Trees (1994) 9: 41–46

Structure and Function
Trees

Phenological and growth patterns of the Mediterranean oak *Quercus suber* L.

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Received: 25 October 1993/Accepted: 19 January 1994

Abstract. The phenology of *Quercus suber* L., a dominant species of the montados in the Iberian Peninsula, was studied for 2 years in southwest Portugal. The seasonal progression of phenological events was analyzed in seven trees. Selected branches were examined monthly for shoot elongation, leaf number, branching, flowering, and fruiting. Radial stem growth and specific leaf weight were also studied. Active growth was observed from early spring to early summer. Reserves accumulated during winter and high photosynthetic activity in early spring apparently supported this strong development. The growth flush started with stem radial increment, which seemed to be impaired by spring rainfall. Male inflorescence production was the next phenological event. Old leaves were shed during new twig and leaf emergence. Shoot elongation and the number of new leaves produced were well correlated with the previous-year shoot's length, and were not clearly related to climatic factors. Radial growth resumed in autumn at a lower rate than in the previous spring, a possible consequence of a reserve depletion due to lower photosynthetic production in summer and investment on fruit maturation, which was complete by late autumn. Premature and excessive new leaf production were apparently subjected to self-pruning strategies related to the development of each tree's crown. Younger cork-oaks produced shorter and fewer shoots per module, and more sclerophyllous leaves than the older ones. A high intra-specific variability was observed in all the results.

Key words: Phenology – Growth – Specific leaf weight – Trees – *Quercus suber* L.

Introduction

Growth of woody species has two components, one relating to increment of biomass, the other to the architectural arrangement of matter in space (Küppers 1985). Plants grow by iteration of modular units and, as a consequence, growth can be described in terms of the population dynamics of these structural units (Watkinson and White 1985). Mechanisms have evolved to limit growth of certain subunits and coordinate their development, so that the whole plant responds opportunistically to favorable environmental patches, while minimizing investment in areas that are shaded or otherwise innapropriate for growth (Waller 1986). Among others, phenological events can reflect the adaptative strategies of a species in a particular kind of ecosystem. Many factors such as temperature, soil conditions, genetical differences, age, herbivory, and below-ground competition, may affect shoot elongation, branching and leaf survivorship in natural forests.

During the past few years considerable attention has been given to the phenological and physiological responses of plants in Mediterranean climates (Mooney et al. 1974; Montenegro 1987; Tenhunen et al. 1987; Correia et al. 1992). In the Iberian Peninsula the montados (called dehesas in Spain) are extensive. Characterized by a low-density tree cover, these traditional "man-made" systems are mainly used for forestry and livestock farming, frequently associated with cereal crops. However, recent agricultural policies and social changes are leading to new land-use strategies and abandonment of rural areas, which make the stability and future of the montados and dehesas uncertain (Joffre 1991). It is thus important to characterize plant function within these ecosystems to obtain a basis for appropriate management purposes.

These systems are dominated by the evergreen oaks, *Quercus ilex* L. and *Quercus suber* L. There is not much literature available about the growth and phenology of these species under natural conditions (Pereira et al. 1987; Picolo and Terradas 1989; Cartan-Son et al. 1992). The present work is a first approach to the above-ground phenology of *Q. suber* emphasizing the leaf demography, flowering, shoot elongation and stem growth events, as well as the variation ranges occurring within a stand. These studies are integrated in a research project concerned with the relationships between climatic conditions and water relations, nutrient cycling and growth in this species.

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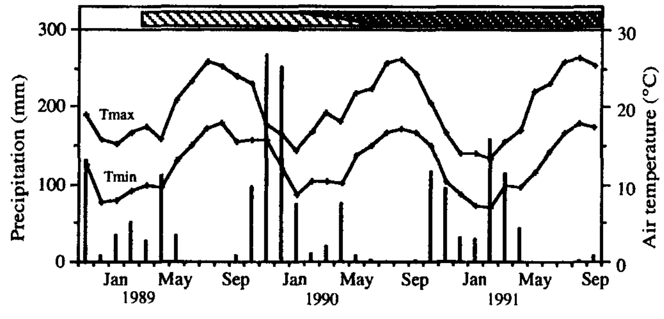

Fig. 1. Climatic characteristics recorded at the Monte Chãos weather station, 22 km SW of the study site. Air temperatures (monthly means) are represented by *lines*, and total precipitation by *vertical bars*. Duration of the phenological ▨, and the radial growth ▩ studies

Materials and methods

Site and climate. The study took place in a semi-natural cork-oak stand approximately 10 km north of Santiago do Cacém (38 ° 05′ N, 8 ° 39′ W, altitude 290 m), in southwest Portugal. The stand is a typical montado, with scattered *Q. suber* trees (93 trees/ha) of various ages, mainly exploited for cork production, and a herbaceous layer used for grazing, sometimes with pasture improvement. The soil is of sandy silt-loam nature and established on a Carbonic turbiditic bedrock.

