Summer-drought constrains the phenology and growth of two coexisting Mediterranean oaks with contrasting leaf habit: implications for their persistence and reproduction

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Abstract This study analyses how coexisting evergreen and deciduous oaks adjust their phenology to cope with the stressful Mediterranean summer conditions. We test the hypothesis that the vegetative and reproductive growth of the winter deciduous (*Quercus faginea* Lam.) is more affected by summer drought than that of the evergreen [*Quercus ilex* L. subsp. *ballota* (Desf.) Samp.]. First, we assessed the complete aboveground phenology of both species during two consecutive years. Shoot and litter production and bud, acorn and secondary growth were monitored monthly. Second, we identified several parameters affected by summer conditions: apical bud size, individual leaf area (LA), leaf mass per area (LMA) and acorn yield in both species, and leaf-fall in *Q. faginea*; and analysed their variation over 10 years. *Q. ilex* performed up to 25% of shoot growth and most leaf development during summer, whereas *Q. faginea* completed most of both phenophases during spring. Secondary growth was arrested in summer under drought conditions. Approximately, 30–40% of bud and 40–50% of acorn growth was undertaken during summer in both species. Summer drought related to differences in LA, LMA and leaf senescence, but not to acorn yield. Both species had similar year-to-year patterns of acorn production, though yields were always lower in *Q. faginea*. Bud size decreased severely in both species during extremely dry years. In *Q. ilex,* bud size tended to alternate between years of large and small buds, and these patterns were followed by opposite trends in stem length. In *Q. faginea*, bud size was more stable through time. *Q. ilex* was more phenologically active during summer than *Q. faginea*, indicating a higher tolerance to drought. Furthermore, bud and fruit growth (the only two phenophases that both species performed during summer) were more severely affected by summer drought in *Q. faginea* than in the evergreen. The differential effects of summer drought on key phenophases for the persistence (bud growth) and colonization ability (fruit production) of both species may have consequences for their coexistence.

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Introduction

The coexistence of species with different leaf habits under similar environmental conditions has long been a central topic in ecological theory (Damesin et al. 1998). Evergreen sclerophylls and winter deciduous species frequently coexist in Mediterranean ecosystems. Such coexistence is puzzling, because summer drought shortens the favourable

season for carbon assimilation of winter deciduous species to a few months in spring and autumn (Milla et al. 2005b). Deciduous species may compensate these productive limitations by advancing bud burst and delaying leaf senescence (Peñuelas and Filella 2001). However, such protraction of the vegetative activity into spring and autumn entails increased risks of suffering damage from early and late frosts (Mediavilla and Escudero 2003a). Alternatively, winter deciduous species may increase the overlap of phenophases in spring, with the drawback of increased demands for resources at this time of the year (Castro-Díez and Montserrat-Martí 1998; Montserrat-Martí and Pérez-Rontomé 2002; Montserrat-Martí et al. 2004).

Despite these limitations, mixed forests of deciduous and evergreen broadleaved trees, mainly composed by oaks, are widespread in the Mediterranean Basin (Quézel and Médail 2003). In the NW Mediterranean, the most frequent pairs of coexisting evergreen/deciduous oaks are *Quercus ilex* subsp. *ilex*/*Q. pubescens* and *Q. ilex* subsp. *ballota*/*Q. faginea*. Some studies have tried to explain the co-occurrence of these oak species by focusing on their different responses to disturbance and seedling performance (Bonfil et al. 2004). Others have followed an ecophysiological approach, comparing stomatal responses, water and nutrient use efficiencies and photosynthetic rate at the leaf level (Epron and Dreyer 1990; Salleo and Lo Gullo 1990; Del Arco et al. 1991; Acherar and Rambal 1992; Escudero et al. 1992; Tretiach 1993; Damesin et al. 1998; Mediavilla et al. 2001; Mediavilla and Escudero 2003b, 2004, Juárez-López et al. 2008). These studies show that several features related to water and carbon economy are different between both pairs of species which helps explain their different distribution.

Damesin et al. (1998) suggested that the key factors controlling the coexistence of evergreen and deciduous Mediterranean oaks are mostly related to processes affecting the whole tree rather than individual organs. However, comprehensive studies of aboveground growth processes at the tree level are scarce. Detailed phenological studies inform of the timing of vegetative and reproductive growth events at the whole-tree level and hence enable the identification of the most relevant sinks and sources within the plant at any given time. Provided that summer drought is the most limiting environmental factor for plant growth in Mediterranean-type ecosystems (Mooney 1983), understanding how evergreen and deciduous oak species arrange their growth phenophases during summer seems to be crucial to explain their co-occurrence in Mediterranean areas. Indeed, the degree of overlap between phenophases seems to be relevant for the adaptation of plants to Mediterranean climate (Castro-Díez and Montserrat-Martí 1998).

This study aimed to explain how coexisting oak species with contrasting leaf habits adjust their phenological patterns to cope with Mediterranean summer conditions. We analysed the aboveground phenological pattern of a winter deciduous (*Q. faginea*) and an evergreen (*Q. ilex* subsp. *ballota*) oak growing in the same locality. According to their distribution, *Q. ilex* seems to be better adapted to withstand summer drought than *Q. faginea*, which normally grows in moister sites (Amaral Franco 1990; Mediavilla and Escudero 2004) or in soils with higher water storage capacity (Castro-Díez et al. 1997; Villar-Salvador et al. 1997). The phenological patterns of these species have been described elsewhere (Floret et al. 1989; De Lillis and Fontanella 1992; Cabezudo et al. 1993; Castro-Díez and Montserrat-Martí 1998). However, detailed studies are lacking, and we are not aware of any previous studies focusing on phenology and growth patterns during summer on coexisting populations of evergreen and deciduous Mediterranean oaks. Here we test the hypothesis that summer growth of vegetative and reproductive organs in the winter deciduous species will be more severely limited by drought than that in the evergreen. To test this hypothesis, we identified the phenophases that took place in summer in both species and assessed their development during two consecutive years. We also analysed the inter-annual variation and the relation to climate (temperature and rainfall) of several parameters related to summer phenology over a period of 10 years.

Methods

Study area

The study site was located in an almost flat south-facing slope near Agüero (Huesca) in NE Spain (42°18′N, 0°47′W, 750 m a.s.l.). Soil in this area is a Calcisol (FAO 1998), formed on Miocene clays with a bedrock of calcareous sandstone. Vegetation is an open tall scrub with scattered low trees, dominated by *Q. ilex* L. subsp. *ballota* (Desf.) Samp., *Q. faginea* Lam., *Arbutus unedo* L. and *Pinus halepensis* Mill., approximately with similar dominance, and the less abundant *Juniperus oxycedrus* L., *Viburnum tinus* L., *Lonicera implexa* Aiton, *Buxus sempervirens* L., *Smilax aspera* L., *Pistacia lentiscus* L., *Quercus coccifera* L., *Amelanchier ovalis* Medicus and *Sorbus domestica* L. Most of the trees and large shrubs are multi-stemmed as a result of the historical firewood-gathering carried out until 1970s. Since then no fires or wood harvests have taken place in this area. Climate is continental Mediterranean, with 635 mm of annual average rainfall, a mean minimum temperature of the coldest month (January) of 4.3°C and a mean maximum temperature of

the hottest month (July) of 28.4°C (data derived from the closest meteorological station, Ayerbe, 42°16′ N, 0°41′ W, 585 m).

Study species

Quercus ilex L. is an evergreen oak tree with semi-ring-porous wood widespread in the western Mediterranean Basin (Barbero et al. 1992). Two subspecies are present in the Iberian Peninsula: subsp. *ilex,* which is mostly distributed near the coast, and subsp. *ballota* (Desf.) Samp. (*Q. rotundifolia* Lam.), which grows preferentially inland and in many continental areas (Amaral Franco 1990).

    Quercus faginea Lam. is a deciduous oak tree with ring-porous wood and with a wide distribution in Mediterranean and sub-Mediterranean areas of the Iberian Peninsula (Amaral Franco 1990). It frequently coexists with *Q. ilex* subsp. *ballota* in NE Spain, although it tends to grow in moister areas (Castro-Díez et al. 1997; Villar-Salvador et al. 1997).

