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ORIGINAL PAPER

Revisiting the fate of buds: size and position drive bud mortality and bursting in two coexisting Mediterranean *Quercus* species with contrasting leaf habit

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Abstract Understanding the relationships between bud size and position and bud fate through time is crucial for identifying and subsequently modeling the mechanisms underlying tree architecture. However, there is a lack of information on how bud size drives crown architectural patterns in coexisting tree species. We studied bud demography in two coexisting Mediterranean oak species with contrasting leaf habit (*Quercus ilex*, evergreen; *Q. faginea*, deciduous). The main objective was to analyse the effect of bud size on the fate of buds with different positions along the shoot (apical, leaf axillary and scale-cataphyll axillary buds). The number, length and position of all buds and stems were recorded in marked branches during 4 years. Study species presented different strategies in bud production and lifespan. The evergreen species showed greater mortality rate than the deciduous one, which produced larger buds. Bud size and position were highly related since apical buds where longer than axillary ones and bud length declined basipetally along the stem. Apical buds had also higher chances of bursting than axillary ones. Within positions, longer buds presented a higher probability of bursting than shorter ones, although no absolute size threshold was found below which bud bursting was impaired. In *Q. ilex*, four-year-old buds were still viable and able to burst, whereas in *Q. faginea* practically all buds burst in their first year or died soon after. Such different bud longevities may indicate contrasting strategies in primary growth between both species. *Q. ilex* is able to accumulate viable buds for several ages, whereas *Q. faginea* seems to rely on the production of large current-year buds with high bursting probability under favourable environmental conditions.

Keywords Bud demography · Bud size · Bud position · Budburst · *Quercus ilex* subsp. *ballota* · *Quercus faginea*

Introduction

Bud production and survival in combination with shoot length and orientation within the crown determine tree architecture (Maillette 1982a; Harmer 1991, 1992). Identifying the factors that determine budburst is hence crucial to manage forest trees and construct reliable models on tree canopy development (Barthélémy and Caraglio 2007). After overwintering, and except in the rare buds that produce shoots in the same year of their formation (lammas

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shoots), most buds grow into new shoots in the next spring, whereas the rest die and abscise or become dormant, persisting in older shoots (Ward 1964; Gill 1971; Wilson and Kelty 1994). It is well established that the ultimate fate of buds depends strongly on bud position, both within the crown and along the shoot, and on shoot age (Maillette 1982a; Macdonald et al. 1984; Jones and Harper 1987; Sabatier and Barthélémy 2001). For example, buds within the crown may produce either long or short shoots in birch (Maillette 1982a) but young branches produce more buds and have lower bud mortality than older ones, thus leading to a variable amount of living buds between years (Jones and Harper 1987). In tree species with preformed shoots, such as *Quercus* species (Fontaine et al. 1999; Barthélémy and Caraglio 2007), bud size might also determine bud fate and explain different patterns in bud production (Maillette 1982b). However, as far as we know, the potential effects of bud size on the bud fate of broadleaf trees remain unexplored (Maillette 1982a, 1987; Jones and Harper 1987; Lehtilä et al. 1994; Tolvanen et al. 2002; Negi 2006).

Mediterranean *Quercus* species display a large year-to-year variability in bud size related to different factors like climate, tree vigour and size, and the position of buds within the crown (Alla et al. 2013). Bud size also depends on the position of buds along the parent shoot (Buck-Sorlin and Bell 2000). For instance, it is well established that apical buds exert a strong dominance over the other buds in the shoot, i.e. they display higher vigour and have greater probabilities to produce shoots than the rest of buds (Sabatier and Barthélémy 2001; Puntieri et al. 2002). However, no previous study has assessed the relationship between bud size and bud fate on the following years, how such relationship depends on bud position within the shoot, and the inter-annual variability of the relationship between bud size and fate in broadleaved tree species.

The aim of this study was to analyse the effect of bud size on the fate of buds of two coexisting Mediterranean oak species with contrasting leaf habit: *Q. ilex* L. subsp. *ballota* (Desf.) Samp. (evergreen; hereafter abbreviated as *Q. ilex*) and *Q. faginea* Lam. (winter deciduous), considering different bud positions within the shoot (apical, leaf axillary and scale-cataphyll axillary buds). Both oak species present scaled buds and preformed shoot growth (Nitta and Ohsawa 1998; Alla et al. 2013). Specifically, we tested