The annual rainfall averages 760 mm and the mean annual temperature is 15.5 °C, while 6.0 °C is the mean minimum temperature of the coldest month (values from 1941–70). Climatic data from the nearest station (Monte Chãos, approx. 22 km SW of the site) was provided by the Instituto Nacional de Meteorologia e Geofísica. Rainfall and air temperatures occurring during the study are displayed in Fig. 1.

Monthly mean maximum air temperatures reached similar values during the 3 years of study (approx. 26 °C). In 1988/9 and 1990/1 the mean minimum air temperatures of the colder months were lower (8 °C and 7 °C, respectively), and lasted longer than in 1989/90 (9 °C). Spring 1990 was characterized by the earliest rise of air temperatures and low rainfall (Fig. 1). For 1990, the soil recharged with water during the previous season (October-January), contrasting with 1989 and 1991, when most rain fell in autumn and early spring. Cumulative values of rainfall from November to April show that 1990 was the wettest year (713 mm) and 1989 was the driest (380 mm). In spite of the different amounts of precipitation, soil water availability to the trees seemed to be similar on 1989 and 1990, as shown by the predawn values measured at the site (approx. –0.3 MPa throughout the year, except during summer, Oliveira et al. 1992).

Data collection. The work was carried out from March 1989 to mid-October 1991. Four mature and three young trees, all growing within 1 ha at the site, were selected and labelled A–G. Some of their characteristics are presented in Table 1.

Table 1. Some characteristics of the studied trees (*Q. suber*). Last year of stripping (YS), diameter at breast height (Dbh), height (H) and average crown diameter (CD)

Tree	YS	Dbh (m)	H (m)	CD (m)
A	1988	0.40[a]	12.5	17.0
B	1988	0.38[a]	8.0	9.0
C	1988	0.50[a]	9.5	14.5
D	1986	0.27[a]	7.0	9.0
E	1988[b]	0.21[a]	5.0	6.5
F	never stripped	0.18	3.5	5.5
G	never stripped	0.19	4.0	5.0

[a] measured upon the stripped surface

[b] stripped for the first time

For each tree, ten previous-year shoots from the lower canopy (1.5–2 m height) were labelled in March 1989. The development of these individual modules was followed and main axis length, branching, leaf number, and phenological events were recorded at monthly intervals. In each tree the coefficient of variation found for these parameters varied widely from 7 to 66%.

Radial stem growth (including cork and cambium) was measured on the stripped individuals using a depth micrometer (Series 129-Mitutoyo, MFG Co. Ltd., Tokyo, Japan) according to Fonseca (1989). Data refer to the south side of the trunk at breast height, and are expressed as basal area increments.

On a monthly basis, leaf samples were taken at random from the outer edge of each canopy (in all directions, at 2.5–3.5 m height), kept in polyethylene bags and brought to the laboratory for specific leaf weight determinations. Leaf area measurements were made with an area meter (model 3000, LICOR Inc., Lincoln, Neb., USA). Leaves were then oven dried (80 °C) for 24 h, and weighed.

Results

Phenology and shoot growth

Active growth was observed from April to late June (Fig. 2). The first obvious phenological event was the development of male inflorescences from axillary buds (data not shown). New shoots and leaves emerged afterwards, also from axillary buds. Old leaf fall began just before new shoot and leaf emergence and continued until late spring. Shoot elongation stopped before leaf emergence and expansion were complete. Female spikes appeared on the new shoots and bore 2–4 flowers each. The acorns, although scarce in the studied branches, were particularly abundant in trees A, B, and C. They became visible in July and attained full maturity by late autumn, in the same year. No flowers or fruits were observed in tree F during this study.

Current-year shoots were all produced from previous-year shoots and not from older ones, and lateral bud growth appeared to be as vigorous as that of terminal buds. Good correlations were found between the previous-year shoot's length and main shoot elongation ($P = 0.0297$), number of new leaves ($P = 0.0001$), and number of lateral twigs ($P = 0.0001$) produced. By the end of the growing season each previous-year's shoot had 2–8 lateral twigs, each with 4–10 leaves.