Study site and period

A homogeneous and almost flat area (800 × 100 m), with at least 60 adult trees per each species, was delimited in the above location. The site was located on a flat plateau, with no lateral inputs of water or nutrients, and homogeneous soil and vegetation. The two species were evenly distributed in the study area with no signs of habitat segregation. Ten individuals per species were marked as reference plants for phenological description and the remaining trees were used for plant material collection and additional measurements. The field study was carried out from December 1996 to October 2006 (for *Q. faginea* since February 1997) with monthly visits throughout 1997 and 1998 (Table 1). The monthly monitoring of secondary growth was carried out in 2006. From 1999 to 2006 sampling was done annually at mid October. October was selected as the most adequate time for annual sampling because by that time of the year shoot development and leaf development are completed, most leaves of *Q. faginea* remain in the crown and are still green, buds have reached more than a 50% of their final size, acorns are almost developed and acorn shedding has not started yet. Consequently leaf parameters, bud development and acorn yield can be accurately estimated in both oak species.

Climatic data and water deficit

Climate data on the monthly maximum and minimum temperature and monthly total precipitation for the period 1995–2006 were obtained from the closest weather station (Ayerbe, situated at ca. 11 km from the study population).

Table 1 Variables measured in the study together with sample sizes and frequency and period of sampling

Variable	Sample size	Frequency	Period
Aboveground phenology	10	Monthly	1997–1998[a]
Bud development	30	Monthly	1997–1998[a]
Apical bud weight	30	Annual	1997–2006
Secondary growth	15	Monthly	2006
Acorn development	50	Monthly	1997–1998[a]
Acorn production	25	Annual	1997–2006
Leaf senescence in *Q. faginea*	25	Annual	1997–2006
Demography of branch elements	10	Monthly	1997–1998[a]
Shoot length	50	Annual	1997–2006
Litterfall	10	Monthly	1997–1998[a]
LA	25	Annual	1997–2006
LMA	25	Annual	1997–2006

[a] Measurements started in December 1996 for *Q. ilex* and in February 1997 for *Q. faginea*

Cumulative water deficit was subsequently calculated as follows. Soil water balance for the study site was estimated by using a modified Thornthwaite water-budget procedure based on the monthly mean temperature and total precipitation data (Willmott et al. 1985). Following this procedure, soil–water balance is modelled by estimating soil-water withdrawal (actual evapotranspiration), recharge, and surplus. Actual evapotranspiration is related to the percentage of the current soil at the available water capacity, and to potential evapotranspiration, which is estimated empirically from monthly mean temperature and day length. We calculated the cumulative water deficit from January through June, when both study species perform most of their growth, and most of the water that these deep-rooted oaks will use in summer falls. We also calculated the cumulative water deficit from August to September, when rainfall is scarce and infiltration through soil surface is low. Calculations were done by using the Actual Evapotranspiration (AET) calculator software, developed by Daniel G. Gavin (http://geography.uoregon.edu/gavin/software.html).

Aboveground phenology, bud development, shoot length and secondary growth

Phenological patterns were obtained on ten marked individuals per species (see Table 2 for the main size descriptors of these individuals as measured in December 2006) by following Montserrat-Martí and Pérez-Rontomé (2002), and Montserrat-Martí et al. (2004). Six phenophases were considered: dolichoblast (i.e. long shoots) vegetative

Table 2 Size (dbh, diameter at 1.3 m; height) and number of stems for ten individuals of each species that were followed for phenological variables

Species	Dbh (cm)	Height (m)	No. stems per individual
Q. faginea	12.4 ± 0.9a*	5.5 ± 0.3a	4 ± 1a
Q. ilex subsp. ballota	10.6 ± 0.6b	4.1 ± 0.1b	9 ± 1b

Data were measured on December 2006. Values are mean ± SE

* Different letters indicate significant differences between species (P < 0.05, ANOVA)

growth (DVG), flower bud formation (FBF), flowering (F), fruit set (FS), seed dispersal (SD), and leaf shedding of dolichoblasts (LSD). The last phenophase indicated leaf abscission instead of leaf death, so that phenological records could be compared with data from litterfall traps (see below). The percentage of each phenophase was estimated in the canopy of each individual and then compared with observations made on other unmarked individuals. This allowed getting an integrated measure of the occurrence of each phenophase in the population. To graphically represent the intensity of each phenophase within the population in the diagrams, three categories were considered: (1) when a phenophase is present in more than 25% of study plants, (2) when it is present in between >5 and 25% of the individuals, (3) when it is present in 5% or less of the individuals. The third category was calculated in the whole studied population. Only those individuals that showed a phenophase in more than 5% of their branches were considered for categories 1 and 2. Phenophases observed in less than 5% of the branches were included in category 3.

To monitor bud development, 30 shoots were randomly collected at the mid crown of non-marked trees. Very big and very small shoots were excluded. The apical bud of each shoot was removed under a stereomicroscope (10×, MS5 Leica Microsystems, Heerbrugg, Switzerland). Buds were oven-dried at 60°C to a constant weight before being individually weighted with a precision scale. Only apical buds were considered as the average dry weight of apical buds is significantly correlated to the weight of subapical buds in both species (G. Montserrat-Martí, unpublished data). The mean rate of bud growth (mg day^{-1}) was estimated as the weight difference between consecutive sampling dates (mg) divided by the time elapsed between consecutive harvests (days). Shoot length was measured with a ruler to the closest 0.5 mm in 50 shoots randomly collected at the mid crown of non-marked trees.

Radial-growth rates were estimated using dendrometer bands (Agriculture Electronics Corporation, Tucson, USA) during the last year of study. In March 2006, dendrometers were placed at 1.3 m on the thickest stem of 15 individuals per species. Bark was brushed off before installing the

dendrometers, which were read at 24-day intervals on average. Displacement measurements were taken with a precision of 0.1 mm. To estimate radial-growth rates (mm day^{-1}), consecutive readings of cumulative perimetrical growth were converted to cumulative radial growth (mm), subtracted and divided by the number of days elapsed between successive readings.

Acorn production and development and percentage of senescent leaves in Q. faginea

Acorn production was visually estimated in October between 1997 and 2006 in 25 individuals of each species by using the method proposed by McDonald (1992). This semi-quantitative method classifies fruit production into five categories: 0 minimal = no fruits or a few fruits on less than 5% of the individuals, 1 very light = few fruits on less than 25% of the individuals, 2 light = few fruits on more than 25% of the individuals, 3 medium = many fruits on 25–50% of the individuals, and 4 heavy = many fruits on more than 50% of the individuals. To measure acorn development, 50 healthy acorns were randomly collected from different individuals on every sampling date (see Table 1). They were oven-dried at 60°C and weighed (including cupules) to the nearest 0.01 mg. The percentage of senescent leaves in the canopy of Q. faginea was visually estimated in mid October in the same 25 individuals used to estimate acorn production.

Demography of branch elements, litterfall collection, leaf area and leaf mass per area ratio

Demography of branch elements was monitored in one well-developed 3-year-old branch randomly selected at the mid crown of every marked tree (n = 10 individuals per species). Five of the branches were exposed to the south at full sun light, and five to the north at full shade. Each branch was labelled and all its elements (leaves, inflorescences and acorns) were drawn and counted every month between January 1997 and December 1998.

Litterfall was collected every month from March 1997 to January 1999 by placing 19-cm diameter traps below the canopy of each marked tree (n = 10 individuals per species). Once in the laboratory, litterfall was fractionated, oven-dried at 60°C and weighed to the closest 0.01 mg. Stems with or without abscission band were separated in two groups, to have an estimate of the amount of branches shed by cladoptosis and those merely broken off the plant.

To calculate mean individual leaf area (LA mm^2), 25 current-year leaves were randomly taken from non-marked individuals and their leaf area was measured individually with a digital leaf-area meter (Delta-T Devices LTD, Cambridge, England) coupled to a Skye Analysis System

(Skyeleaf 1.11, Powys, UK). Leaves were oven-dried to a constant weight at 60°C and their leaf mass per area ratio (LMA mg cm^{-2}) calculated by dividing their dry weight by their area.

