary approaches: (i) organogenesis, which identifies the timing of organ initiation and development in different bud types; and (ii) phenology and phenomorphology, which examine the timing of phenophases and morphological changes in plants and their organs in natural populations (Orshan et al., 1989).

We address two general objectives: (1) to integrate the information on canopy phenology and organogenesis in the apical buds of *Qi* and *Qf*; and (2) to examine the overlap in the growth of canopy organs in order to infer potential competition among them, specifically (a) whether fruit development overlaps with the initiation and development of vegetative and reproductive primordia, (b) whether this overlap affects vegetative and reproductive growth in the following year, and (c) whether the more proximal position of female inflorescences in *Qi*, compared to *Qf*, influences these interactions.

In line with these objectives and based on previous research (Fig. 1), we address two hypotheses concerning the following growth and developmental processes.

1. *Competition between organogenesis and shoot extension.* It is hypothesised that these processes may compete for resources when they overlap temporally. This competition is expected to be more limiting in summer, particularly for the evergreen (Qi), which initiates bud burst later and requires a longer period for shoot development than the deciduous (Qf). The overlap between shoot and bud development during the summer may account for the alternating pattern of high and low primary growth observed in Qi but not in Qf (Montserrat-Martí et al., 2009). In Qf, early bud burst and rapid shoot extension may result in the peak phase of bud development (labelled "3" in Fig. 1) occurring during a prolonged period of reduced resource competition (i.e. reduced overlap), thereby supporting more regular annual bud development. Conversely, in Qi, this peak phase is expected to be considerably shorter due to the later completion of shoot growth and leaf hardening.

2. *Synchrony between female inflorescence initiation and bud/fruit development.* In both species, the initiation of female inflorescences is expected to coincide with critical phases of bud and fruit development, potentially leading to resource competition. This may explain the smaller buds and reduced fruit production typically observed in the year following a mast year (Camarero et al., 2010; Gordon et al., 2006; Koenig and Knops, 2000; Sharp and Sprague, 1967; Sork et al., 1993).

2 Material and methods

The data and materials used in this study were derived from a long-term phenological research programme (1997–2010) conducted on the same populations of the two coexisting *Quercus* species. Previously published findings from this programme (Alla et al., 2013; Montserrat-Martí et al., 2009) provided the temporal framework for identifying key phenological events (see Fig. 1).

2.1 Target species

Quercus ilex L. is an evergreen oak tree that is widespread in the western Mediterranean basin (Barbero et al., 1992). Two subspecies occur on the Iberian Peninsula: subsp. *ilex*, found mainly near the coast; and subsp. *ballota* (Desf.) Samp. (*Q. rotundifolia* Lam.), hereafter referred to as Qi, which predominates in inland and more continental areas (Amaral Franco, 1990). *Quercus faginea* Lam. (Qf) is deciduous and widely distributed in Mediterranean and sub-Mediterranean regions within the Iberian Peninsula (Amaral Franco, 1990). It frequently coexists with Qi in northeastern Spain, but Qf is more typical of moister habitats (Castro-Díez et al., 1997). Putative hybrids between Qf and *Q. humilis* are common and are generally assigned to *Q. cerrioides* Willk. and Costa (Gobierno de Aragón, 2026). In our study population, the morphological characteristics of Qf predominate. Although this group of oaks remains in need of further taxonomic clarification (Aissi, 2023; Amaral Franco, 1990), for simplicity, we treat all individuals as Qf sensu lato.

2.2 The study site

The study site is located on an almost flat, south-facing slope near Agüero (Huesca) in northeastern Spain (42°18′ N, 0°47′ W, at 750 m a.s.l.). The climate is continental Mediterranean, with an average annual rainfall of 635 mm; spring and autumn are the wettest and most favourable seasons for plant growth, whereas winter is cold and relatively dry, and summer is hot and very dry; the mean minimum temperature is 4.3 °C in the coldest month (January), and the mean maximum temperature is 28.4 °C in the hottest month (July) (data from the nearest meteorological station, Ayerbe, 42°16′ N, 0°41′ W, at 585 m a.s.l.). Further details of the study site, climate, and populations are presented in Montserrat-Martí et al. (2009) and Alla et al. (2013).

The soil is a Calcisol (FAO, 2026), formed on Miocene clays overlying calcareous sandstone bedrock. The vegetation consists of open, tall scrub with scattered trees, dominated by a mixture of Qi, Qf, *Arbutus unedo* L., and *Pinus halepensis* Mill. Most trees and large shrubs are multi-stemmed, a consequence of past firewood gathering and clearing fires; however, these activities ceased in the 1970s.

Our studies were conducted on a small plot (800 × 100 m) where both soil and vegetation appeared homogeneous, with no evident lateral inputs of water or nutrients. The plot contained over 60 adult trees of each oak species, evenly distributed, with no evidence of habitat segregation.

2.3 Phenological measurements

In the phenological study of the two species, only canopy phenophases that are visually discernible were considered. Phenological sampling was conducted from December 1996 to October 2006 (with some results summarised in Montserrat-Martí et al., 2009) and from January 2006 to December 2009 (unpublished data). During the second study period, 15 individuals of both Qi and Qf were selected. All trees were well developed with clearly visible crowns, a prerequisite for accurately assessing the percentage occurrence of each phenophase. For multi-stemmed trees, only the branches of the trunk considered most representative were measured. Where necessary, binoculars (8 × 42) were used to inspect inaccessible parts of the canopy.

Sampling was carried out monthly, except in spring, when it took place every 2–3 weeks. At each sampling event, several branches of each species were preserved in a phenomorphological herbarium, providing a historical record and allowing for future verification when necessary (Orshan et al., 1989).

The phenophases adopted were defined as follows: 0: winter dormancy. 1: swollen buds (the onset of this phenophase was difficult to determine in both species due to the subtle early stages of bud swelling). 2: bud burst (from the beginning of bud opening, when leaves or male inflorescences became visible, until part of the stem starts to emerge). 3: vegetative growth of shoots (from the end of phenophase 2 until stem elongation ceased and tender leaves were fully extended). 4: formation of scaly buds (from the end of phenophase 3, when tender hypsophyllary buds were present, until scaly buds became visible). 5: presence of growing scaly buds (buds actively growing until around November, when they entered dormancy and returned to phenophase 0). 6: swelling of buds of the additional growth units (following the same criteria as phenophase 1). 7: bud burst and vegetative growth of the additional growth units (as in phenophases 2 and 3). 8: formation of scaly buds of the additional growth units (as in phenophase 4). 9: pre-flowering (the period when flower buds were visible to the naked eye, starting with

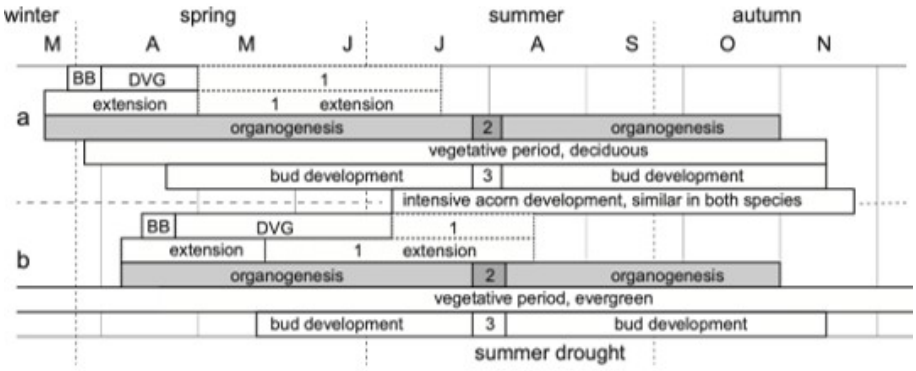

Figure 1. Temporal representation of phenophases, events, and key hypotheses for **(a)** *Quercus faginea* and **(b)** *Q. ilex* subsp. *ballota*. BB – budburst, DVG – shoot vegetative growth, 1 – additional shoot growth (lammas shoots, generally less significant than DVG), 2 – expected timing of female flower initiation, 3 – period of maximum bud development. Shaded in grey are hypothetical assumptions for which insufficient information is available (organogenesis and 2). The phenophases indicated in the figure correspond to the classes used in this study (see the material and methods section for further details), as follows: BB = 2, DVG = 3, additional shoot growth = 6 and 7, and bud development = 4 and 8. Organogenesis is the period of primordia initiation, and extension is the period of primordia growth up to their final size. Data sources: Montserrat-Martí et al. (2009) for phenology; Alla et al. (2013) for bud development. Secondary stem growth is not included in the graph.