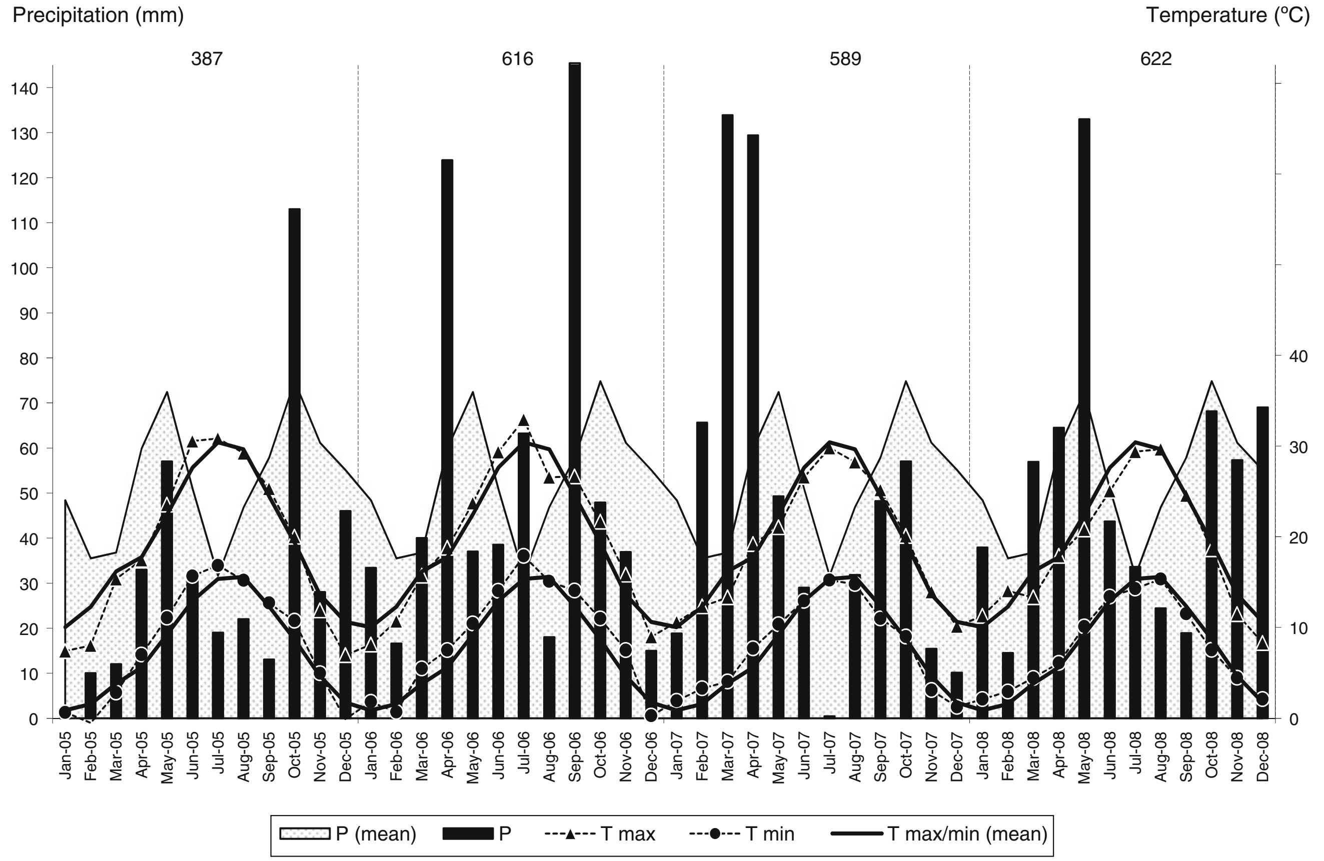


Fig. 1 Total monthly precipitation (P) and mean monthly maximum and minimum temperatures ($T_{\max}$ and $T_{\min}$, respectively) during the studied period, and long-term average values [abbreviations followed by "(mean)"]. Climatic data were obtained from Ayerbe station (north eastern Spain). The numbers at the top of each year indicate total annual precipitation

Table 1 Morphological features of study trees (mean ± SE) and numbers of sampled trees and branches, plus shoots and buds measured in the different study years

Species	Diameter at 1.3 m (cm)	Height (m)	No. stems per tree	Age at 1.3 m (years)	No. trees (branches)				No. shoots				No. buds			
					2005	2006	2007	2008	2005	2006	2007	2008	2005	2006	2007	2008
Q. ilex	10.3 ± 0.9b	4.9 ± 0.3b	5.2 ± 0.9	29 ± 4	10 (20)	10 (20)	10 (10)	7 (7)	131	205	86	52	987	1367	571	262
Q. faginea	13.7 ± 0.8a	7.4 ± 0.4a	3.8 ± 0.7	33 ± 2	10 (20)	10 (20)	8 (8)	7 (7)	135	310	174	155	845	1725	1140	774

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

the following hypotheses: (1) larger buds will have higher chances to burst on the following years than smaller buds, and (2) there will be a threshold of bud size below which budburst will be impaired, such size threshold will be larger in apical buds than in the rest of buds. The fulfilment of these objectives may allow disentangling some coexistence mechanisms of both oak species related to contrasting patterns of bud size, bud fate and shoot production.

Materials and methods

Study site and species

The study site is located in Agüero, Huesca province, Aragón, northeastern Spain (42°18′N, 0°47′W, 750 m a.s.l.). Climate is Mediterranean and continental being characterized by a dry summer and a cold winter with 631 mm and 13.8 °C of total annual precipitation and mean annual temperature, respectively. Monthly climatic data for the past 50 years and also for the study years (2005–2008) were obtained from Ayerbe meteorological station (42°16′ N, 0°41′ W, 585 m a.s.l.) located at ca. 10 km from the study site. The study years were characterized by wet spring conditions except for 2005 when warm and dry conditions prevailed in the first half of the year (Fig. 1). In fact, year 2005 recorded the second most severe drought affecting the study area since 1950, reaching a water deficit 66 % higher than the long-term mean (Supplementary Information, Fig. S1). Soil in this area is a Calcisol (FAO 1998), formed on Miocene clays with bedrock of calcareous sandstone. Vegetation is an open scrubland with scattered low trees, dominated by *Q. ilex*, *Q. faginea*, *Arbutus unedo* L. and *Pinus halepensis* Mill., approximately with similar dominance, and other less abundant woody species. For further details on the study site see Montserrat-Martí et al. (2009).