Calculations and statistical analyses

To evaluate annual shoot production, we calculated the mean number of current-year (n) stems (S) and leaves (L) produced per previous-year ($n - 1$) stem (Sn/S$n - 1$ and Ln/S$n - 1$, respectively). These indexes were calculated from the data obtained with branch demography in December 1996, 1997 and 1998. To avoid underestimating shoot production due to the branch shedding of *Q. faginea* throughout late spring and summer, the first index was also calculated by using data from May, when the number of current-year shoots is maximum (Sn max/S$n - 1$).

All data were checked for normality and homoscedasticity prior to statistical testing. Those variables that did not fit a normal distribution were log or arcsin (x) transformed. Differences between monthly or annual means were assessed by one-way ANOVAs followed by Bonferroni tests when variances were equal, or Dunnett's T3 test otherwise. In the case of variables which could not be transformed to follow a normal distribution, such as the percentage of senescent leaves, paired comparisons were based on the U Mann–Whitney tests. Analyses were performed with SPSS 12.0 (SPSS, Chicago, USA).

Correlation analyses were performed to evaluate the relationship between growth and climatic variables (mean monthly minimum and maximum temperatures, total precipitation and cumulative water deficit from January through June). Pearson correlation coefficients were calculated for all paired correlations (r) except when acorn production (not continuous) was involved, in which case Spearman rank correlation coefficients (r_s) were calculated. To account for the effects of temporal autocorrelation in correlation analyses between growth and climatic variables, we estimated the corrected 95% confidence intervals for the correlation coefficients using stationary bootstrap estimates with an average block length proportional to the maximum estimated autocorrelation of the data (Park and Lee 2001; Mudelsee 2003). The temporal relationships between previous-year apical-bud weight (year $n - 1$) and stem length of the next year (year n) were assessed using cross-correlation analysis considering lags from 0 to 4 years.
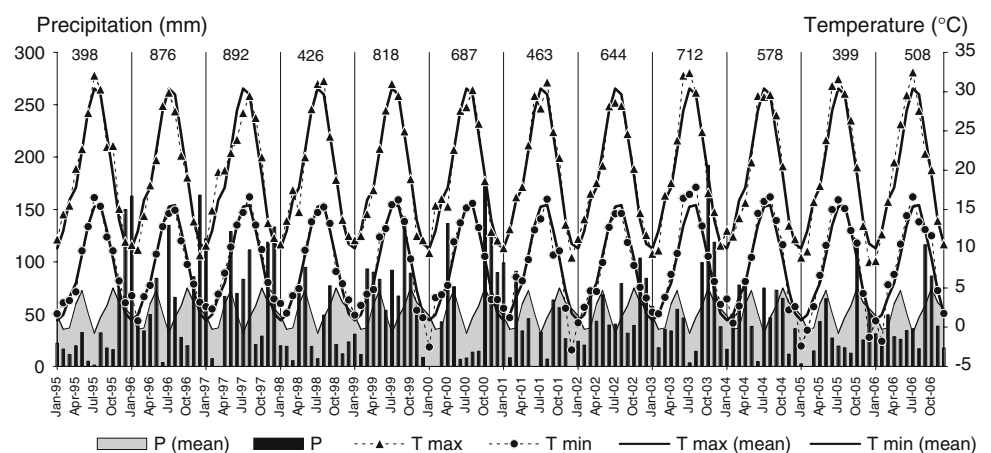
Results

Climate and cumulative water deficit over the study period

Climate was markedly different between the first 2 years of study, since 1997 was quite wet (WD = 65 mm) and 1998 had a similar cumulative water deficit (WD = 222 mm) to the 1995–2006 mean (WD = 224 mm) (Fig. 1). 2001 (WD = 278 mm) and 2005 (WD = 339 mm) were years with low annual rainfall and high maximum temperatures. The periods 1994–1995 and 2004–2005 were amongst the driest episodes recorded in NE Spain during the past 50 years. For instance, the cumulative water deficit from January to June was 43.0 and 29.7 mm in 1995 and 2005, respectively, whereas the mean value for the 1995–2006 period was 14.0 mm.
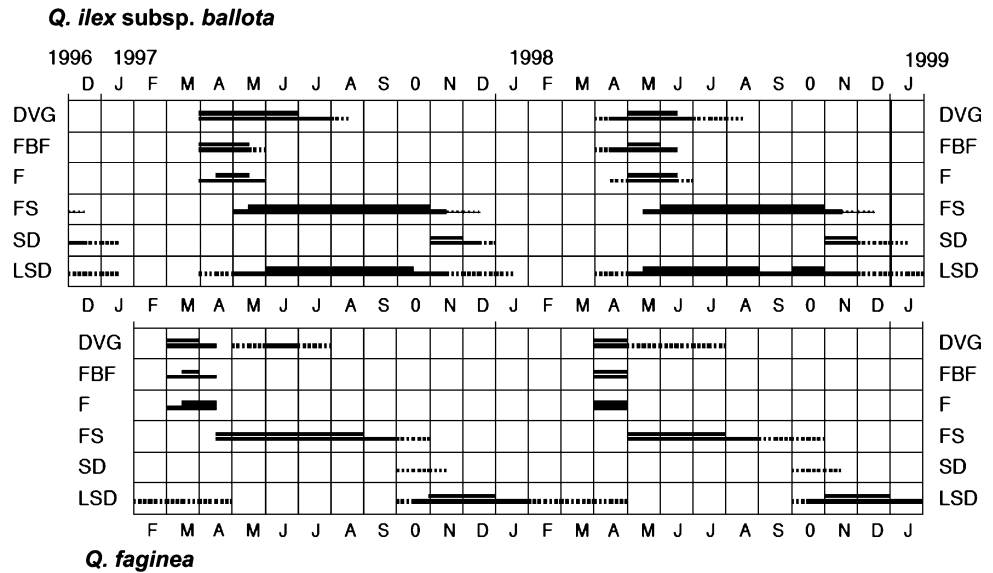
Phenological patterns and summer drought

Study species showed remarkable differences in the timing of shoot growth (DVG) and its extension into summer. Although both species avoided developing many shoots during the driest part of the year, the period of maximum shoot development occurred earlier and was much shorter in *Q. faginea* than in *Q. ilex* (Fig. 2). The first flush of shoot growth of *Q. faginea* was almost finished by late April, and by May leaves were completely developed.

Fig. 1 Total monthly precipitation (P) and mean monthly maximum and minimum temperatures (T_{max} and T_{min}, respectively) during the studied period, and average values for the last 31 years series available at the Ayerbe weather station [Huesca, NE Spain); P (mean), T_{max} (mean) and T_{min} (mean)]. The *numbers* at the top of each year indicate total annual precipitation

From that time on, only some epicormic shoots and some additional flushes (lammas shoots) were produced, and DVG was completely finished by the end of July. Contrastingly, in *Q. ilex* almost 25% of DVG and most of leaf maturation occurred during summer. DVG was almost finished by the end of July 1997 in *Q. ilex*, but a residual growth (few epicormic shoots and lammas growth) continued up to mid August. In 1998, DVG of *Q. ilex* finished earlier, by late June.

The period of fruit development was quite similar in both species, although *Q. faginea* finished 2–4 weeks earlier than *Q. ilex* (Fig. 3). Acorns started to enlarge in July. They emerged from the cup in early August and continued growing until fruit dispersal in October–November. From August to October an important shedding of undeveloped acorns was observed (data not shown). Maximum acorn growth took place between August and October (Fig. 3), and fruit development during summer accounted for approximately 40–50% of the dry weight at maturity in both species (Fig. 3). *Q. ilex* presented large variations in the acorn dry weight at mid October throughout the study period. In *Q. faginea*, most acorns aborted before mid October, and acorn numbers in the population were frequently too low to get a representative sample (Fig. 3), so inter-annual variability in fruit size could not be assessed.