Most leaves emerged and expanded within 1 month but the period of leaf emergence lasted about 2 months. Leaf longevity was 11–12 months, although some leaves lasted longer (Fig. 3). A substantial mortality was observed for 1- to 4-month-old leaves in trees with high foliar production (A, B, E). Part of this mortality was directly related to the abcission of newly emerged twigs. Stress factors like drought or herbivory were not clearly connected to this mortality. The last cohort of leaves (emerged in July) did not appear to be more susceptible to early shedding than the leaves that emerged in June. Moreover, May leaves very seldom survived until the next growth season (Fig. 3). Herbivory can only partially explain mortality during periods of high leaf production (June 1989), since leaf mortality values in 1990 were still high (data not shown) but no obvious herbivory was then observed.

Shoot elongation was generally more pronounced in mature oaks (2.8–9.3 cm year^{-1}) than in young ones (trees F

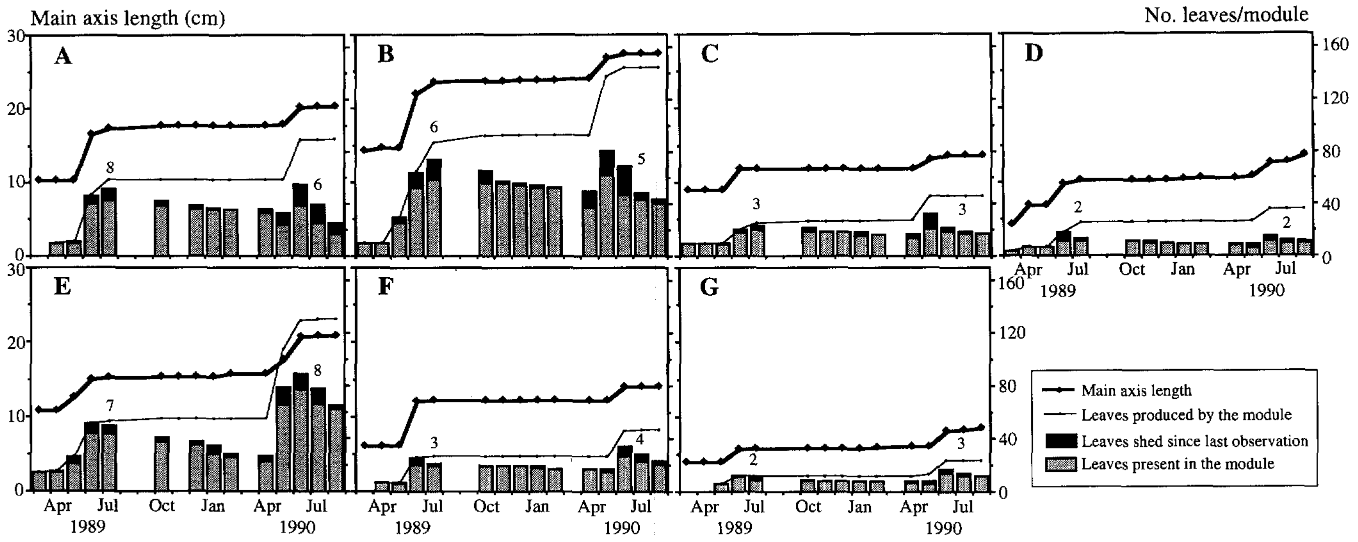

Fig. 2 A–G. Seasonal development of phenological parameters for the seven cork-oaks under study (A–G). *Numbers* indicate the average number of new lateral twigs produced per main shoot. Data refer only to the tagged modules surviving by the end of the study