the emergence of male inflorescences and ending with the last flower bud at the end of flowering; primarily assessed through observation of conspicuous male flowers). 10: flowering (presence of male and/or female flowers at anthesis). 11: fruit development (presence of pollinated female flowers or developing fruits). 12: fruit dispersal (shedding of ripe, viable fruits). 13: senescence and death of leaves. 14: dry leaves remaining on canopy branches.

At each sampling time, the percentage of the crown exhibiting the 14 phenophases was estimated. Tree crowns were subdivided into four to six subunits, and within each, a visual assessment was made of the proportion of branches displaying the respective phenophases. Data from all subunits were then averaged to obtain a mean phenophase value, which was summarised in phenophase diagrams.

2.4 Leaf, stem, and apical bud traits

From 2006 to 2010, 20 current-year leaves were collected at random in mid-July from each of the 15 replicate trees of each species. We collected leaves on 3-year-old medium-sized branches from the sun-exposed area of the crown, at approximately mid-height. The mean individual leaf area (LA, mm^2) was measured using a digital leaf area meter (Delta-T Devices Ltd, Cambridge, UK) connected to a Skye Analysis System (SkyeLeaf 1.11, Powys, UK). Leaves were then oven-dried at 60 °C to constant weight, and their leaf mass per unit area (LMA, $mg\,cm^{-2}$) was calculated.

In January, buds were randomly harvested from 30 to 40 medium-sized shoots located in the sun-exposed mid-crown region of each tree. Buds were subsequently oven-dried at 60 °C and weighed individually.

2.5 Organogenesis

Plant organogenesis and phenology are closely related aspects of plant biology: organogenesis concerns the development of organs from meristems, whereas phenology addresses the relationship between phenophases (developmental stages) and environmental factors. The temporal pattern of organogenesis may also be regarded as a phenological event. To avoid overlap and confusion between these processes in the phenological analysis, only visually distinguishable phenophases were considered.

Since the leaf units were very densely packed within the small buds, the complete dissection of even a single bud proved to be an extremely labour-intensive task. For this reason, the study was limited to a single year, from January to December 2007, and included only two replicate individuals per species (Qi-1, Qi-2, Qf-1, and Qf-2) (Table 1). Within both populations, many individuals flowered infrequently and produced few acorns. Accordingly, the selected individuals were among the fruit-bearing trees in the population, to ensure that the initiation and development of reproductive structures within the developing buds were represented in the material sampled.

To maintain consistency, two additional selection criteria were applied. First, measurements were confined to a single zone within the canopy: 3-year-old medium-sized branches from the sun-exposed area of the crown, at approximately mid-height. Second, only buds from medium-sized shoots were sampled.

Typically, four to five 3-year-old branches were collected from each tagged individual during each visit. These branch samples yielded approximately 25–40 medium-sized shoots bearing viable apical buds. Samples were dried at 50–60 °C

Table 1. General information on the four trees studied for organogenesis. Maximum tree height (m) was measured at the beginning of the study, in January 2006. AB: dry weight of apical buds (mg); St: stem length (mm); LA: leaf area (mm^2); LMA: leaf mass per area ($mg\,cm^{-2}$). The number of recorded items over the 5-year period (2006–2010) is shown in parentheses. Values are presented as means ± standard error. Significant differences between individuals are indicated by a difference in capital letters using a multiple comparisons test ($P<0.05$).

	Qi-1	Qi-2	Qf-1	Qf-2
Max height (m)	3.7	5.0	8.3	6.0
AB (mg)	1.47 ± 0.16 C (40)	4.07 ± 0.31 C (50)	12.44 ± 0.69 A (50)	9.70 ± 0.64 B (50)
St (mm)	39.7 ± 0.91 A (488)	45.1 ± 0.81 A (663)	33.1 ± 0.85 B (310)	37.8 ± 1.34 B (191)
LA (mm^2)	334.7 ± 12.29 C (100)	297.9 ± 6.45 C (100)	908.9 ± 20.07 A (100)	746.2 ± 18.27 B (100)
LMA ($mg\,cm^{-2}$)	22.9 ± 0.33 A (100)	23.5 ± 0.32 A (100)	13.2 ± 0.13 C (100)	14.3 ± 0.16 B (100)

and preserved. As the sampled individuals were large, the collected branches represented only a minimal proportion of the above-ground biomass. As a result, continuous collection of plant material throughout the study period did not cause any observable growth response to branch removal.

Prior to subsequent measurements of bud contents, shoots were rehydrated for 12 h at 4 °C, or until all bud components closely resembled the turgor and texture of fresh buds. Apical buds were then excised, with three replicates per tree per sampling occasion. Apical buds from additional growth units were too poorly represented to be included.

Dissection and measurement of the size and number of each organ within the bud were performed at 10–100× magnification under a stereomicroscope (Leica MZ125; Leica Microsystems, Heerbrugg, Switzerland) equipped with a digital camera (Leica DFC295) and an ocular micrometer.

The criteria of Nitta and Ohsawa (1998) and Ohsawa et al. (2011) were followed to distinguish the types of protective organs present in the apical buds. A growth unit produced by a scaly apical bud comprises several foliar organs, arranged from proximal to distal as scales, cataphylls, photosynthetic foliage leaves, and hypsophylls. Scales, cataphylls, and hypsophylls primarily serve protective functions. Scales and their associated internodes remain unchanged during budburst, whereas cataphylls and their internodes undergo some elongation. Hypsophylls are produced at the distal end of the growth units and gradually decrease in size towards the apex. By the winter bud stage, hypsophylls are typically desiccated and often severely damaged, precluding further development during subsequent budburst.

To determine the precise number of leaf units of each type, we followed the methodology of Ohsawa et al. (2011), examining buds at the swollen and budburst stages. In addition, we analysed the shoots bearing all dissected apical buds to accurately determine the number of cataphylls, foliage leaves, hypsophylls, and reproductive structures included in the buds from which they originated. Although node counts within the buds were reasonably accurate, distinguishing between scales (S) and cataphylls (C) was often difficult; therefore, these categories were combined into a single group: S + C.

2.6 Statistical analysis

Differences over time in the composition of vegetative and reproductive structures were assessed using the *emmeans* function (version 1.4-13) from the *emmeans* package in R (Lenth et al., 2026), with individual trees and year (only in Table 2) as fixed factors. Estimated marginal means were obtained via a linear regression model. Differences among individuals were assessed by ANOVA, and when differences were significant, we used a multcomp package (Hothorn et al., 2008) to assess multiple comparisons. The relationship between apical bud length and leaf primordium length was also examined using linear regression, with months and individuals included as random factors, and the significance of differences was assessed using ANOVA. All statistical analyses were conducted using R version 4.0.2 (R Core Team, 2023).