Quercus ilex is an evergreen oak tree usually forming shrubby-type crowns in the study area (Table 1), which in the Iberian Peninsula grows preferentially inland under continental conditions (Amaral Franco 1990). *Q. faginea* is a deciduous oak tree with tree-like crowns (Table 1) and a wide distribution in sub-Mediterranean areas mainly in the Iberian Peninsula (Amaral Franco 1990). The study species coexist in the study area forming multi-stemmed trees of similar age, but *Q. faginea* individuals are taller than *Q. ilex* ones (Table 1).

Branch demography

In January 2006, 10 mature individuals per species were randomly selected, tagged and their size (diameter at 1.3 m and height) and number of stems per tree were measured

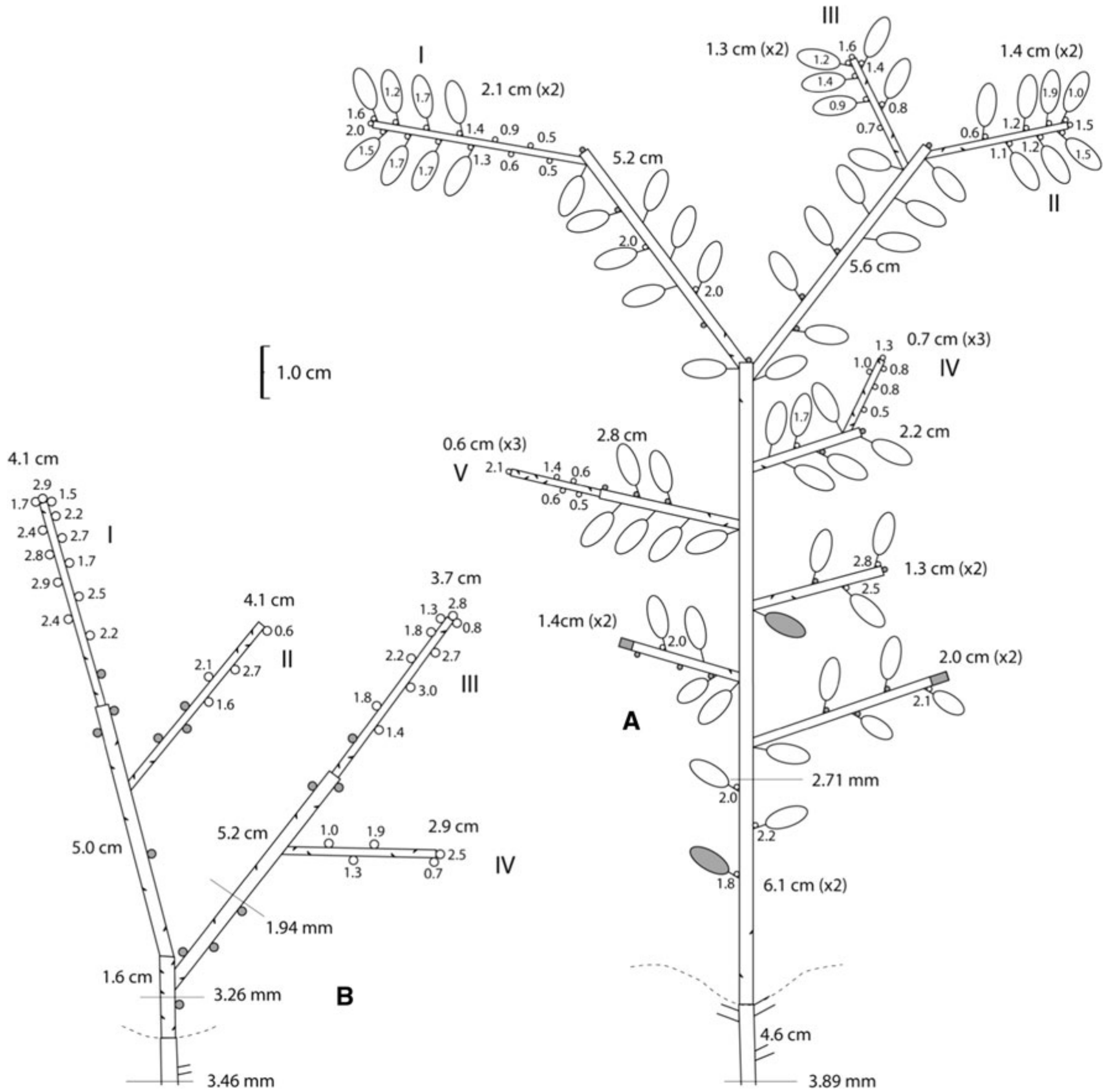


Fig. 2 Schematic representation of representative 3-year-old branches of *Q. ilex* (**a**) and *Q. faginea* (**b**) with all their components (shoots, leaves and buds) as measured in January. *Dashed lines* denote the base of the 3-year-old branch while straight continuous lines indicate stem diameters. Real stem-unit-growth lengths are displayed in *Q. faginea*, whereas the shoot lengths of *Q. ilex* were multiplied (in *parentheses*) to improve the visual clarity of the drawings. *Grey* apical parts of stems are dead. Current-year shoots were numbered from the apex to the base using Roman numbers. Leaves were only present in the branches of the evergreen species (*Q. ilex*). *White circles* represent living buds and *grey ones* dead buds. The length of buds (in mm) is presented near the living ones. *Scars* left by shed buds are shown by ticks

(Table 1). At this time of the year shoot development has been completed and canopies are in winter quiescence. Age of trees was estimated by taking radial cores at 1.3 m using a Pressler increment borer and counting annual tree rings. Within each tree, two 3-year-old branches were selected on the southern side of the crown. Branches were marked, drawn in synthetic diagrams and the numbers and length of their different cohorts of shoots, buds and leaves (in *Q. ilex*) recorded (see an example in Fig. 2). Number and position of dead buds at the beginning of the census were also recorded.