Active bud development began at the end of shoot elongation in both species, and during summer buds gained up to 30–40% of their final dry weight (Figs. 4, 5). However, due to their differences in the timing of shoot development, bud growth started earlier in *Q. faginea*, and by the beginning of summer buds had already 20% of their final dry weight. Contrastingly, the buds of the evergreen had only gained 7% of their final size by the same time, and hence summer was an intensive period of bud development
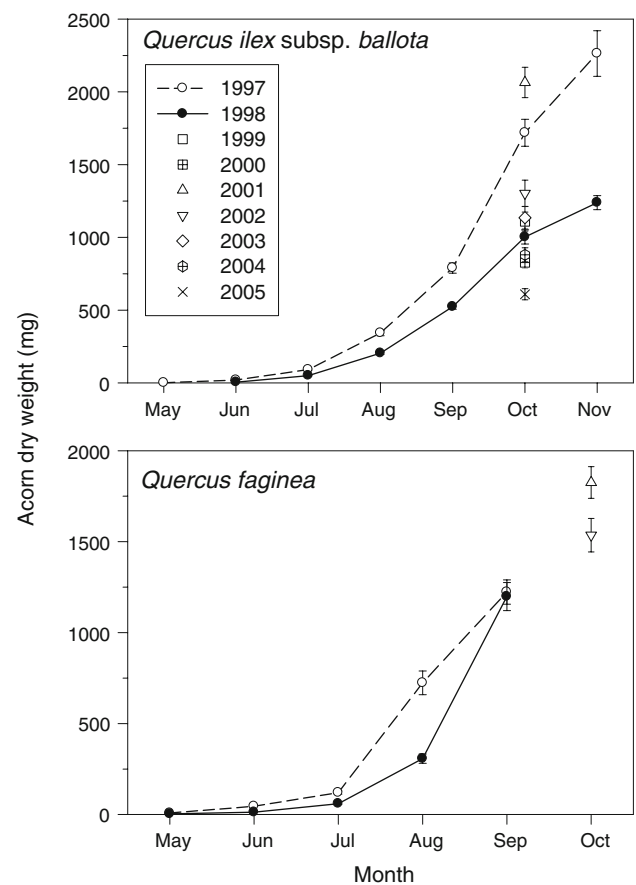
Fig. 3 Individual weight of acorns of *Quercus ilex* subsp. *ballota* (*upper graph*) and *Quercus faginea* (*lower graph*) during the study period (1997–2006). Values are mean ± SE (*n* = 50)

in this species (Fig. 4). Indeed, most of the differences in the bud development of the evergreen between 1997 and 1998 occurred during summer months (Fig. 5). In
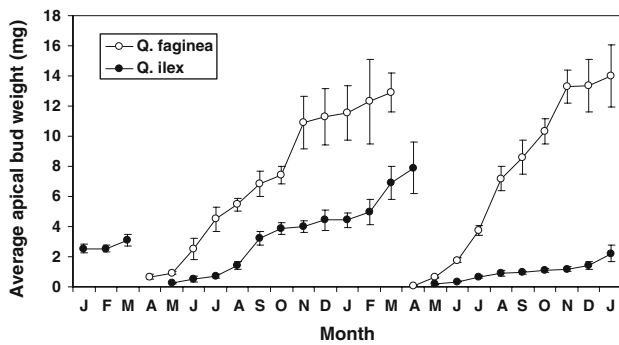
Fig. 4 Seasonal variation in the individual weight of the apical buds of *Quercus ilex* subsp. *ballota* (*black circles*) and *Quercus faginea* (*white circles*) between January 1997 and January 1999. Values are mean ± SE ($n = 30$)

Q. faginea, buds showed a second period of growth between October and November (Fig. 5), and they were always larger than in the evergreen (Fig. 4).

Leaf shedding in *Q. ilex* occurred throughout the year, but most leaf litter fell between May and January (Fig. 6). A peak of leaf fall was recorded in early June in 1998, indicating abundant leaf shedding after the end of shoot production in May. Contrastingly, no clear peaks were detected in 1997, when shoot production was much lower.
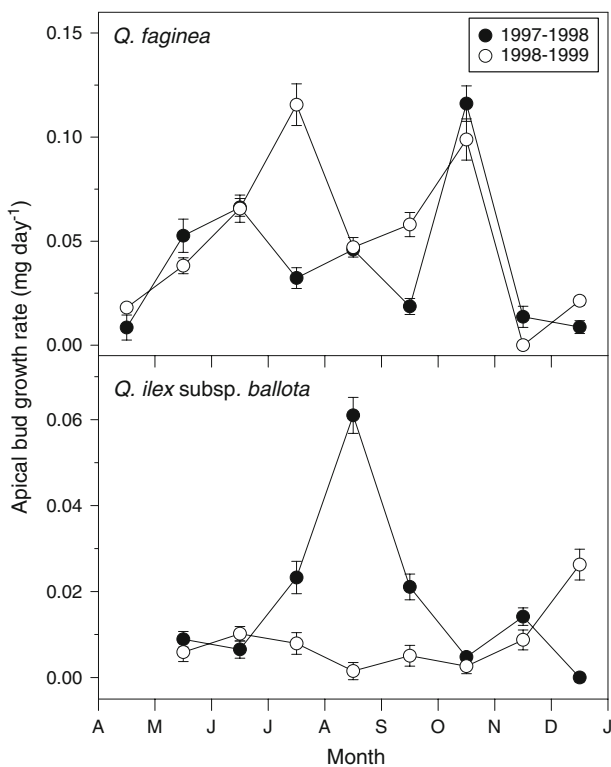
Fig. 5 Apical bud growth rate of *Quercus faginea* (*upper graph*) and *Quercus ilex* subsp. *ballota* (*lower graph*) during the 2 years of detailed phenological monitoring (1997–1998). Values are mean ± SE ($n = 30$)

Leaf shedding in *Q. faginea* was more regular between both years. Most leaves were shed in late autumn and early winter, though leaf shedding also occurred throughout most of the year due to marcescent leaf fall. Both species shed stems throughout the year, but *Q. faginea* shed a larger amount of stems than *Q. ilex* (Fig. 6). The percentage of abscised stems was higher and more regular between years in *Q. faginea* than in *Q. ilex* (Fig. 6). Also, *Q. faginea* shed a similar amount of litterfall between both years of monitoring ($P = 0.88$), whereas *Q. ilex* shed more litterfall in 1998 than in 1997 ($P = 0.03$). Most of the branches shed by *Q. faginea* were only 1 or 2 years old, while those of *Q. ilex* were frequently older and bigger (data not shown).

Both species had a similar seasonal pattern of secondary growth in 2006, showing a main peak of growth in late spring and early summer (June), a secondary peak in autumn (September–October), and arrested growth during summer, from July to August (Fig. 7). Nevertheless, in *Q. ilex*, ca. 72% of the annual tree-ring width was completed between March and July, whereas in *Q. faginea* it was ca. 90%. Consequently, the winter deciduous species showed a lower secondary growth activity during summer than the evergreen.

Inter-annual variability of bud size, leaf traits, growth, and acorn yield, and relationship to climate

In *Q. ilex*, the average apical bud weight (ABW) varied markedly throughout the 10 years of study (CV = 49.3%), alternating between years of large and years of small buds (Fig. 8). Oscillations were specially marked between 1997 and 2003, but the pattern was broken in 2005, a very dry year, when ABW was very low instead of high as expected from the pattern. The significant positive correlation at lag 1 in *Q. ilex* indicates that the dry weight of apical buds is positively related to the length of stems in the following year (Fig. 8). In *Q. faginea* buds were much larger and the variation in the ABW (CV = 24.3%) was smaller than in *Q. ilex*, but ABW decreased markedly after masting (2002) and severe drought (2005). Similarly to *Q. ilex*, large apical buds tended to produce shoots with long stems, except in the very dry years, such as 2005 (Fig. 8). No significant correlations were found between bud size and climate variables in any of the two species.