3 Results

3.1 General features

3.1.1 Characteristics of species and replicates

Quercus ilex subsp. *ballota* and *Q. faginea* differed in trait expression (Table 1). Both replicates of Qi exhibited smaller buds and leaves, longer twigs, and a higher leaf mass per area compared to Qf. Some intraspecific variation was also observed (Table 1): Qi-1, a relatively short tree with small apical buds, exhibited moderate fecundity during the study period. In contrast, Qi-2, a taller tree with larger buds, produced numerous acorns. This tree bore large, elongated leaves that represented the extreme of leaf variation among individuals in the population (Fig. 2). Similarly, Qf-1, a vigorously tall tree with large buds and leaves, differed from Qf-2, a moderately sized tree with slightly smaller buds and leaves. However, both Qf replicates produced many acorns.

3.1.2 Bud size and contents

The two *Quercus* species differed in bud size and in the number of leaf units per bud. Qf generally produced more nodes in its larger buds than Qi, despite Qi having more leaf pri-

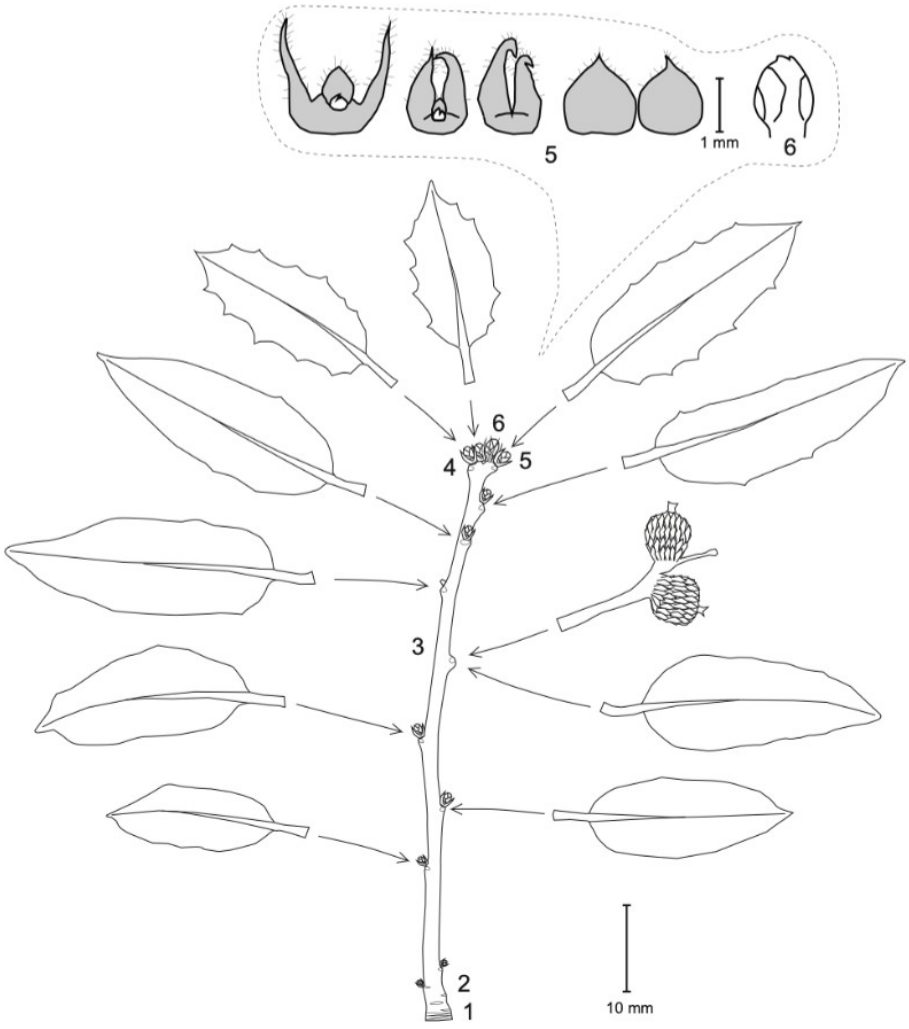

Figure 2. Diagram of a current-year shoot of Qi-2. The branch was collected on 6 July 2012 and had 24 nodes. All buds were in the process of transitioning into scaly buds, with tender and actively developing bud organs. Diagrams are drawn to scale. 1 – scale scar zone: region of scars with no appreciable axillary buds. 2 – cataphyll scar zone: five male inflorescence scars on the proximal nodes and two axillary buds (0.7 mm) on the distal nodes. 3 – zone of long internodes: seven leaves, five axillary buds (1.0–1.6 mm), one infructescence, and one aborted female inflorescence. 4 – subapical zone: three leaves and three subapical buds (1.3–1.4 mm). 5 – hypsophyll zone: four nodes, two hypsophylls with axillary buds (0.3 mm), and two pairs of stipules without axillary buds. Drawings of the hypsophylls are shown at the top of the figure, shaded mostly in grey to indicate dryness. 6 – apical bud: (1.4 mm) containing 14 nodes or leaf units. The apical meristem is actively engaged in organogenesis, initiating leaf primordia. A drawing of the apical bud is shown in the upper right of the figure.

mordia and a similar number of hypsophylls (Table 2). Differences were also observed between the two individuals of each species (Table 2). The number of nodes showed some variation among individuals, years, and branches in each plant. Moreover, the leaf primordia in the winter buds of Qf were notably longer than those of Qi, with a tendency for larger buds to contain longer leaf lamina primordia (Table 3).

In the analysis of bud contents carried out on two individuals per species throughout 1997, a total of 123 buds of Qf and 111 of Qi were fully dissected down to the apical meristem, and all their components – including leaf blades and stipules, axillary meristems and buds, reproductive primordia, and the apical meristem – were measured.

The scaly buds of both oak species contained numerous leaf units, each comprising two stipules and often an axillary vegetative bud or an inflorescence primordium. The apical buds consisted of the following elements arranged in sequence: outer protective scales, followed by cataphylls, then leaf primordia, and finally hypsophylls. An apical bud generates a complete growth unit, as illustrated by the Qi-2 branch in Fig. 2.

By the end of organogenesis in late summer, the bud contained the entire preformed shoot for the following year,

including axillary buds and male inflorescence primordia. However, the hypsophylls, distal axillary buds, and female inflorescence primordia exhibited little or no differentiation.

3.1.3 Position of inflorescences

The position of female inflorescences along the shoot axis varied between and within both species. In Qi, female inflorescences were typically formed in the axils of mid to distal leaves, generally between the second and ninth leaves below the proximal hypsophyll, and most frequently between the fourth and seventh leaves. Conversely, Qf produced female inflorescences in the axils of distal leaves, occasionally in the axil of the proximal hypsophyll – specifically between the axil of the proximal hypsophyll and that of the fifth leaf – but most commonly in the three distal leaves. Hence, the apical meristems of Qi initiate the leaf primordia associated with female inflorescence meristems earlier than those of Qf.

In both populations studied, male inflorescences were consistently observed in the axils of cataphylls, and occasionally in those of small leaves or intermediate forms between cataphylls and leaves. Buds containing four or more male inflorescence primordia showed a slightly higher average number of cataphylls compared with other buds, although the differences were not significant (data not shown).

3.2 Phenology

The phenological cycle of Qi commenced between mid-April and early May, with most vegetative and reproductive phenophases peaking in spring. By summer, Qi had already formed most of its scaly buds, reached peak bud development, and completed approximately half of its maximum fruit growth period. The second half of active fruit development, along with the cessation of bud development, occurred in autumn (Fig. 3b, c). In contrast, Qf initiated its phenological cycle between mid-March and early April, approximately 1 month earlier than Qi. Most peaks in its vegetative and reproductive phenophases also occurred in spring. During summer, Qf exhibited peaks in bud and fruit development only later in the season. Autumn marked the conclusion of active fruit and bud development (Fig. 4b, c). These phenological patterns were consistently observed throughout the 2006–2009 study period.