The length and fate (survival or abscission and, in buds, also burst) of the different cohorts of buds and shoots, and the number of leaves (just for *Q. ilex*) of each branch was measured annually during four consecutive years (from 2006 to 2009). The demography of the different elements within the branch was evaluated by comparing the diagrams drawn on each sampling year (Fig. 2). All elements within the branch were numbered from the apex to the base of the branch to facilitate their monitoring on each annual survey. On every sampling date, the following variables were measured in one-year-old shoots: length of living buds, number of living and dead buds and bud scars (the sum of these three numbers rendered total bud number per shoot). Living buds were categorized according to their position within the shoot as: apical, leaf axillary (buds arranged in leaf axes or in leaf scars in the case of the deciduous species; see Fig. 2) and scale-cataphyll axillary (buds in the axil of scales and cataphylls). Dead buds were mostly distinguished by their shrivelled typical appearance and branches without living buds were considered dead. This visual method for detecting dead buds was reliable since monitored dead buds did not burst and almost all of them were shed during the study period (2006–2009). The fate of buds was monitored in subsequent years by comparing consecutive drawings of the same branch. Shoots may remain or die and abscise, whereas buds may burst, die or remain dormant as part of the bud bank of the next winter. Data of all branches for the first 2 years were obtained non-destructively, but by the second and third year of sampling, several selected branches were cut down to reduce the number of studied shoots and buds (Table 1). We assume this would not affect the bud break probability of the remaining branches, given the large size of the crowns of the studied trees. In January 2009, all remaining branches were also harvested and the different measurements taken in the laboratory. Shoot and bud length were measured in the field at 10-× magnification using a measuring magnifier (Befort Wetzlar, Germany) and a centesimal calliper (Mitutoyo, Kawasaki, Japan), whereas in the laboratory, buds were measured to the nearest 0.1 mm under a stereomicroscope (MZ12.5 Leica Microsystems, Heerbrugg, Switzerland).

Data analyses

To test if bud position affected bud size, differences in the absolute frequencies of apical and axillary buds classified according to their size were assessed using the *G*-test (Sokal and Rohlf 1995). To estimate the probability of bud bursting in the next growing season as a function of bud length, we fitted binary logistic regressions. Since these data do not follow normal distributions, the differences in length between bursting and non-bursting buds were also assessed using Mann–Whitney *U* tests.

Bud mortality (*m*) was calculated using the formula proposed by Sheil et al. (1995) as:

$$m = 1 - (N_{\mathrm{t}}/N_{\mathrm{t}-1})^{1/t} \qquad (1)$$

where $N_{\mathrm{t}-1}$and N_{t} are bud counts at the beginning and end of the measurement interval, and t is the time between two measurements. Since in our case $t = 1$ year the equation may be simplified to $m = 1 - (N_{\mathrm{t}}/N_{\mathrm{t}-1})$.

We also calculated the annual production rate [$\lambda(t)$] of buds and current-year shoots to evaluate if the amounts of both branch components are in a net equilibrium or whether there is a deficit or a surplus of formed buds or shoots (Maillette 1982a). The rate $\lambda(t)$ was calculated following Ishihara and Kikuzawa (2009) as:

$$\lambda(t) = N(t)/N(t-1) \qquad (2)$$

where N is the total number of living buds or shoots in years t and $t-1$.