Shoot production in *Q. ilex* showed also an alternate pattern, parallel to stem length and opposite to ABW (Table 3; Fig. 8). *Q. faginea* showed higher shoot and leaf production in 1997 than in 1998, but differences were not significant when the index of production was calculated for the month with a maximum amount of current-year shoots (Sn max/$Sn - 1$). This was probably a consequence of the intense branch shedding observed from April to December (Fig. 6).
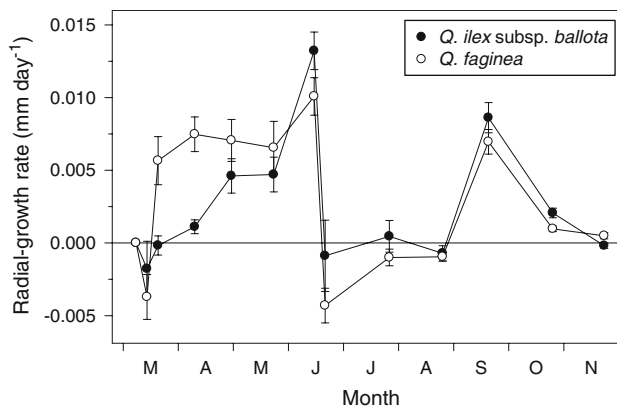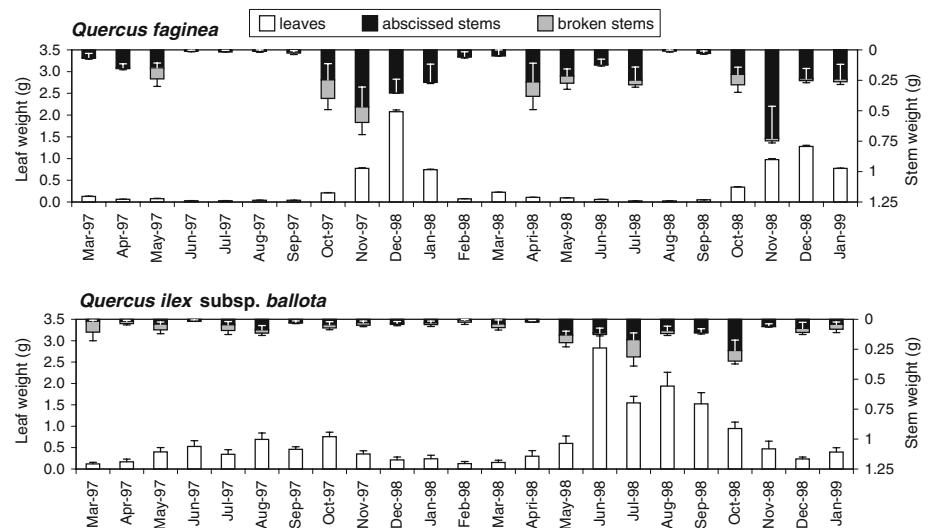
Fig. 7 Seasonal dynamics of radial growth rate (mm day^{-1}) in *Quercus ilex* subsp. *ballota* and *Quercus faginea* between March 2006 and November 2006. Values are mean ± SE (*n* = 15)

Individual leaf area (LA) did not change significantly in *Q. faginea* during the 10 years of study (*P* = 0.98), while in *Q. ilex* it was high (250–300 mm^2) from 1997 to 2000, and decreased since then (178–255 mm^2) (*P* < 0.01) (Fig. 9). In both species, LA was low in 2002 when masting occurred. High rainfall in April promoted large LA in *Q. ilex* (Table 4). LA in both species was significantly but oppositely correlated with the average water deficit between January and June: the relation was negative in *Q. ilex* and positive in *Q. faginea* (Table 4).

Leaf mass per leaf area ratio (LMA) showed significant differences between years in both species (*F* = 7.47–10.97, *P* < 0.001; Fig. 9). In *Q. faginea*, LMA was negatively related to April and June precipitation (Table 4) and tended to show higher values in drier years, whereas *Q. ilex* tended to produce current-year leaves with low LMA values in dry years (e.g. 1998, 2001) (Fig. 9).

Acorn yield varied greatly throughout the 10 years of study, following a similar pattern in both oak species (r_s = 0.82, *P* < 0.01), but crops were always smaller in *Q. faginea* (Table 5). In both species, acorn yield peaked in 2002 (masting year), whereas individual acorn dry weight was maximum in 2001, indicating that lower acorn yield was compensated by increased fruit size (Table 5). Acorn yield was inversely correlated with the minimum temperatures of September in both species (Table 4).

The percentages of senescent and dry leaves in the canopy of *Q. faginea* estimated at mid October were higher in the years of dry summers (2000, 2001 and 2005) or high acorn production (2002) (Table 5). Indeed, the percentage of senescent leaves of *Q. faginea* was positively correlated with low rainfall in summer (Table 4).

Discussion

Phenology and summer drought

Our results show that an important fraction of the phenological cycle of Mediterranean oaks is undertaken during summer. Both study species performed a small part of their shoot growth, and a significant amount of their bud and fruit growth at this time of the year. This agrees with previous phenological studies on these species (Floret et al. 1989; De Lillis and Fontanella 1992; Cabezudo et al. 1993; Castro-Díez and Montserrat-Martí 1998). Cambial activity was mostly arrested during summer both in *Q. ilex* and *Q. faginea* in the year of study. This was probably a consequence of water stress, which induces the quiescence of cambial activity in many Mediterranean woody species including oaks (Corcuera et al. 2004; Campelo et al. 2007).

In accordance with our hypothesis, the phenological activity of the winter deciduous species during summer
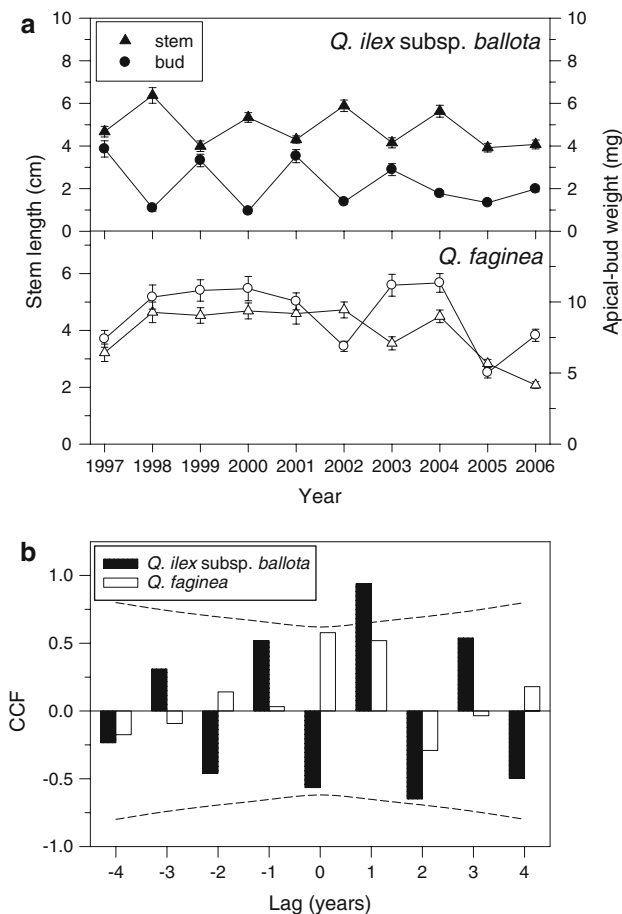
Fig. 8 a Variations in the apical bud dry weight (mg) and stem length (mm) of *Q. ilex* susbp. *ballota* and *Q. faginea* throughout the study period. Values are mean ± SE (*n* = 30). The cross-correlation function (CCF) (**b**) shows significant associations (bars above or below the 95% confidence intervals, *dashed lines*) between stem length and apical-bud weight for both species and for different temporal lags. For instance, lag 0 corresponds to buds and stems of the same year and lag 1 shows the association between bud size of year *n* − 1 and stem length of year *n*

(DVG) and most leaf development during summer, whereas *Q. faginea* only performed a very small fraction of DVG and its leaves were already mature before summer. The summer stop of wood growth was also severer in *Q. faginea* than in *Q. ilex*, since radial-growth rates during summer were more negative in the winter deciduous. These results indicate that *Q. ilex* can endure summer conditions better than *Q. faginea*, explaining its occurrence in more arid areas. This agrees with the results of several studies conducted on the ecophysiology of both species (Mediavilla et al. 2001; Mediavilla and Escudero 2003b, 2004). Also, fruit growth, the phenophase more intensively developed during summer, achieved higher success in terms of yield and final fruit size in the evergreen species. Buds grew significantly during summer in both species, which may be possible thanks to the tight protection of the numerous scales and cataphylls in scaled buds (Nitta and Ohsawa 1998). Nevertheless, bud size was more severely decreased in dry years in the winter deciduous species. Both bud and fruit growth are highly relevant for the persistence and colonization ability of oaks, as they determine primary growth on the following year and the ability to spread and colonize new sites. Differences in the performance of both phenophases during extremely dry years or unusually wet summers may have consequences for the coexistence of both species.