In both species, additional summer growth occurred in 5 %–10 % of branches, primarily in the upper canopy zone (Figs. 3b, 4b). This growth typically occurred in ≥ 5 % of crown branches and occasionally in up to 80 % of branches, as recorded for Qf-1 in 2008. Among the four individuals studied in 2007, such growth was observed in only 5 %–10 % of branches (Figs. 3b, 4b).

3.3 Organogenesis

The two replicate individuals within each species gave very similar results (Table 2, Figs. A1–A4). Therefore, in Figs. 3 and 4, only the data for individuals Qi-2 and Qf-2 have been presented. The results from the stem analyses were consistent with those obtained from their dissected apical buds (Table 2). Phenological and organogenetic patterns were found to be strongly interconnected (Figs. 3, 4). Organogenesis appeared to commence during bud swelling in Qf and at the onset of bud break in Qi, ceasing in both species by the end of summer, whereas bud growth continued until November (Figs. 3a, 4a).

3.3.1 Vegetative organogenesis

Vegetative organogenesis commenced in spring with the initiation of the first leaf unit, consisting of two scales. Subsequently, the remaining leaf units were initiated (Figs. 3a, 4a, A1–A4). Comparable numbers of scales and cataphylls were produced, each corresponding to a stipule of its respective leaf unit. All scale units failed to develop lamina and generally also lacked an axillary bud. Moreover, early in their development and following exposure, scale units hardened to form most of the outer covering of the scaly bud. Cataphyll units usually did not produce lamina, except for distal ones, where a small lamina was occasionally formed. Each cataphyll unit contained an axillary meristem capable of developing into either an axillary bud or a male inflorescence. Subsequently, leaf primordia developed, producing two stipules, a leaf lamina, and a new axillary meristem. Many of these meristems gave rise to an axillary bud; however, certain proximal ones (in small leaves or intermediate forms with cataphylls) developed into male inflorescences, while some distal ones formed female inflorescences. Finally, the hypsophylls were the last foliar units of the heteroblastic series and the final elements contained in the winter bud. The proximal hypsophyll typically formed two stipules, a small leaf lamina, and an axillary bud (or, occasionally, a female inflorescence in Qf only), whereas the distal hypsophyll produced only two acute, triangular stipules resembling those of scales (Fig. 2).

The pattern of organogenesis within axillary buds was similar to that observed in apical buds. However, axillary buds lacked Hy, and the prophylls fulfilled their developmental role. Moreover, the apical buds of the additional growth units contained fewer scales and cataphylls than ordinary buds. The buds of additional growth units probably developed before scales and cataphylls had hardened, enabling these elements to grow to a certain extent or even to produce normal leaves. Examination of the bases of numerous additional shoots confirmed that scale and cataphyll scars were consistently few, with scale scars frequently absent, especially in Qi.

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Table 2. Bud content and characteristics of the stems supporting the buds analysed in the four studied trees. Reported traits include apical bud (AB) length, number of nodes, number of leaf units composed of scales + cataphylls (S + C) (two S or two C per leaf unit), number of leaf primordia (Lp), male and female inflorescence primordia or meristems (p M Infl and p F Infl), leaves above female inflorescences/infructescences (L above infl), and hypsophylls (Hy). The number of recorded items is shown in parentheses. Significant differences between individuals identified using multiple comparisons test ($P < 0.05$) are indicated, as in Table 1, by capital letters.

	Qi-1		Qi-2		Qf-1		Qf-2	
	2006	2007	2006	2007	2006	2007	2006	2007
Bud content								
AB length	2.11 ± 0.06 E (17)	1.70 ± 0.08 E (11)	3.14 ± 0.09 D (15)	3.06 ± 0.13 D (11)	5.98 ± 0.19 A (9)	5.62 ± 0.30 A (6)	4.87 ± 0.09 B (9)	4.10 ± 0.10 C (20)
Nodes	17.47 ± 0.39 D (17)	15.45 ± 0.64 D (11)	20.53 ± 0.47 C (15)	20.82 ± 0.67 C (11)	23.22 ± 0.32 BC (9)	23.85 ± 0.44 AB (13)	26.38 ± 0.80 A (12)	25.63 ± 0.62 AB (27)
S+C	5.82 ± 0.18 (17)	5.29 ± 0.14 (17)	8.27 ± 0.18 (15)	8.06 ± 0.22 (17)	13.00 ± 0.37 (9)	12.90 ± 0.32 (21)	14.71 ± 0.46 (12)	13.95 ± 0.22 (38)
L p	7.59 ± 0.29 (17)	6.71 ± 0.32 (14)	8.00 ± 0.37 (15)	7.76 ± 0.37 (17)	5.44 ± 0.24 (9)	6.38 ± 0.24 (13)	6.67 ± 0.19 (12)	6.93 ± 0.34 (27)
p M Infl	0.70 ± 0.27 (23)	0.44 ± 0.22 (16)	3.53 ± 0.39 (15)	3.45 ± 0.51 (20)	1.89 ± 0.73 (9)	1.35 ± 0.39 (26)	0 (12)	0.04 ± 0.04 (25)
p F Infl	1.40 ± 0.16 AB (10)	1.68 ± 0.33 ABC (3)	1.40 ± 0.16 AB	1.86 ± 0.14 A	0.33 ± 0.17 D (9)	0.53 ± 0.26 BC (17)	0.83 ± 0.34 ABC (12)	0.36 ± 0.13 C (25)
L above infl	3.67 ± 0.41 A (9)	3.67 ± 0.67 A (3)	3.70 ± 0.21 A (190)	3.57 ± 0.20 A (7)	0.00 ± 0.00 B (3)	0.33 ± 0.33 B (6)	0.00 ± 0.00 B (6)	0.90 ± 0.31 B (10)
Hy	4.06 ± 0.16 AB (17)	3.73 ± 0.14 B (11)	4.27 ± 0.23 AB (15)	4.99 ± 0.09 AB (11)	4.78 ± 0.32 AB (9)	4.87 ± 0.21 A (26)	5.01 ± 0.44 A (12)	4.76 ± 0.21 AB (27)
Stem analysis								
Nodes	17.89 ± 0.59 DE (18)	17.31 ± 0.39 E (24)	20.09 ± 0.80 CD (17)	20.69 ± 0.51 C (27)	23.40 ± 0.37 AB (10)	23.29 ± 0.25 B (48)	24.85 ± 0.44 AB (13)	25.64 ± 0.27 A (45)
S+C	5.61 ± 0.40 D (18)	5.54 ± 0.16 D (23)	7.56 ± 0.30 C (17)	7.61 ± 0.32 C (27)	13.80 ± 0.33 AB (10)	12.88 ± 0.13 B (48)	14.92 ± 0.28 A (13)	14.43 ± 0.11 A (45)
L	8.00 ± 0.59 A (18)	7.60 ± 0.38 AB (24)	8.12 ± 0.47 A (17)	8.24 ± 0.40 A (27)	5.40 ± 0.31 C (10)	5.83 ± 0.21 C (48)	6.08 ± 0.39 BC (13)	6.39 ± 0.17 BC (45)
M Infl	0.42 ± 0.29 (18)	0 (23)	0.28 ± 0.19 (18)	0.70 ± 0.30 (27)	0 (10)	0 (48)	0 (13)	0 (45)
F Infl	0.56 ± 0.15 (18)	0.26 ± 0.11 (23)	1.11 ± 0.20 (18)	1.11 ± 0.13 (27)	0.10 ± 0.10 (10)	0.21 ± 0.0 (48)8	0 (13)	1.02 ± 0.10 (45)
L above infl	5.00 ± 0.47 A (10)	3.50 ± 0.87 A (4)	4.62 ± 0.31 A (13)	4.34 ± 0.30 A (22)	1.00 ± 0.00 B (1)	0.22 ± 0.15 B (9)	0.00 ± 0.00 B (0)	0.30 ± 0.08 B (33)
Hy	4.28 ± 0.16 AB (18)	4.17 ± 0.13 AB (24)	4.41 ± 0.21 AB (17)	4.84 ± 0.15 AB (28)	4.20 ± 0.29 AB (10)	4.58 ± 0.16 AB (48)	3.85 ± 0.22 B (13)	4.82 ± 0.18 A (45)

Table 3. Mean lengths of the middle and longest leaf primordium laminae in apical buds of the four studied trees of *Quercus ilex* (Qi) and *Q. faginea* (Qf). Only apical buds from the resting period (December to March) were included. The values correspond to the year 2007, with additional data for Qf from the first 3 months of 2008. The number of apical buds analysed was 15 for Qi-1, 14 for Qi-2, 25 for Qf-1, and 22 for Qf-2. Abbreviations: Lp, leaf primordium; St, stipules; Lam, lamina of the leaf primordium; Position, the position of the longest lamina counted from the proximal to the distal leaf primordium. Values are presented as means ± standard error. Significant differences between individuals identified using multiple comparisons test ($P < 0.05$) are indicated by capital letters.