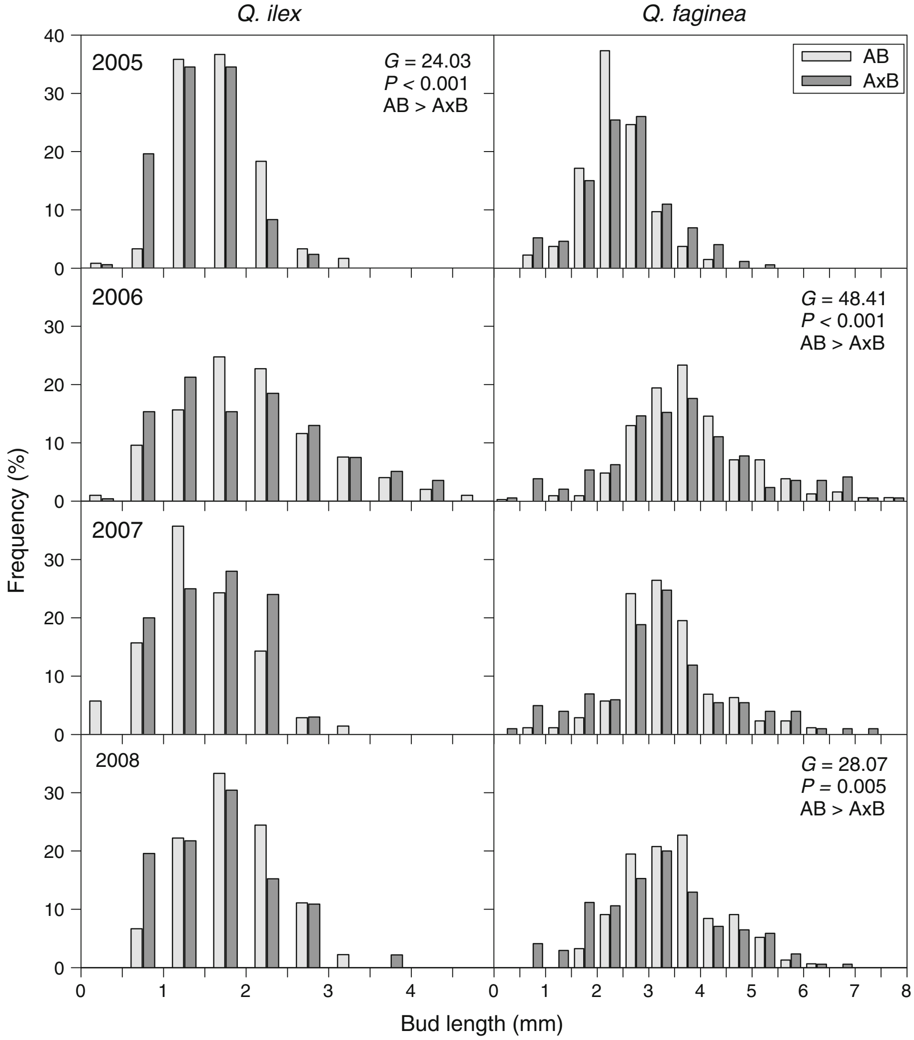
The effect of bud size on the fate of buds was explored by using Generalized Linear Mixed Models (GLMMs) taking into account the position of buds and the size of the parent shoot. Since there seemed to be a relationship between bud position and bud length, we first explored the relationship between both variables, evaluating if there were any differences in the size of buds with different positions along the parent shoot. To do this, a GLMM with "year" and "bud position" (apical/axillary) as fixed factors, "individual tree" and "branch" as random factors and the "length of the bearing shoot" as a covariate was fitted to the bud size data. Leaf and scale-cataphyll axillary buds were grouped as "axillary buds", since scale-cataphyll axillary buds produced very few shoots and could not be adequately analysed as a separate group. This analysis showed that bud position drove bud size to a high extent ($F = 695.1$, $P < 0.001$ and $F = 849.4$, $P < 0.001$, for *Q. ilex* and *Q. faginea*, respectively). Indeed, both variables were strongly correlated in both species ($r > 0.85$), when included as separate factors in the analysis. For this reason, and to avoid collinearity issues (Zuur et al. 2009), we explored the effect of bud size on bud fate by considering the interaction between "bud position" and "bud length" as a fixed factor, while disregarding individual effects of each factor separately. The model was completed as above by including "year" as a fixed factor, "individual tree" and "branch" as random factors and the "shoot length of the bearing shoot" as a covariate. Factor effects were tested by fitting a bimodal distribution to the response variable "bud fate". The stepwise analysis showed that the interaction between "year" and "bud position x bud size" led to collinearity issues, and was hence not considered in our analysis (Zuur et al. 2009). Finally, the individual effect of bud position on bud fate (irrespective of bud size) was explored by bimodal GLMMs with "bud position" and "year" as fixed factors, "individual tree" and "branch" as random factors and the "shoot length of the bearing shoot" as a covariate. Variables were introduced following a stepwise procedure to avoid collinearity issues. When required, variables were transformed to meet normality and/or homoscedasticity. Statistical analyses were performed using the "lattice" and "lme4" packages of the R program (R Development Core Team 2011).

Table 2 Mean (standard error) values of bud numbers per shoot, length of apical, leaf axillary and scale-cataphyll axillary buds, stem length and the percentage of buds bursting, persisting or dying within each bud position for the two species and the 4 years of study