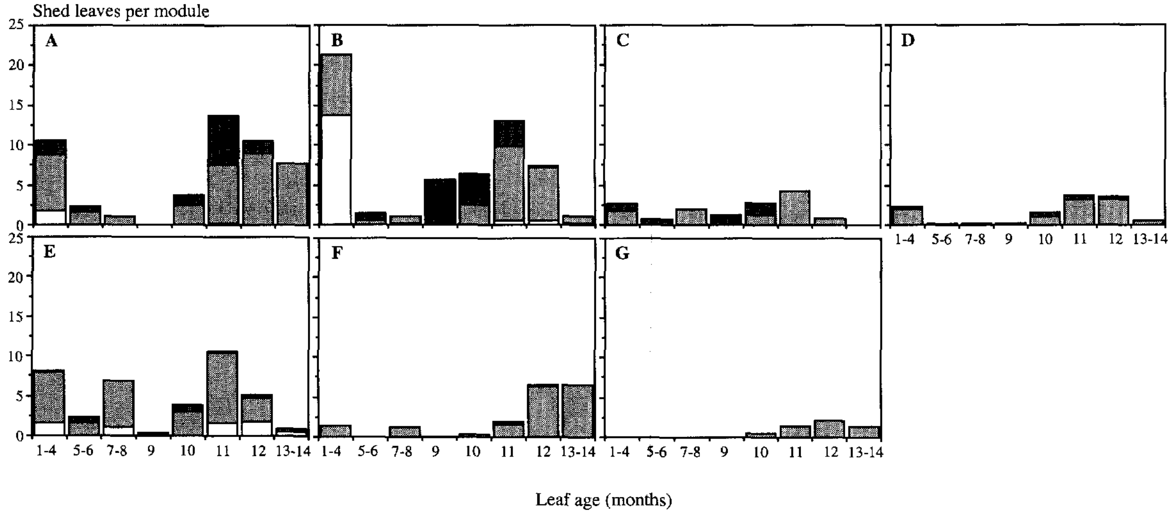

Fig. 3 A–G. Age and average number of shed leaves along the year (1989/90). Leaves emerged in May ☐, June ▨, and July ▩ 1989

and G with 1.8–6.2 cm year^{-1}). Shoot mortality was highly variable among trees, but tended to be more pronounced during the growth periods (Table 2).

Stem growth

Radial stem growth flush started before, and was more synchronous between trees, than all the other phenological events. It occurred throughout the year (though at different rates), in contrast to shoot elongation. Two different periods could be identified – one with a high growth rate, during spring; and a second one, corresponding to a smaller area increment, from early autumn to the next spring (Fig. 4). In 1990 the more intensive growth started in March and lasted about 4 months, resulting in a stem area increment of 14.8–57.2 cm^2. In the following year it began later (April) and basal area increment was smaller (14.5–41.3 cm^2).

Slight decreases in basal area were recorded during summer which may have derived from stem shrinkage at the time of measurements.

We observed a high variability in the stem area increment among trees (Fig. 4) which was apparently related to their sizes (Table 1). Larger trees (A and C) had higher area increments than smaller ones. Although it had the highest

Table 2. Percentage of dead shoots (relative to the ten shoots tagged on March 1989). Values are shown for each tree (A–G) and three consecutive periods. Total percentages of dead shoots (March 1989 to August 1990) are also shown

	A	B	C	D	E	F	G
Mar 1989–Jul 1989	20	30	30	30	10	0	0
Aug 1989–Feb 1990	40	0	30	0	0	0	10
Mar 1990–Aug 1990	0	30	0	20	20	30	0
Total	60	60	60	50	30	30	10

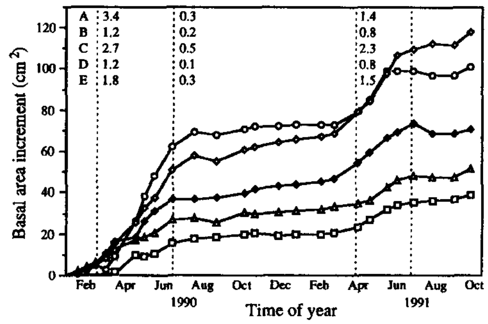

Fig. 4. Seasonal progression of basal area increment of the stripped trees. Trees A -○-, B -△-, C -◇-, D -□-, and E -◆-. Growth rates (cm^2 week^{-1}) are indicated for each tree in three different periods

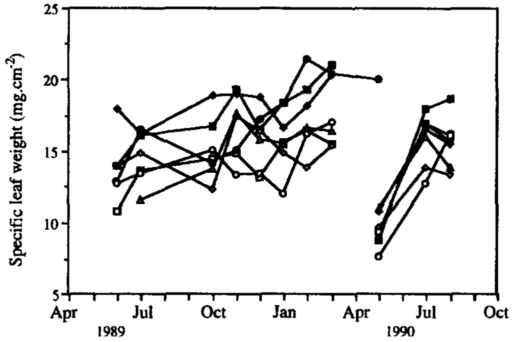

Fig. 5. Seasonal progression of specific leaf mass found for the seven trees under study. Trees A -○-, B -△-, C -◇-, D -□-, E -◆-, F -●-, G -■-. *Line gaps* indicate different leaf cohorts. Each point is the mean of the measurements on three subsamples

radial increment (data not shown), tree E only presented intermediate values of area increment as a consequence of its small girth.