		Qi-1	Qi-2	Qf-1	Qf-2
Middle Lp	AB (mm)	2.04 ± 0.077 D	3.17 ± 0.097 C	5.72 ± 0.131 A	4.45 ± 0.110 B
	N°nodes	17.07 ± 0.565 D	20.67 ± 0.454 C	23.40 ± 0.340 B	25.98 ± 0.534 A
	N°Lp	7.27 ± 0.358 AB	8.03 ± 0.427 A	5.80 ± 0.173 C	6.73 ± 0.273 BC
	Stp (mm)	0.85 ± 0.026 C	1.65 ± 0.103 AB	2.15 ± 0.109 A	1.76 ± 0.068 B
	Lam (mm)	0.38 ± 0.017 B	0.56 ± 0.030 B	1.43 ± 0.098 A	1.22 ± 0.055 A
The longest Lp	Stp (mm)	1.05 ± 0.060 B	1.83 ± 0.096 A	2.15 ± 0.119 A	1.94 ± 0.104 A
	Lam (mm)	0.44 ± 0.019 B	0.64 ± 0.027 B	1.53 ± 0.103 A	1.40 ± 0.088 A
	Position	2.70 ± 0.319 A	3.53 ± 0.443 A	3.38 ± 0.154 A	3.32 ± 0.202 A

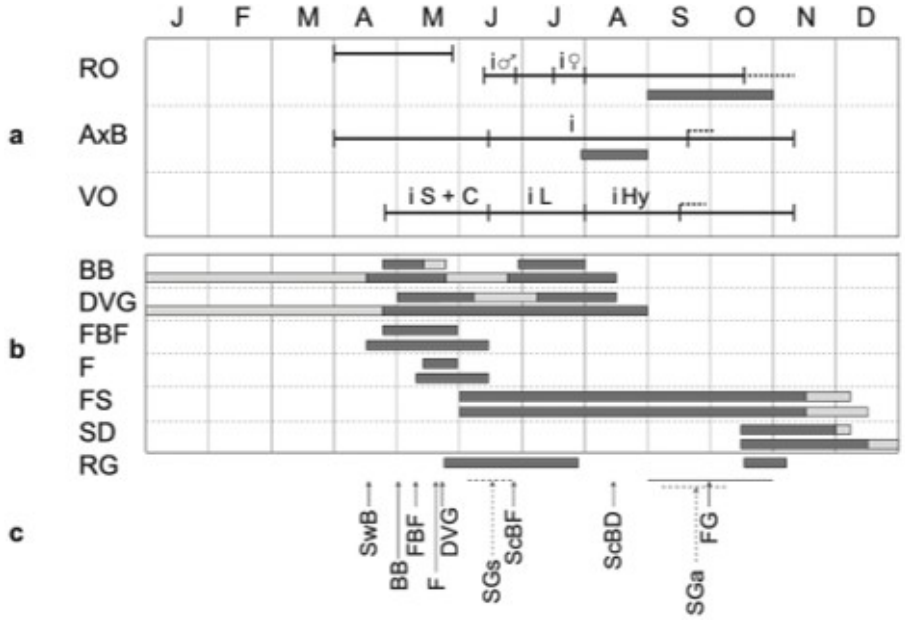

Figure 3. Organogenesis and phenological diagrams for *Quercus ilex* subsp. *ballota* in 2007 (Qi-2). **(a)** Diagram depicting the organogenesis of Qi-2. Two dark-grey rectangles represent the periods of maximum fruit (upper) and bud (lower) growth. The continuous line indicates the periods of development of the initiated primordia, and the letter "i" denotes the periods of initiation of the following organs: male and female inflorescences, scales (S), cataphylls (C), leaves (L), and hypsophylls (Hy). The dashed line indicates a possible minor time extension. **(b)** Phenophase diagrams for Qi. The upper bars correspond to Qi-2, and the lower bars represent the entire population in 2007. Light bars indicate phenophases occurring in fewer than 5 % of individuals or in fewer than 5 % of branches within single individuals, whereas dark bars indicate phenophases occurring in ≥ 5 %. **(c)** Medians of different phenophases for the Qi population sample, from 2006 to 2009 ($n = 15$). The periods of maximum secondary growth were approximately determined based on Albuixech et al. (2012). Abbreviations: BB (1, 7 in part) – budburst, DVG (3, 7 in part) – shoot vegetative growth, FBF (9) – flower bud formation, F (10) – flowering, FS (11) – fruit setting, SD (12) – seed dispersal, RO – reproductive organogenesis and primordia development, AxB – axillary bud initiation and development, VO – vegetative organogenesis, SwB (1) – swollen buds, ScBF (4) – scaly bud formation, ScBD (5) – scaly bud development, SGs – secondary growth in spring, Sga – secondary growth in autumn, FG (12 in part) – intensive fruit growth, RG – growth periods of coarse roots during 2007–2014, based on Alday et al. (2020). In parentheses are indicated the phenophases used in the study (see the material and methods section).

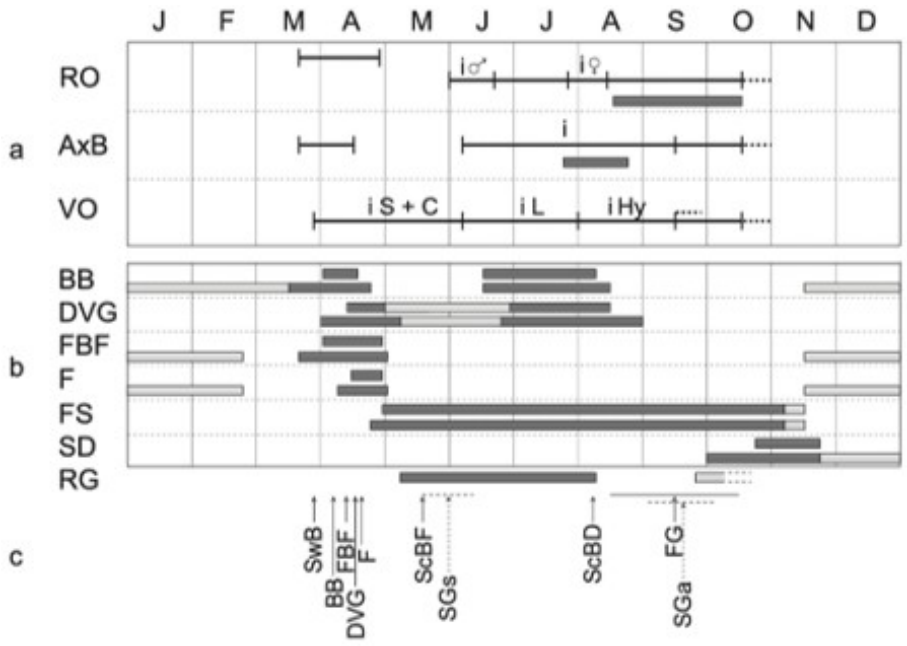

Figure 4. Organogenesis and phenological diagrams for *Quercus faginea* in 2007 (Qf-2). The format and conventions are identical to those in Fig. 3.