Relationship between climate and leaf, fruit and bud production

In *Q. ilex*, LA decreased with water deficit, whereas in *Q. faginea* tended to increase. The results obtained for the evergreen are in agreement with previous experiments on artificial drought on this same species (Ogaya and Peñuelas 2006) and may show a mechanism to reduce water losses through transpiration. We cannot provide an explanation for the positive relationship between LA and water deficit in the deciduous species. Nevertheless, the low year-to-year variation of LA in *Q. faginea* can be explained by its earlier development of shoots and leaves,

was lower than the evergreen, indicating that *Q. faginea* tends to avoid rather than tolerate summer drought. Accordingly, *Q. ilex* performed up to 25% of shoot growth

Table 3 Shoot production in *Quercus ilex* susbp. *ballota* and *Q. faginea*

Index	*Q. ilex* subsp. *ballota*			*Q. faginea*	
	1996	1997	1998	1997	1998
Sn/Sn − 1	2.76 (1.11)a	1.02 (0.76)b	2.89 (1.37)a	2.90 (0.39)a	2.40 (0.79)b
Sn max/Sn − 1	–	1.02 (0.76)a	3.04 (1.34)b	2.76 (0.47)a	2.01 (0.55)a
Ln/Sn − 1	19.68 (8.18)a	7.01 (5.28)b	17.33 (9.63)a	16.26 (3.37)a	8.69 (2.37)b

Sn/Sn − 1 = mean number of current-year (*n*) stems (S) produced per previous-year (*n* − 1) stem, Ln/Sn − 1 = mean number of current-year leaves (L) produced per previous-year stem, as measured in December 1996, 1997 and 1998. Sn max/Sn − 1 = mean number of current-year stems produced per previous-year stem as measured in the month with maximum number of current-year shoots. Different letters in a row indicate significant differences between years within species (ANOVA followed by Bonferroni test; *P* < 0.05). Values are mean (SD in parentheses; *n* = 10)
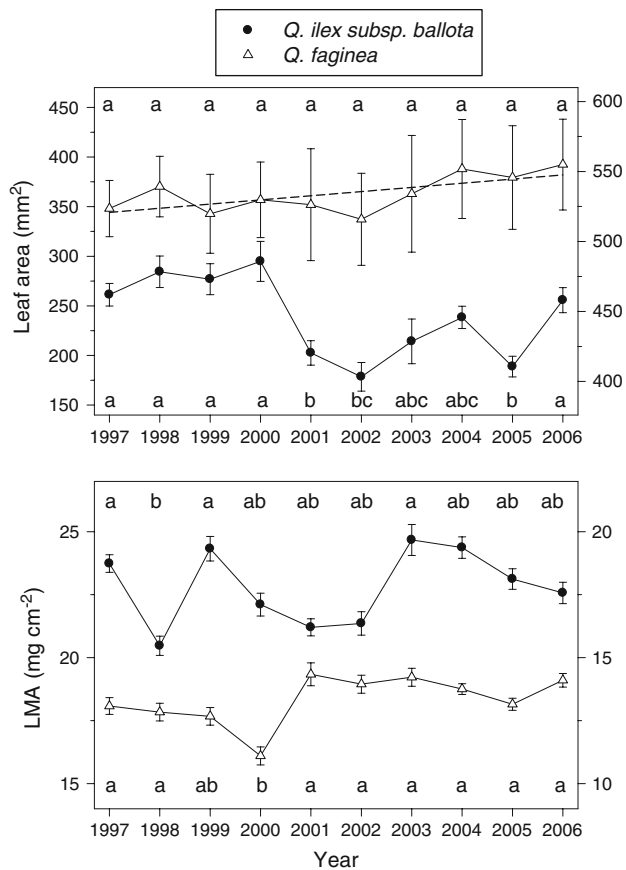
Fig. 9 Inter-annual variability in individual leaf area (*LA* mm²) and leaf mass per area (*LMA* mg cm⁻²) in current-year leaves of *Quercus ilex* subsp. *ballota* and *Quercus faginea*. *Different letters* indicate significant differences between years within species (Dunnett's T3 test). Values are mean ± SE (*n* = 25)

Table 4 Relationship between phenological and climatic variables in *Quercus ilex* susbp. *ballota* (Qi) and *Q. faginea* (Qf)

Phenological variables	Climatic variables	
Acorn production Qf	Ti Sep	
	−0.69 (0.03)	
Acorn production Qi	Ti Sep	
	−0.67 (0.03)	
DW acorn Qi	Ti Mar	
	0.86 (0.001)	
LA Qf	Ti Feb	WD Jan–Jun
	−0.78 (0.001)	0.62 (0.05)
LA Qi	P Apr	WD Jan–Jun
	0.77 (0.01)	−0.64 (0.05)
LMA Qf	P Apr	P Jun
	−0.86 (0.001)	**−0.71** (0.02)
Leaf senescence Qf	P Jul–Aug	WD Aug–Sep
	−0.63 (0.05)	**0.77** (0.01)

Values are Pearson coefficients, except for acorn production and leaf senescence where Spearman coefficients were calculated. Only significant ($P < 0.05$) correlations are shown (*P* values are indicated in parentheses). Significant correlations after correcting for temporal autocorrelation are indicated in bold (see text for further details on calculations)

Ti and *Tx* mean monthly minimum and maximum temperatures, respectively, *P* precipitation; *WD* cumulative water deficit

thus avoiding summer drought. Both species showed minimum LA in the masting year (2002). In *Q. ilex,* intense fruit production is related to substantial flowering (García-Mozo et al. 2007), and both leaf and inflorescence growth occur at the same time during spring. Therefore, the low LA of 2002 might well be the result of within-branch competition for resources between developing leaves and inflorescences.

Patterns of inter-annual variability of LMA seem also to follow opposite trends in the two study species. In *Q. faginea,* LMA was negatively related to spring precipitation and tended to increase in dry years. This was probably a result of increased allocation of biomass to structural components (Reich et al. 1999), as LMA was negatively related to the concentration of soluble sugars in leaves ($r = -0.63$, $P = 0.05$, data from Montserrat-Martí et al. submitted). Similar patterns have been described for other winter deciduous species (Salleo and Lo Gullo 1990). The tendency of *Q. ilex* to decrease LMA during dry years has been reported before by Ogaya and Peñuelas (2006), and could be due to a delay in the leaf development of this

species caused by drought, as LMA seems to increase throughout leaf lifespan.

Summer rainfall was negatively related to the percentage of senescent leaves by mid October, indicating that summer drought advances leaf senescence in *Q. faginea*. Similar results were found in *A. ovalis*, a Mediterranean winter deciduous shrub which advanced leaf shedding in summer as a result of drought (Milla et al. 2005b). Earlier or more scattered leaf shedding implies a decrease in nutrient use efficiency (Del Arco et al. 1991; Milla et al. 2005a). Leaf senescence of *Q. faginea* was also advanced in the masting year (2002), probably as a result of increased demand of resources from developing acorns (Hikosaka 2005).

We could not find any significant effect of summer drought or water availability on acorn development or yield, but according to our results, the higher the minimum temperatures in September, the lower the acorn yield. September is an important month for acorn development in both species, as it accounts for up to 30% of the final acorn weight (Fig. 3), and many acorns are aborted during this time of the year (Pulido and Díaz 2005). Temperatures in September are still high at the study site (average temperature is 18.9°C), and an increase in night minimum temperatures may result in increased respiratory losses, with negative consequences for acorn development. A temperature-induced summer water stress seems also to

Table 5 McDonald's categories for annual acorn yield based on McDonald (1992) index, average ripe acorn dry weight ($n = 50$) in *Quercus ilex* susbp. *ballota* and *Q. faginea*, and percentage of senescent leaves ($n = 25$) measured in mid October in the canopy of *Q. faginea* throughout the 10 years of study

Year	Acorn crop		Acorn dry weight (g)		Senescent leaves (%)
	Q. ilex	Q. faginea	Q. ilex	Q. faginea	Q. faginea
1997	2	1	1.72 (0.66)a	1.22 (0.47)a	2.92 (1.32)a
1998	1	0	1.00 (0.34)b	1.20 (0.39)a	4.06 (2.43)a
1999	1	0	1.11 (0.41)b	0.63 (0.26)c	2.28 (0.98)b
2000	2	0	0.83 (0.25)b	–	17.42 (5.08)c
2001	2	2	2.06 (0.74)a	1.82 (0.62)b	7.96 (4.24)d
2002	4	3	1.30 (0.64)abc	1.54 (0.65)ab	12.64 (5.48)e
2003	2	1	1.13 (0.43)b	–	3.96 (2.28)a
2004	2	1	0.84 (0.34)b	–	4.00 (3.93)a
2005	2	2	0.61 (0.27)d	–	18.90 (4.57)c
2006	1	0	*	–	1.84 (0.69)b

Values are mean and SD as indicated in parentheses. Different letters indicate significant differences ($P < 0.05$) within species between annual mean in acorn dry weight (Dunnett's T3 test) and percentage of senescent leaves of *Q. faginea* (*U* Mann–Whitney test)

* Most of the few acorns produced in 2006 by *Q. ilex* were very small and fell before October

affect the synchrony and amount of acorn production in similar Mediterranean oak species (Espelta et al. 2008).