Specific leaf weight (SLW)

A wide variability was apparent among trees, and mature individuals seemed to have less sclerophyllous leaves (Fig. 5). As expected, SLW was minimum in juvenile leaves (9.4 mg cm^{-2}, May 1990). Leaf emergence and expansion (and thickening) were very rapid, and the measurements frequency did not allow us to record the minimum SLW values on the first year.

The seasonal progression of SLW is not clear from our data, but maximum values were generally reached in early spring (approx. 21 mg cm^{-2} in March, trees F and G). The largest changes of SLW occurred in spring, during and immediately after leaf expansion. There was no clear decrease of SLW in the old leaves, prior to shedding.

Discussion

The growth patterns presented here are similar to those described for sclerophyllous species which have a very short growth period (Montenegro 1987; Correia et al. 1992). In the Mediterranean ecosystems the most favorable time for metabolic activity is in late spring when temperatures have become warm, but prior to limitations of summer drought (Mooney et al. 1974).

Stem area growth was the earliest and longest phenological event in *Q. suber*, only stopping (or strongly decreasing) when summer drought became too severe for photosynthetic activity (Oliveira et al. 1992). Different growth rates were recorded in autumn-winter and in spring. Although light and temperature were not apparently limiting after the first autumn rains, stem area did not greatly increase thereafter. It is possible that the strong vegetative and reproductive effort in the previous seasons had depleted the internal reserves of carbohydrates and thus, only a low stem growth rate could be maintained. In sclerophyllous species, carbon reserves accumulate during the mild Mediterranean winters (Larcher and Thomaser-Thin 1988). Such reserves are likely to support the strong stem development which started in early spring, as soon as the environmental conditions became favorable for growth.

Annual basal area increment was different between the 2 years of study, which might be related to different early spring water availabilities or to the lower winter and spring temperatures in 1991 (Fig. 1). Zhang and Romane (1991) suggest that spring rainfall probably plays a negative role in stem growth, either by affecting root development and thus, all the subsequent above-ground growth, or by diverting most of the energy to new shoots and leaves formation. Our results seemed to agree with this, since a smaller radial increment corresponded to a wetter early spring (Fig. 1). However, the timing and duration of stem growth might also be associated to previous winter rainfall or to spring temperatures (Pilcher and Gray 1982). Moreover, the regeneration rate of cork decreases gradually after the second year following bark-stripping (Natividade 1950). This probably also accounts for the smaller growth we observed in the second year of study.

Our results coincide with reports from Fritts (1976) and Caritat et al. (1992) in which young trees present the strongest radial growth. Nevertheless, the strongest stem area increment was observed in the larger trees. Basal area increment seemed to decrease with decreasing girth values. However, the area increment of the youngest tree was higher than could be expected from its diameter at breast height. This is explained by the strong radial development of this tree, probably due to the fact that it had been stripped for the first time in 1988. According to Natividade (1950), cork regeneration is faster after the first stripping than after the subsequent cork removals, and the regenerated cork layer is rather thick and porous.

Stem shrinkage has been described by Hinckley and Bruckerhoff (1975) for *Q. alba* under drought conditions. They measured diurnal variations of up to 0.6 mm in stem circumference. In cork-oak this shrinkage may be even more pronounced due to desiccation and contraction of an additional stem layer, the cork. At our study site, and especially in summer 1991, there was a marked decrease in relative air humidity (data not shown) and this might be the main reason for the "negative" increments measured during summer in some trees.

It is likely that the intense growth of new shoots in spring depends strongly on reserves accumulated from autumn and winter photosynthesis (Mooney et al. 1974; Pereira et al. 1987), but it was not clear from our study if it was triggered by rainfall and/or spring temperature events.

The importance of rainfall for shoot elongation referred by Sharifi et al. (1983) and Molinas et al. (1992) was not obvious in our results because the smaller main shoot elongation was observed in the wettest year (1990), the last year of study. Any positive effects of water availability on main axis growth might have been hidden by the fact that elongation seemed to become progressively smaller with the module's age (Fig. 2). This phenomenon, also referred by Molinas and Caritat (1989), might be typical of this species. Similarly to *Q. rubra* (Heichel and Turner 1984), *Q. suber* probably invests as much on lateral branching as on apical growth.