3.3.2 Reproductive organogenesis

Reproductive organogenesis was closely integrated with vegetative organogenesis (Figs. 3a, 4a), with male and female inflorescences initiating shortly after the leaf primordia that subtend them. Male inflorescences were initiated in spring, prior to their female counterparts. Their development commenced within the bud immediately after initiation and continued until autumn. By this time, the inflorescences appeared fully preformed. At this point, the buds entered a state of dormancy. Development resumed during bud swelling and was complete by the onset of flowering (Fig. 5).

Female inflorescences followed a distinct and later developmental pattern. Following initiation, they exhibited minimal growth or persisted as simple axillary meristems – slightly larger and taller than the vegetative ones – making them difficult to distinguish morphologically. By summer, they had either initiated a few bracts before entering winter dormancy or remained as simple axillary buds. Development resumed with bud swelling, leading to the initiation of flowers in the bract axils, and growth continued until flowering occurred (Fig. 5). The developmental patterns of inflorescences in Qi were very similar to those observed in Qf; however, the lower frequency of inflorescence initiation in Qf compared to Qi prevented the inclusion of Qf data in Fig. 5.

Female inflorescence initiation in Qi occurred in the latter half of July, shortly before the period of maximum bud development and well before the phase of maximal fruit development. In contrast, initiation in Qf occurred later, approximately during the first half of August, fully coinciding with the period of peak bud development and just preceding the onset of maximal fruit development. Nevertheless, in both species, the initiation of female inflorescences preceded the onset of peak fruit development (Figs. 3a, 4a).

3.4 Integrating reproductive and vegetative organogenesis

The number of scale and cataphyll nodes was greater in Qf than in Qi, resulting in a significant delay in the initiation of female inflorescences in Qf (Table 2). As a result, both species were found to initiate male inflorescences at approximately the same time. However, Qf produced female inflorescences in the axils of distal leaves and the proximal hypsophyll, whereas Qi did so in more proximal leaves. This accounts for the earlier initiation in Qi compared to Qf. Thus, at all levels of organisation, vegetative and reproductive organogenesis were tightly coordinated.

4 Discussion

This study provides the first detailed synthesis of phenology and organogenesis in *Quercus* species. In one respect, the inclusion of organogenesis represents a significant limitation: the dissection of apical buds is so time-consuming that replication remains unacceptably low. Nevertheless, no area of investigation should be avoided solely because it is slow and technically demanding. Despite the limited replication, the inclusion of this information introduces a valuable new di-

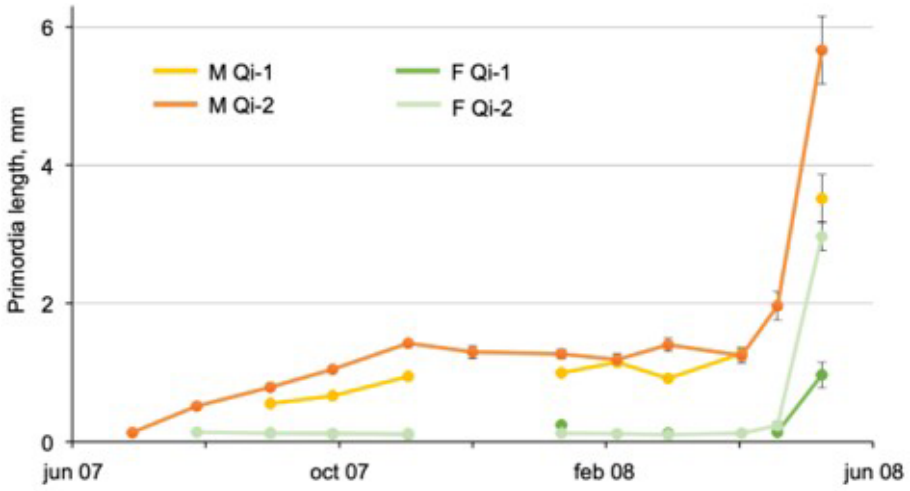

Figure 5. Length of male (M) and female (F) inflorescence primordia or meristems in dissected apical buds of Qi. Mean values (in mm) are presented with standard errors. Data from 2007 are organised by developmental stage, covering the period from 4 July to 4 December, followed by data from 13 January to 9 May. Number of inflorescence primordia measured in dissected buds: MQi-1 (31), FQi-1 (19), MQi-2 (135), FQi-2 (27).

mension to phenological research, and we anticipate that future studies will further validate the utility of this approach.

Our investigation of phenology and organogenesis in two coexisting *Quercus* species revealed three key interrelationships, each at least partially identified through organogenetic analysis. The first two pertain to strategies of annual growth and bud development (Hypothesis 1), and the third concerns resource competition between vegetative growth and fruit production (Hypothesis 2).

4.1 Phenology and organogenesis are synchronised

In both Qi and Qf, phenology and organogenesis progressed in parallel and were closely coupled. However, a notable divergence was detected. From approximately the time of meiosis and fertilisation, phenophases advanced at a significantly slower rate, whereas organogenesis remained highly active. This observation allows the identification of two temporally distinct phases, demarcated by the timing of meiosis and fertilisation, which occur in late spring or early summer (Johnson et al., 2002; Merkle et al., 1980; Schermer et al., 2019).

- *Phase 1: Extension growth and flowering.* This phase comprises the highly active and overlapping spring phenophases (Castro-Díez and Montserrat-Martí, 1998), such as shoot development, flowering, and most secondary growth. Within the buds, the initiation of scales, cataphylls, proximal leaf primordia, and male inflorescences takes place. Leaf and stem tissues are at maximum hydration: water content peaks at the onset of vegetative shoot growth (Guada et al., 2018; Palacio et al., 2008). This hydration supports turgor pressure, essential for primary growth extension (Hsiao and Xu, 2000). During this period, canopy water demands are primarily met by soil water reserves accumulated during autumn and winter, and supplemented by spring rainfall. Spring is widely recognised as the most favourable season for primary growth in Mediterranean regions (Orshan, 1989).

- *Phase 2: Fructification and bud development.* This phase includes most of the additional growth, all fruit development, limited secondary growth, and a substantial portion of bud development. During this stage, the initiation of the remaining leaf primordia, female inflorescences, hypsophylls, and most axillary buds takes place. Spring and summer precipitation may extend the duration of vegetative shoot growth, promoting the formation of additional growth units (Hover et al., 2017) and enhancing secondary growth, particularly the production of latewood (Eilmann et al., 2009). Nevertheless, in contrast to Phase 1, tissue water content at maximum hydration declines markedly (Palacio et al., 2008). In both species, buds appear to function as lower-priority resource sinks compared to shoots and developing fruits (Alla et al., 2012). Consequently, successful bud development occurs only when water availability is sufficient for all actively growing organs or when competition for resources is relatively low (Alla et al., 2013). Furthermore, successful bud development also depends on robust secondary growth in the stems of associated current-year shoots. This growth includes the formation of wide xylem vessels, which improve hydraulic conductivity (Alla et al., 2011; Cochard et al., 2005). This secondary growth typically occurs prior to the on-

set of severe summer water deficit (Alla et al., 2011). Thereafter, scaly buds – owing to their protective structure – are able to continue organogenesis and growth under relatively dry conditions, even when canopy tissue water content is only moderate (Alla et al., 2013). Nonetheless, during more intense droughts, bud development is significantly impaired (Montserrat-Martí et al., 2009; Camarero et al., 2010). Thus, climate appears to play a crucial role in the completion of the two described phases.