Bud size showed no significant relationship with climate, although ABW was severely reduced in 2005 (an extremely dry year) in both species. Such a lack of relationship could be due to a regulation of ABW by internal mechanisms, except when environmental conditions are extreme or there is a very high allocation to reproduction, as in years of mast fruiting like 2002, when both species showed small ABW. Bud and fruit development overlap during summer, and hence they can potentially compete for resources when fruit yields are large. In *Q. ilex*, shoot length (and production) and bud size showed opposite alternate patterns. Accordingly, years of long stems (high shoot production) and small buds alternated with years of short stems (low shoot production) and big buds. The oscillation continued throughout the 10 years of study, and was only broken by the severe drought of 2005. *Q. ilex* performs an important fraction of both its shoot and bud development during summer and our results indicate that most of the differences between years in the bud growth rate of *Q. ilex* are found during summer months. This seems to indicate that summer is a crucial period for bud development, so that any shortage in resource availability at this time of the year may have an impact on the bud size of this species.

In species with preformed growth such as oaks (Collin et al. 1996; Fontaine et al. 1999), larger buds produce longer shoots with more leaves (Isik 1990; Hanover 1963; MacDonald et al. 1984; Remphrey and Powell 1984; Remphrey and Davidson 1994; Thorp et al. 1994). On the other hand, small buds will produce smaller and less numerous shoots on the following year, because many small buds tend either to abort or to produce short modules. If there is a trade-off between the allocation to developing shoots and buds, more resources will be available for bud growth once shoot growth has been completed and, consequently, larger buds will be formed. On the next year, these large buds will produce many large shoots that will lead to the formation of small buds, and the cycle would start again. We suggest that the fact that the final stage of shoot extension occurs in summer in *Q. ilex* triggers a trade-off between bud and shoot growth, which provides an internal mechanism to regulate both processes. This is supported by the absence of a similar trade-off in *Q. faginea*, which completes most of shoot development in spring.

Years of high shoot production and formation of long stems in *Q. ilex* were followed by an intense leaf shedding in late spring and early summer, which may be the result of source–sink interactions within branches (Hikosaka 2005). The alternation of years of high shoot production and leaf shedding, long stems and small buds, with years of opposite characteristics has not been described for *Quercus* species before. However, several studies report short-time series of alternate leaf shedding and shoot production in *Q. ilex* conforming to this pattern (Rapp 1969; Hernández et al. 1992; Ogaya and Peñuelas 2006).

Implications for the coexistence of evergreen and deciduous Mediterranean oaks

Under the current climatic conditions, coexisting populations of *Q. ilex* and *Q. faginea* in the NW Mediterranean

Basin are found in mountains where climate is relatively moist. According to our results, summer drought has a differential effect on the vegetative and reproductive growth of evergreen and winter deciduous oaks, and consequently, the current equilibrium between coexisting populations of both species may be disrupted if summer conditions change. For example, if summers become longer and drier in the next decades, as predicted by global change models for the Mediterranean region (IPCC 2007), both bud development and acorn production of the winter deciduous would be more severely affected than those of the evergreen. Summer drought can affect the final stages of shoot growth and leaf maturation in *Q. ilex*. However, according to our results, this occurs only when drought episodes are extreme. Therefore, although both species will be negatively affected, harsher summers will decrease both the vegetative growth and the reproductive ouput of the winter deciduous in the following years. If bud development is decreased, the canopy development of *Q. faginea* will be reduced, and this would affect its ability to compete for space and light. Also, if the acorn yield of *Q. faginea* is lower, it would have fewer chances of regenerating and colonizing new sites. All these changes may lead to the competitive exclusion of the winter deciduous species by the evergreen, which would expand its distribution area.

Conclusions

This study shows that coexisting evergreen (*Q. ilex*) and winter deciduous (*Q. faginea*) Mediterranean oaks have important differences in their summer phenology and growth activities. Although both study species perform an important fraction of the phenological cycle during summer, the growth activity of the winter deciduous species was lower as compared to the evergreen in several phenophases (secondary growth, bud development, fruit growth). Furthermore, bud development was more severely affected by summer drought in *Q. faginea* than in *Q. ilex*, which may have important consequences for the subsequent canopy development of *Q. faginea*. Also, fruit production was always lower in the winter deciduous. These results have relevant implications for the coexistence of both species as they show that a shift in summer drought conditions may alter their relative competitive ability, and consequently, future species abundance and distribution.

References

Acherar M, Rambal S (1992) Comparative water relations of four Mediterranean oak species. Vegetatio 99–100:177–184. doi:10.1007/BF00118224

Amaral Franco J (1990) *Quercus*. In: Castroviejo S, Laínz M, López González G, Montserrat P, Muñoz Garmendia F, Paiva J, Villar L (eds) Flora Iberica, vol 2. Real Jardín Botánico CSIC, Madrid, pp 15–36

Barbero M, Loisel R, Quézel P (1992) Biogeography, ecology and history of Mediterranean *Quercus ilex* ecosystems. Vegetatio 99–100:19–34. doi:10.1007/BF00118207

Bonfil C, Cortés P, Espelta JM, Retana J (2004) The role of disturbance in the coexistence of the evergreen *Quercus ilex* and the deciduous *Quercus cerrioides*. J Veg Sci 15:423–430. doi:10.1658/1100-9233(2004)015[0423:TRODIT]2.0.CO;2

Cabezudo B, Pérez Latorre AV, Navarro T, Nieto Caldera JM (1993) Estudio fenomorfológico en la vegetación del sur de España. II. Alcornocales Mesomediterráneos (Montes de Málaga, Málaga). Acta Bot Malacitana 18:179–188

Campelo F, Gutiérrez E, Ribas M, Nabais C, Freitas H (2007) Relationships between climate and double rings in *Quercus ilex* from northeast Spain. Can J Res 37:1915–1923. doi:10.1139/X07-050

Castro-Díez P, Montserrat-Martí G (1998) Phenological pattern of fifteen Mediterranean phanaerophytes from *Quercus ilex* communities of NE-Spain. Plant Ecol 139:103–112. doi:10.1023/A:1009759318927

Castro-Díez P, Villar-Salvador P, Pérez-Rontomé C, Maestro-Martínez M, Montserrat-Martí G (1997) Leaf morphology and leaf chemical composition in three *Quercus* (Fagaceae) species along a rainfall gradient in NE Spain. Trees (Berl) 11:127–134

CC IP (2007) Summary for policy makers. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor MMHL (eds) Climate Change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

Collin P, Badot PM, Millet B (1996) Croissance rythmique et développement du chêne rouge d'Amérique, *Quercus rubra* L, cultivé en conditions contrôlées. Ann Sci For 53:1059–1069. doi:10.1051/forest:19960602

Corcuera L, Camarero JJ, Gil-Pelegrín E (2004) Effects of a severe drought on *Quercus ilex* radial growth and xylem anatomy. Trees (Berl) 18:83–92. doi:10.1007/s00468-003-0284-9

Damesin C, Rambal S, Joffre R (1998) Co-occurrence of trees with different leaf habit: a functional approach on Mediterranean oaks. Acta Oecol 19:195–204. doi:10.1016/S1146-609X(98)80024-6

De Lillis M, Fontanella A (1992) Comparative phenology and growth in different species of the Mediterranean maquis of central Italy. Vegetatio 99–100:83–96. doi:10.1007/BF00118213