Leaf longevity was similar to that reported by Pereira et al. (1987) studying young *Q. suber* individuals, but the high leaf mortality they observed was generally not found in our young oaks. It seemed to depend on the amount of new leaves produced, or on their prematurity, rather than on the tree's age or size.

Studying cork-oaks in NE Spain, Caritat et al. (1992) found the more vigorous shoot elongation in young trees. The opposite was observed in our case possibly due to the absence of a strong competition for light in our rather open forest system. Moreover, stronger competition for water by the larger trees might have also played an important role in this result.

It is possible that the vascular system was still not entirely efficient when the first new twigs and leaves emerged. This would partially explain their high mortality. Moreover, twig abscission during the growth season was described for several *Quercus* species (including *Q. suber*) by Escudero et al. (1987) and is probably related to an architectural "prearrangement" of the typically open canopy in this oak. The fact that the smaller trees in our study presented the lowest values of shoot mortality seems to agree with this.

The wide range of SLW values obtained was probably a consequence of the great variability in leaf area mass, density, and thickness resulting from environmental effects, and which is apparent even between leaves on the same plant (Witkowski and Lamont 1991). The fact that younger trees' crowns were more homogeneously exposed to high light intensities than the others might be directly responsible for the higher SLW values they presented. Nevertheless (or as a consequence of their variability) our values were similar to the ones reported for *Q. suber* by several authors (Pereira et al. 1987; Picolo and Terradas 1989; Santos Loureiro 1990). Only Salleo and LoGullo (1990) found lower SLW for cork-oak, studying 5-year-old plants, and accordingly they suggested that this species might not be regarded as a true sclerophyll. The values found in our work do not support this idea. The decrease of SLW in the old leaves prior to shedding, reported for deciduous species (Jurik 1986; Harrington et al. 1989), was not clearly apparent for this evergreen oak. The fact that most of the leaf biomass was invested in structural components might explain this, as well as the need for fully functional leaves when environmental conditions favour photosynthetic activity (early spring).

The rapid leaf emergence, expansion, and thickening observed in this study suggest not only a protection strategy against desiccation and herbivory (Mooney et al. 1974), but also an opportune investment while water availability and climatic conditions are still suitable for maximum photosynthetic production (Dougherty et al. 1979; Oliveira et al. 1992). According to McLaughlin and McConathy (1979), most of the carbon was probably incorporated into new leaves and shoots during this period. Later, it might have been supplied to the developing acorns (Mooney and Hays 1973), which would explain the decrease of specific leaf weight values observed for some trees during the fruit maturation period (Fig. 5). Decreases in specific leaf weight recorded in mid-summer and winter might be related to starch depletion, reported by Larcher and Thomaser-Thin (1988) for several Mediterranean sclerophylls. Such a requirement for reserves would result from a lower photosynthetic activity during those periods (Oliveira et al. 1992).

The importance of the root system development should also be considered. The growth trends here described for this evergreen species are similar to those reported for a deciduous oak by Dougherty et al. (1979), and it is likely that an equivalent below-ground dynamics occurs for *Q. suber*. Those authors observed that root and stem cambial growth were the first phenological events, ceasing by the time of leaf expansion, and resuming after leaves became a major exporter of photosynthate.

The date of the last stripping was not clearly related to the phenological trends and growth rates, but our results suggested a strong development for young trees stripped for the first time.

Since crown position and location along the branch are discriminative factors for several phenological parameters in *Q. suber* (Picolo and Terradas 1989) our results from low branches should only be extrapolated to the whole tree with care. However, we believe that differences between lower and upper crown phenology are not very important in this oak growing in open systems and developing rather low and wide canopies (Oliveira et al. 1993). The absence of a strong competition for light among trees in this sort of open forest is probably responsible for a more or less homogeneous branch elongation and development, not favouring the apical growth of "main" shoots.

The onset of the phenological events was not simultaneous for all trees and their duration was also different. For all the studied parameters a clear intraspecific variability was apparent. Younger trees showed a different growth pattern, producing shorter and fewer new shoots than mature individuals. They further presented the lowest rates of leaf and branch mortality, and the more sclerophyllous leaves. However, even among the mature oaks there were sharp differences in the number of leaves and lateral twigs produced, shoot elongation, leaf longevity and stem growth. As stated by Crawley and Akhteruzzaman (1988), theoretical models based on the assumption that populations consist of groups of uniform individuals, must be viewed with caution.

Acknowledgements. We thank the many people who assisted in field data collection. This work was supported by JNICT grants FSE/A-160 and BD/1630-IE to G. Oliveira.

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