Consistent with this, the influence of climate on phenology is well documented (Chuine et al., 2010; Laube et al., 2014), with the most pronounced effects observed in vegetative growth, flowering, and the senescence-abscission phenophases (Delpierre et al., 2017). By contrast, its impact on reproductive phenophases is recorded as less significant (Liu et al., 2021). However, the response of organogenetic patterns to changing climate or to gradients in climate and elevation remains unstudied. These patterns are expected to align with phenological ones, in a manner consistent with our findings.

The advancement of bud burst observed in the deciduous Qf compared to the evergreen Qi can be considered advantageous, as it prolongs the vegetative period and enhances carbon assimilation (Keenan et al., 2014; Kolářová et al., 2014). However, any advantage will be lost if late frosts damage the early bud burst or if the summer proves excessively long and dry (Didion-Gency et al., 2024), resulting in poor bud development and, consequently, reduced shoot production, flowering, and fruiting in the following year (Ogaya and Peñuelas, 2006). In our view, the capacity of the species studied to persist in specific locations and respond to climate change will depend on their ability to synchronise phenological patterns with seasonal climatic conditions and to maintain adequate summer growth.

4.2 Different patterns of temporal overlap between vegetative and reproductive growth with organogenesis

At the bud level, we observed potential resource competition between leaf organs and their axillary male inflorescence primordia in both species. The development of male inflorescences appears to inhibit normal leaf growth, resulting in the formation of cataphylls or, at most, small leaves or intermediate structures between cataphylls and fully developed leaves. However, buds containing numerous male inflorescence primordia had only slightly higher numbers of cataphylls than the other buds analysed, with the differences being non-significant. Thus, our bud dissection data do not provide significant support for such competition. Nevertheless, a recent study by Le Roncé et al. (2023) found that in Qi, fruit removal in mid-June led to a decrease in the production of male inflorescences and an increase in the production of leaves and female inflorescences during the subsequent year. These findings are consistent with our observations regarding organogenesis and phenology in Qi. The removal of fruits in mid-June may enhance the availability of resources for bud development, thereby increasing the initiation and development of leaves and female inflorescence meristems. If, however, such removal were to occur while cataphylls and male inflorescence primordia were already initiated, an increase in their production would not be expected.

This hypothesis assumes that competition for resources occurs among the organs within the buds. An increase in resource availability should favour the initiation of leaf primordia over that of cataphylls (and their associated axillary male inflorescences), while also promoting the initiation of female inflorescence primordia towards the end of the leaf primordia initiation period. This hypothesis warrants further investigation. However, it would necessitate a greatly increased sampling intensity, which would, in practice, be difficult to achieve. Even the low replication achieved here was extremely time-consuming and labour-intensive.

In contrast to their male counterparts, female inflorescences are located in the axils of normal, generally well-developed leaves. When the primordia of female inflorescences begin to develop, they exhibit minimal growth (Fig. 5), suggesting that competition for resources with leaf primordia is likely to be minimal.

At the whole-plant scale, the initiation and development patterns of vegetative and reproductive primordia are remarkably similar in both species. Nevertheless, the temporal overlap with shoot development is notably different. Qf has an early onset of first-flush shoot growth and initiates leaf primordia in the buds once the leaves have already matured, around early June. In contrast, Qi produces its first flush later, and the maturation of its thicker leaves extends until approximately early September. Consequently, leaf development in Qi spans the entire leaf primordia initiation phase and a significant portion of hypsophyll initiation.

Qf must delay the initiation of leaf primordia by nearly 2.5 months to avoid overlapping with shoot development and leaf maturation, whereas Qi can only postpone it by approximately 2 months. This results in a near-synchronous period of leaf primordia initiation in both species. The presence of numerous scales and cataphylls in both species facilitate this adjustment, although Qf may exhibit a greater delay owing to the presence of more scales and cataphylls. This pattern is consistent with observations in other temperate tree species, where the initiation of leaf primordia in developing buds often follows the extension of first-flush shoots (Puntieri et al., 2002; Sabatier et al., 2003).

The time available for bud development also differs between species. It is longer in Qf, due to its earlier bud burst, and more rapid shoot growth and leaf maturation. This distinction is ecologically relevant, as Qf is deciduous and must renew a complete set of buds each year to reconstruct the following year's canopy. In contrast, Qi is evergreen and does

not need to produce as many new shoots annually. It usually maintains three cohorts of leaves, with the number of leaves shed each year being closely linked to the number of new leaves formed (Montserrat-Martí et al., 2009; Misson et al., 2011). Furthermore, in rainfall exclusion experiments, leaf longevity tended to increase under drought conditions (Misson et al., 2011; Limousin et al., 2012). This physiological flexibility allows Qi to maintain adequate canopy even when shoot production is reduced: its survival is less dependent on high levels of annual growth and organogenesis.

In summary, our findings on the temporal overlap between vegetative and reproductive growth with organogenesis support our first hypothesis. The development of large versus small buds in consecutive years appears to be determined by their performance during the peak summer growth period, typically spanning late July to mid-August (see Fig. 4 in Montserrat-Martí et al., 2009; Alla et al., 2013). During this period, Qf displays minimal phenological activity, favouring consistent annual bud development. In contrast, Qi exhibits more intense phenological activity due to its later bud burst, and slower shoot growth and maturation. This delay reduces the optimal window for bud development, particularly when shoot production is high. This may explain the alternating pattern of high and low shoot production observed in Qi, a pattern not found in Qf (Alla et al., 2013; Montserrat-Martí et al., 2009; Ogaya and Peñuelas, 2006; Rambal et al., 2014). The window for bud development is narrower in years of large shoot production than in years with limited shoot growth, leading to the formation of smaller buds and reduced shoot production in the following year.

4.3 The initiation of female inflorescences did not coincide temporally with the periods of maximum bud and fruit development

According to our second hypothesis, we expected the period of female inflorescence initiation to coincide in both species, or to be slightly delayed in Qi, thereby overlapping with the peak of bud development and the onset of maximum fruit development (which are similar in both species; see Figs. 3 and 4). Such an overlap might serve as a regulatory mechanism governing bud and fruit production in the year following one of high fruit output (Camarero et al., 2010; Sharp and Sprague, 1967). However, during the study year, this overlap was not observed. Surprisingly, Qi initiated female inflorescences almost 15 d earlier than Qf, despite the later onset of organogenesis in Qi. This discrepancy may be attributed to two morphological characteristics: (1) Qf produces a greater number of scales and cataphylls than Qi, enabling both species to initiate leaf primordia at approximately the same time; (2) female inflorescences in Qf are located more distally than in Qi, thereby postponing their initiation until the hypsophyll initiation phase. Delaying the initiation of leaf primordia may constitute an additional function of scales and cataphylls in *Quercus*, beyond their role in protecting the meristems and primordia (Alla et al., 2013; Magnin et al., 2012; Nitta and Ohsawa, 1998).

Throughout the study years, we consistently observed that Qf produced fewer fruits than Qi within the study population (Montserrat-Martí et al., 2009). This difference may be attributed to a greater requirement in Qf for (a) wetter summers to fully develop buds and initiate numerous female inflorescences, and (b) its delayed initiation of female inflorescence primordia, which more closely overlaps with the period of maximum fruit development.

Although our results did not support our second hypothesis, we acknowledge that fruit development can constrain bud development on the same shoot, even in years of normal fruit production (Gordon et al., 2006; Alla et al., 2012). This suggests that even early stages of fruit development, prior to the peak development period, may compete for resources with bud development. The most extreme case of fruit production, such as masting, depends on abundant initiation of inflorescences in the preceding year. Sharp and Sprague (1967) observed that in *Quercus alba*, the conditions determining years of high acorn production appear to be set at the onset of the flowering phase. In such instances, the peduncles of pollinated flowers begin to develop more rapidly from May onwards, even before syngamy occurs. This early divergence in inflorescence/infructescence development suggests that active fruit development must also begin earlier.