Del Arco JM, Escudero A, Vega Garrido M (1991) Effects of site characteristics on nitrogen retranslocation from senescing leaves. Ecology 72:701–708. doi:10.2307/2937209

Epron D, Dreyer E (1990) Stomatal and non stomatal limitation of photosynthesis by leaf water deficits in three oak species: a

comparison of gas exchange and chlorophyll a fluorescence data. Ann Sci For 47:435–450. doi:10.1051/forest:19900503

Escudero A, Del Arco JM, Sanz IC, Ayala J (1992) Effects of leaf longevity and retraslocation efficiency on the retention time of nutrients in the leaf biomass of different woody species. Oecologia 90:80–87. doi:10.1007/BF00317812

Espelta JM, Cortés P, Molowny-Horas R, Sánchez-Humanes B, Retana J (2008) Masting in acorn production mediated by summer drought reduces acorn predation in two sympatric Mediterranean oaks. Ecology 89:805–817. doi:10.1890/07-0217.1

FAO (1998) World reference base for soil resources, Roma

Floret C, Galan MJ, Floc'h El, Leprince F, Romane F (1989) France. In: Orshan G (ed) Plant pheno-morphological studies in Mediterranean type ecosystems. Kluwer, Dordrecht, pp 9–97

Fontaine F, Chaar H, Colin F, Clément C, Burrus M, Druelle JL (1999) Preformation and neoformation of growth units on 3-year-old seedlings of Quercus petraea. Can J Bot 77:1623–1631. doi:10.1139/cjb-77-11-1623

García-Mozo H, Gómez-Casero MT, Domínguez E, Galán C (2007) Influence of pollen emission and weather-related factors on variations in holm-oak (Quercus ilex subsp. ballota) acorn production. Environ Exp Bot 61:35–40. doi:10.1016/j.envexpbot.2007.02.009

Hanover JW (1963) Geographic variation in ponderosa pine leader growth. For Sci 9:86–95

Hernández I, Gallardo JF, Santa Regina I (1992) Dynamic of organic matter in forests subject to a Mediterranean semi-arid climate in the Duero basin (Spain): litter production. Acta Oecol 13:55–65

Hikosaka K (2005) Leaf canopy as a dynamic system: ecophysiology and optimality in leaf turnover. Ann Bot (Lond) 95:521–533. doi:10.1093/aob/mci050

Isik K (1990) Seasonal course of height and needle growth in Pinus nigra grown in summer-dry Central Anatolia. For Ecol Manage 35:261–270

Juárez-López J, Escudero A, Mediavilla S (2008) Ontogenetic changes in stomatal and biochemical limitations to photosynthesis of two co-occurring Mediterranean oaks differing in leaf life span. Tree Physiol 28:367–374

MacDonald AD, Mothersill DH, Caesar JC (1984) Shoot development in Betula papyrifera. III. Long-shoot organogenesis. Can J Bot 62:437–445. doi:10.1139/b84-066

McDonald PM (1992) Estimating seed crops of conifer and hardwood species. Can J Res 22:832–838. doi:10.1139/x92-112

Mediavilla S, Escudero A (2003a) Relative growth rate of leaf biomass and leaf nitrogen content in several Mediterranean woody species. Plant Ecol 168:321–332. doi:10.1023/A:1024496717918

Mediavilla S, Escudero A (2003b) Photosynthetic capacity, integrated over the lifetime of a leaf, is predicted to be independent of leaf longevity in some tree species. New Phytol 159:203–211. doi:10.1046/j.1469-8137.2003.00798.x

Mediavilla S, Escudero A (2004) Stomatal responses to drought of mature trees and seedlings of two co-occurring Mediterranean oaks. For Ecol Manage 187:281–294

Mediavilla S, Escudero A, Helmeier H (2001) Internal leaf anatomy and photosynthetic resource-use efficiency: interspecific and intraspecific comparisons. Tree Physiol 21:251–259

Milla R, Castro-Díez P, Maestro-Martínez M, Montserrat-Martí G (2005a) Does the gradualness of leaf shedding govern nutrient resorption from senescing leaves in Mediterranean woody plants? Plant Soil 278:303–313. doi:10.1007/s11104-005-8770-z

Milla R, Castro-Díez P, Maestro-Martínez M, Montserrat-Martí G (2005b) Environmental constraints on phenology and internal nutrient cycling in the Mediterranean winter-deciduous shrub

Amelanchier ovalis Medicus. Plant Biol 7:182–189. doi:10.1055/s-2005-837469

Montserrat-Martí G, Pérez-Rontomé C (2002) Fruit growth dynamics and their effects on the phenological pattern of native Pistacia populations in NE Spain. Flora 197:161–174

Montserrat-Martí G, Palacio-Blasco S, Milla Gutiérrez R (2004) Fenología y características funcionales de las plantas leñosas mediterráneas. In: Valladares F (ed) Ecología del bosque mediterráneo en un mundo cambiante. Ministerio de Medio Ambiente, Madrid, pp 129–162

Mooney HA (1983) Carbon-gaining capacity and allocation patterns of Mediterranean climate plants. In: Kruger FJ, Mitchell DT, Jarvis JUM (eds) Mediterranean-type ecosystems. The role of nutrients. Springer, Berlin, pp 103–119

Mudelsee M (2003) Estimating Pearson's correlation coefficient with bootstrap confidence interval from serial dependent time series. Math Geol 35:651–665. doi:10.1023/B:MATG.0000002982.52104.02

Nitta I, Ohsawa M (1998) Bud structure and shoot architecture of canopy and understorey evergreen broad-leaved trees at their northern limit in East Asia. Ann Bot (Lond) 81:115–129. doi:10.1006/anbo.1997.0545

Ogaya R, Peñuelas J (2006) Contrasting foliar responses to drought in Quercus ilex and Phillyrea latifolia. Biol Plant 50:373–383. doi:10.1007/s10535-006-0052-y

Park E, Lee YJ (2001) Estimates of standard deviation of Sperman's rank correlation coefficients with dependent observations. Comm Stat Simul Comp 30:129–142. doi:10.1081/SAC-100001863

Peñuelas J, Filella I (2001) Responses to a warming world. Science 294:793–795. doi:10.1126/science.1066860

Pulido F, Díaz M (2005) Regeneration of a Mediterranean oak: a whole cycle approach. Ecoscience 12:92–102. doi:10.2980/i1195-6860-12-1-92.1

Quézel P, Médail F (eds) (2003) Ecologie et biogéographie des forêts du basin méditerranéen. Elsevier, Paris

Rapp M (1969) Production de litière et apport au sol d'éléments minéraux dans deux écosystèmes méditerranéens: la fôret de Quercus ilex L. et la garrigue de Quercus coccifera L. Oecol Plant 4:377–410

Reich PB, Ellsworth DS, Walters MB, Vose JM, Gresham C, Volin JC, Bowman WD (1999) Generality of leaf trait relationships: a test across six biomes. Ecology 80:1955–1969

Remphrey WR, Davidson CG (1994) Shoot preformation in clones of Fraxinus pennsylvanica in relation to site and year of bud formation. Trees (Berl) 8:126–131. doi:10.1007/BF00196636

Remphrey WR, Powell GR (1984) Crown architecture of Larix laricina saplings: shoot preformation and neoformation and their relationships to shoot vigour. Can J Bot 62:2181–2192. doi:10.1139/b84-298

Salleo S, Lo Gullo MA (1990) Sclerophylly and plant water relations in three Mediterranean Quercus species. Ann Bot (Lond) 65:259–270

Thorp TG, Aspinall D, Sedgley M (1994) Preformation of node number in vegetative and reproductive proleptic shoot modules of Persea (Lauraceae). Ann Bot (Lond) 73:13–22. doi:10.1006/anbo.1994.1002

Tretiach M (1993) Photosynthesis and transpiration of evergreen Mediterranean and deciduous trees in an ecotone during a growing season. Acta Oecol 14:341–360

Villar-Salvador P, Castro Díez P, Pérez Rontomé C, Montserrat-Martí G (1997) Stem xylem features in three Quercus (Fagaceae) species along a climatic gradient in NE Spain. Trees (Berl) 12:90–96

Willmott CJ, Rowe CM, Mintz Y (1985) Climatology of the terrestrial seasonal water cycle. J Climatol 5:589–606. doi:10.1002/joc.3370050602