Bud type	Variable	Units (year)	*Q. ilex*				*Q. faginea*			
			2005	2006	2007	2008	2005	2006	2007	2008
	Bud number per shoot		6.8 (0.3)	5.3 (0.2)	5.2 (0.3)	4.6 (04)	6.0 (0.2)	5.3 (0.1)	6.1 (0.2)	4.6 (0.2)
Apical buds	Length of all buds	mm (*t*)	1.79 (0.06)	2.13 (0.06)	1.49 (0.06)	1.87 (0.08)	2.46 (0.06)	3.92 (0.06)	3.46 (0.07)	3.52 (0.07)
	Length of bursting buds	mm (*t*)	1.91 (0.07)	2.44 (0.14)	2.19 (0.13)	–	2.50 (0.05)	4.01 (0.15)	3.45 (0.10)	–
	Stem length	cm ($t + 1$)	3.20 (0.23)	3.03 (0.35)	1.89 (0.31)	–	2.47 (0.15)	2.17 (0.24)	2.69 (0.05)	–
	Bursting buds	% ($t + 1$)	57.14	34.15	39.39	–	61.70	54.22	57.25	–
	Length of living buds	mm (*t*)	1.68 (0.15)	1.46 (0.15)	1.66 (0.15)	–	–	–	–	–
		mm ($t + 1$)	1.90 (0.19)	1.51 (0.12)	1.93 (0.19)	–	–	–	–	–
	Living buds	% ($t + 1$)	9.53	34.14	12.13	–	0.00	0.00	0.00	–
	Length of dead buds	mm (*t*)	1.62 (0.11)	2.14 (0.07)	1.32 (0.06)	–	2.41 (0.11)	3.66 (0.15)	3.58 (0.16)	–
	Dead buds	% ($t + 1$)	33.33	31.71	48.48	–	38.30	45.78	42.75	–
Leaf axillary buds	Length of all buds	mm (*t*)	1.34 (0.02)	1.75 (0.03)	1.10 (0.09)	1.61 (0.05)	2.14 (0.03)	3.07 (0.04)	2.69 (0.05)	2.91 (0.05)
	Length of bursting buds	mm (*t*)	1.71 (0.04)	2.39 (0.08)	1.40 (0.55)	–	2.59 (0.05)	4.07 (0.12)	3.25 (0.13)	–
	Stem length	cm ($t + 1$)	2.88 (0.11)	2.47 (0.14)	1.93 (0.50)	–	1.76 (0.06)	2.18 (0.15)	1.87 (0.13)	–
	Bursting buds	% ($t + 1$)	18.75	18.45	18.65	–	30.24	30.00	19.13	–
	Length of living buds	mm (*t*)	1.08 (0.04)	1.20 (0.05)	0.40[a]	–	0.97 (0.19)	1.64 (0.43)	2.07 (0.62)	–
		mm ($t + 1$)	1.37 (0.06)	1.48 (0.07)	1.10[a]	–	1.73 (0.70)	1.42 (0.17)	2.17 (0.64)	–
	Living buds	% ($t + 1$)	22.32	22.33	10.37	–	0.44	0.42	0.37	–
	Length of dead buds	mm (*t*)	1.20 (0.03)	1.74 (0.03)	1.10 (0.08)	–	1.91 (0.04)	2.96 (0.05)	2.62 (0.05)	–
	Dead buds	% ($t + 1$)	58.93	59.22	70.98	–	69.32	69.58	80.50	–
Scale-cataphyll axillary buds	Length of all buds	mm (*t*)	0.60 (0.02)	0.69 (0.03)	0.68 (0.05)	0.66 (0.04)	0.79 (0.05)	0.67 (0.03)	0.59 (0.02)	0.91 (0.06)
	Length of bursting buds	mm (*t*)	0.85 (0.05)	–	–	–	1.00[a]	0.70[a]	–	–
	Stem length	cm ($t + 1$)	1.95 (1.35)	–	–	–	1.70[a]	1.70[a]	–	–
	Bursting buds	% ($t + 1$)	1.63	0.00	0.00	–	3.13	0.63	0.00	–
	Length of living buds	mm (*t*)	0.70 (0.06)	0.88 (0.13)	–	–	0.92 (0.18)	1.20 (0.06)	1.65 (1.05)	–
		mm ($t + 1$)	1.15 (0.25)	1.43 (0.33)	–	–	1.26 (0.21)	1.75 (0.95)	2.45 (0.65)	–
	Living buds	% ($t + 1$)	3.25	2.69	0.00	–	14.71	1.39	1.82	–
	Length of dead buds	mm (*t*)	0.59 (0.02)	0.68 (0.03)	0.68 (0.05)	–	0.78 (0.06)	0.64 (0.05)	0.58 (0.01)	–
	Dead buds	% ($t + 1$)	95.12	97.31	100	–	82.16	97.98	98.18	–

[a] $n = 1$

Fig. 3 Distribution of apical (AB) and the largest axillary (AxB) buds according to their length. The distributions of lengths were compared among the two bud types using *G*-tests whose values and related significance levels (*P*) are presented in the case of significant differences ($P < 0.05$)



Results

Bud and shoot size variability across positions and time

Shoot length varied among species and years being usually longer in *Q. ilex* (mean ± SE = 2.90 ± 0.08 cm) than in *Q. faginea* (2.12 ± 0.05 cm) and differences between species were highly significant ($F = 69.87$, $P < 0.001$) (see also Supplementary Information, Fig. S2). The distributions of current-year shoot lengths were skewed towards short length values in both species. The shortest (longest) shoots were produced in 2008 (2006) and 2006 (2007) by *Q. ilex* and *Q. faginea*, respectively. The total number of buds produced per shoot varied as a function of the shoot length (Supplementary Information, Figs. S3 and S4). The mean number of living buds produced per shoot was 5.62 ± 0.14 in *Q. ilex* and 5.44 ± 0.09 in *Q. faginea* and differences between species were not significant ($F = 1.35$, $P = 0.24$) (Table 2).

Bud length varied from 0.2 to 4.7 mm in *Q. ilex* and from 0.2 to 7.8 mm in *Q. faginea*. The minimum bud length did not significantly differ between study years ($F = 0.93$, $P = 0.43$ in *Q. ilex* and $F = 2.68$, $P = 0.06$ in *Q. faginea*) whereas the maximum bud length varied across years in both species ($F = 7.58$, $P < 0.001$ in *Q. ilex* and $F = 7.63$, $P < 0.001$ in *Q. faginea*) with the largest buds being formed in 2006 in both species (Figs. 3, 4 and 5). Bud length varied significantly within shoot positions ($F = 695.11$, $P < 0.001$ and $F = 849.43$, $P < 0.001$, for *Q. ilex* and *Q. faginea*, respectively), declining basipetally along the shoot, i.e. from the largest apical buds to the smallest axillary scale buds (Table 2).