This phenomenon would promote greater overlap between the fruit development period, and the phases of peak bud development and female inflorescence initiation during mast years. This would lead to significantly reduced flowering (Sharp and Sprague, 1967; Sork et al., 1993; Koenig and Knops, 2000; Gordon et al., 2006), and additionally, the production of much smaller buds in the year following a mast year. In the case of Qi, Camarero et al. (2010) reported a significant reduction in bud size in the year following an exceptionally abundant mast event. This mechanism appears to be more effective than the one originally hypothesised, as it would exert minimal influence on bud development and inflorescence initiation during years of normal fruit production.

In line with this notion, Le Roncé et al. (2023) suggested that the timing of reproductive organ development plays a pivotal role in the physiological processes underlying mast seeding.

5 Conclusions

This study presents the first integrated analysis of phenology, pheno-morphology, and organogenesis in two Mediterranean *Quercus* species with contrasting leaf habits. The aim was to elucidate the functional significance of their morphological traits and to test two ecological hypotheses. The first hypothesis – competition between organogenesis and shoot extension – was supported by our findings. In contrast, the second

hypothesis – synchrony between female inflorescence initiation and bud/fruit development – was not.

To account for this discrepancy, we propose that the advancement of fruit development observed during mast years may coincide with the initiation of inflorescence meristems and bud formation, potentially resulting in smaller buds and reduced flowering in the subsequent year. This effect was not evident during years of normal fruiting.

Our observations highlight the flexibility of developmental patterns in response to summer water availability. They underscore the need to consider not only the timing but also the windows of opportunity for organ growth when investigating whole-plant physiological strategies in tree species.

Appendix A

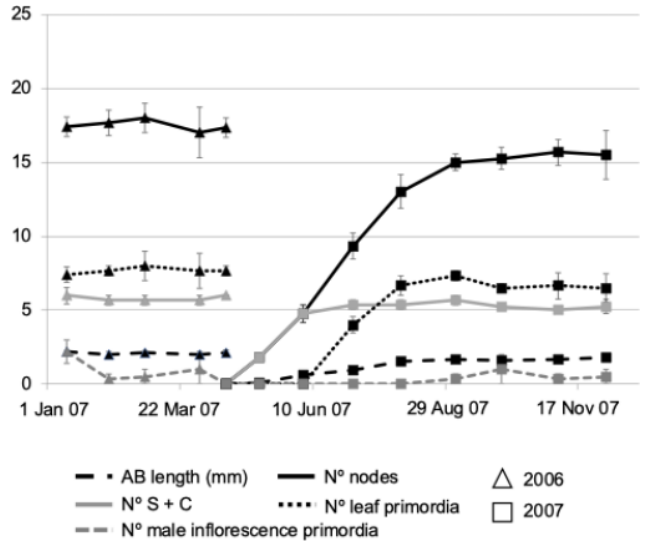

Figure A1. Monthly variation in apical bud (AB) characteristics of Qi-1 in 2007: AB length, node number, number of scales and cataphylls (S + C), number of leaf primordia, and number of male inflorescence primordia. AB 2006 (triangles) from January to April, in the period preceding bud burst, and AB 2007 (squares) from initiation to December.

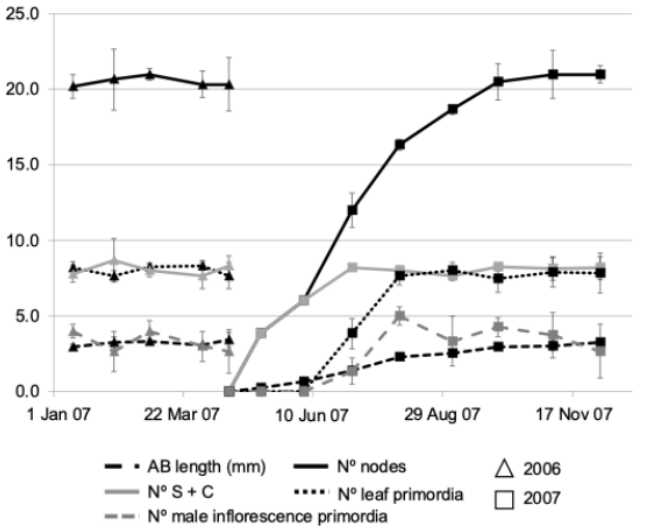

Figure A2. Monthly variation in apical bud (AB) characteristics of Qi-2 in 2007: the legend is the same as in Fig. A1.

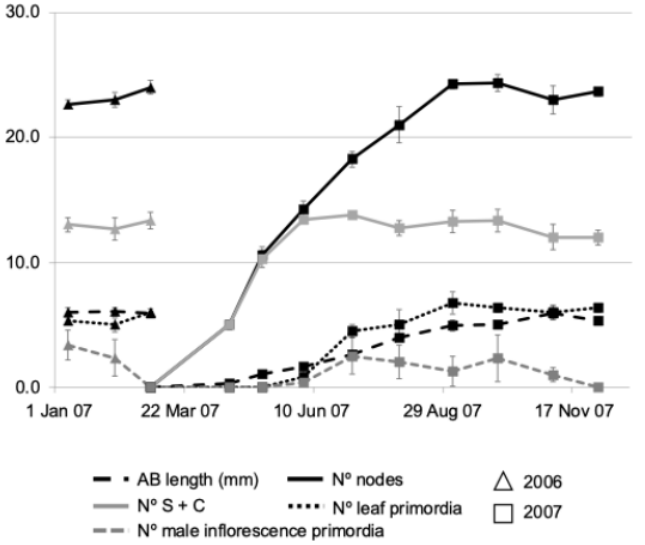

Figure A3. Monthly variation in apical bud (AB) characteristics of Qf-1 in 2007: AB length, node number, number of scales and cataphylls (S + C), number of leaf primordia, and number of male inflorescence primordia. AB 2006 (triangles) from January to March, in the period preceding bud burst, and AB 2007 (squares) from initiation to December.

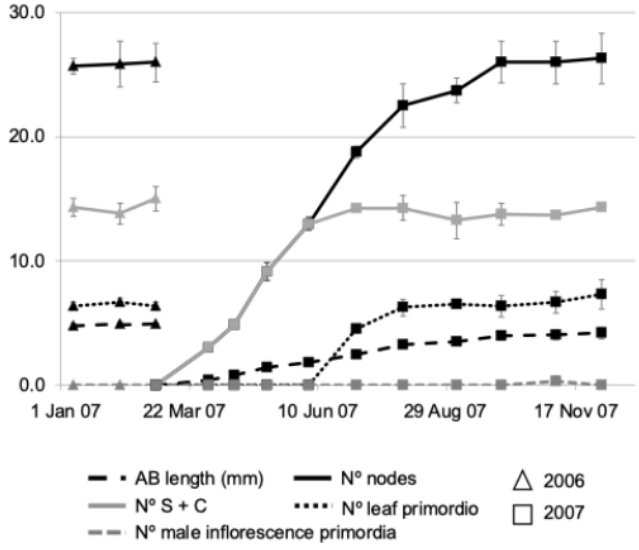

Figure A4. Monthly variation in apical bud (AB) characteristics of Qf-2 in 2007: the legend is the same as in Fig. A3.

Data availability. The herbarium material used in this study is deposited in the JACA herbarium (IPE, CSIC). The datasets are available on request from the corresponding author.

Author contributions. Gabriel Montserrat: writing (original draft, review, and editing), visualisation, methodology, investigation, data curation, conceptualisation, and funding acquisition. Andreu Cera: writing (review and editing), formal analysis, and conceptualisation. John Hodgson: writing (review and editing), supervision, and conceptualisation.

Competing interests. The contact author has declared that none of the authors has any competing interests.

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