The mean length of apical buds was larger than that of axillary buds in all cases ($U = 19771$, $P < 0.001$ in *Q. ilex* and $U = 20955$, $P < 0.001$ in *Q. faginea*). However, apical buds were significantly larger than the largest axillary buds only in the driest year (2005) for *Q. ilex* and in more humid years (2006 and 2008) for *Q. faginea* (Fig. 3).

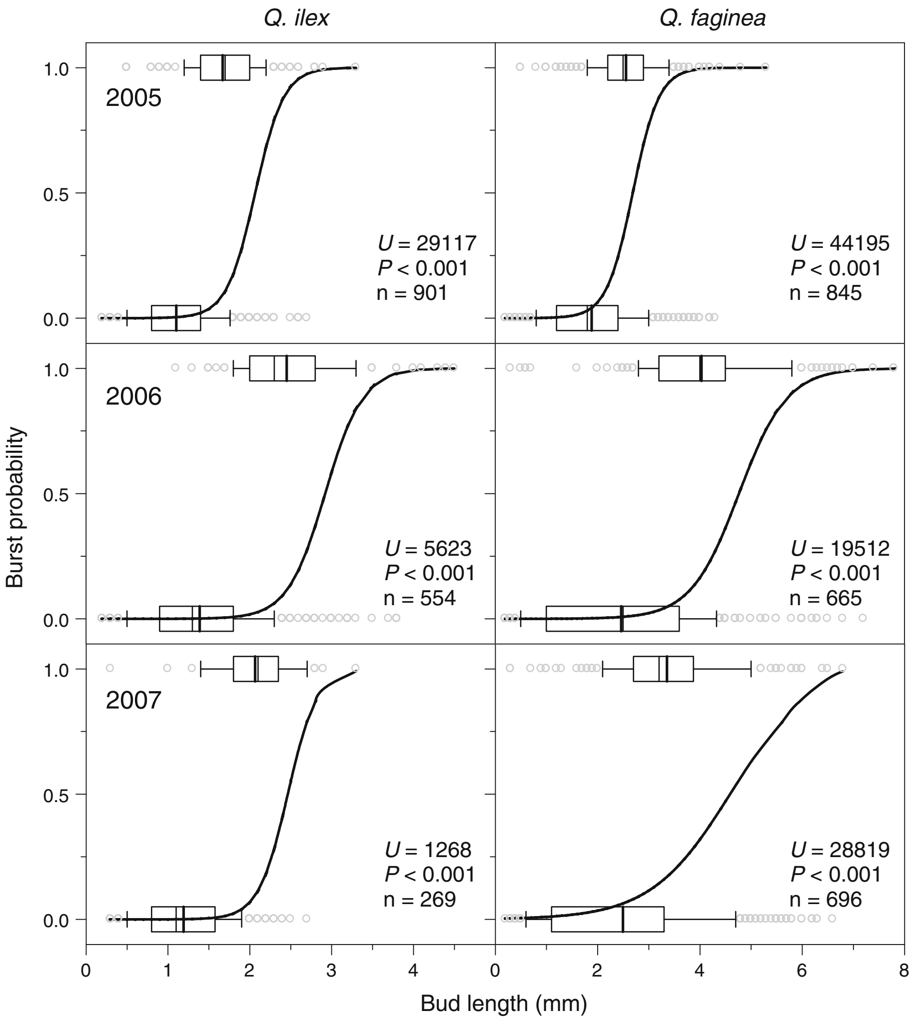


Fig. 4 Bursting probability for all living buds monitored according to their length. *Curves* correspond to fitted logistic models and boxes (showing median values as *thin lines* and *outliers*) to buds that died or remained dormant (0, non-bursting buds) or that developed a new shoot (1, bursting buds) in the following year *t* + 1, respectively. *Thin* and *thick lines* in *box plots* correspond to median and mean values, respectively. The length of bursting and non-bursting buds was compared using Mann–Whitney *U* tests (see "Materials and Methods" for further details)

Relationship between bud size, position and fate

Bud mortality during the year of bud formation ranged between 40 and 50 % and from 30 to 40 % in *Q. ilex* and *Q. faginea*, respectively (Table 2). Buds of *Q. ilex* showed the highest lifespan, since the four-year-old buds of this species were still able to burst. On the contrary, very few *Q. faginea* buds lived up to one (1 bud in 2004) or two (2 buds in 2005) years, but normally they died after the first spring. Indeed, the percentage of buds surviving their first spring varied among years from 9 % (2005) to 16 % (2006) in *Q. ilex* and, on average, 14 % of them were apical buds. Contrastingly, in *Q. faginea* the percentage of buds surviving after their first spring was less than 1 % over all studied years and all of them were axillary (Table 2). Lammas shoots were very scarce in the studied years, accounting for less than 1 % of all shoots, and being more frequent in *Q. faginea* than in *Q. ilex*, where they were present only in the last sampling year (data not shown).

GLMMs showed that bud size had a strong impact on the fate of buds in different positions (Table 3), larger buds having a higher probability to burst than smaller ones across bud positions (Figs. 4, 5). We found highly significant differences in length between bursting and non-bursting buds being more marked in axillary buds than in the case of apical ones. The only exceptions to this finding were the apical buds of *Q. faginea*, where the lengths of bursting buds did not significantly differ from non-bursting buds (Table 2; Fig. 5). Apical buds presented a higher probability of bursting than axillary buds and this difference was more marked in *Q. faginea* (54–62 vs. 17–29 %) than in *Q. ilex* (34–57 % vs. 15–17 %) since the latter species showed a huge variability in bursting probability among years (Table 2). Moreover, apical buds presented a lower mortality, varying from 30 to 50 % in both species, than the largest axillary buds, which presented mortality rates between 50 and 80 %. The relative frequency of bursting buds decreased as branches aged, being 17–25 % and 25–40 % in *Q. ilex* and *Q. faginea*, respectively.

The size of living buds with a 50 % probability to burst varied among years from 2.1 to 2.9 mm in *Q. ilex* and from 2.7 to 4.8 mm in *Q. faginea*, being the largest bursting buds

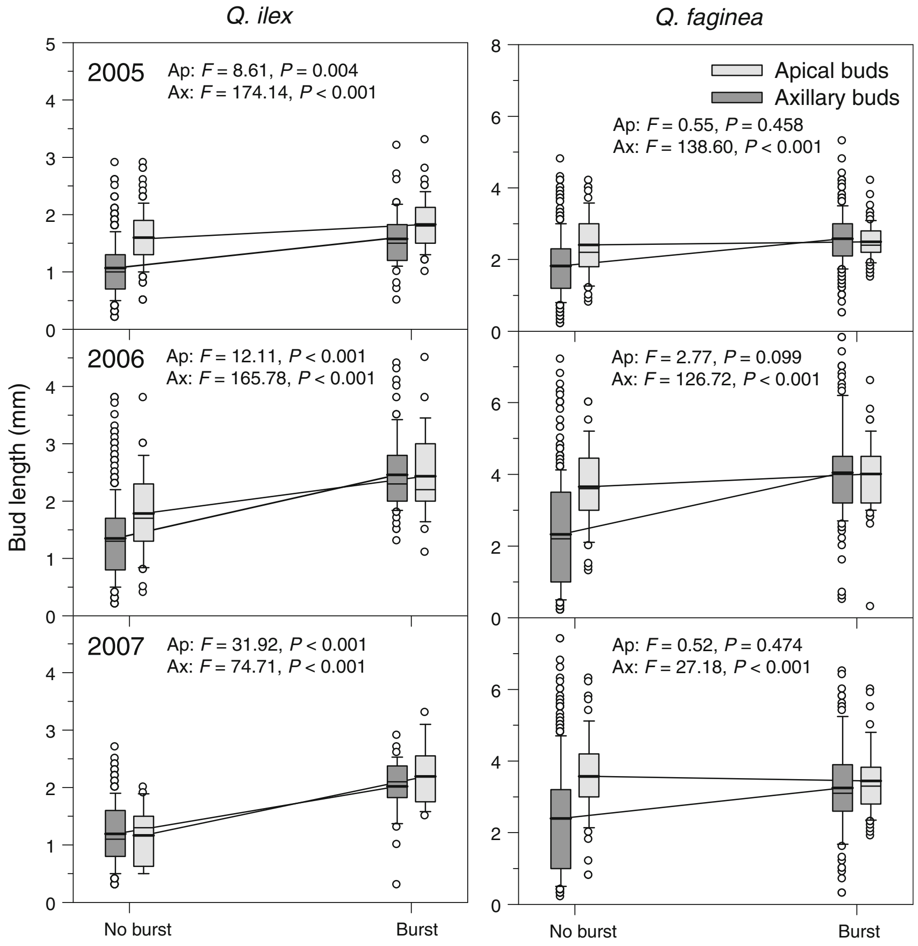


Fig. 5 Length of bursting and non-bursting buds in apical (Ap) and axillary (Ax) positions (including leaf and scale-cataphyll axillary buds). *Thin* and *thick lines* in *box plots* correspond to median and mean values, respectively. *F*-values along with *P* values are shown for each bud position, year and species

formed in 2006 for both species (Fig. 4). However, no size threshold was found below which bud bursting was impaired, since even the shortest buds could burst and produce shoots on the following spring (Figs. 4, 5).

Annual balances between bud and shoot numbers

The total number of current-year buds produced per branch of the same branching order alternated between years of high and low bud production in *Q. ilex* ($F = 0.58$, $P = 0.634$), whereas in *Q. faginea* it increased over time ($F = 9.35$, $P < 0.001$) (Fig. 6). These data represent only current-year buds and shoots, excluding older dormant buds and the shoots produced by them. The number of living buds per branch showed a huge variability among years, since they varied from 28 to 43 in *Q. ilex* and from 36 to 110 in *Q. faginea*. The bud production rates per branch from 2006 to 2008 presented an alternating pattern among years in *Q. ilex* (2006, 1.5 buds year^{-1}; 2007, 0.8 buds year^{-1}; and 2008, 1.1 buds year^{-1}), whereas these rates decreased as branches aged in *Q. faginea* (2006, 1.7 buds year^{-1}, 2007, 1.6 buds year^{-1}; and 2008, 1.1 buds year^{-1}). Moreover, the number of shoots produced per branch showed a similar pattern as the number of buds produced per branch for both species (Fig. 6). The lowest shoot production rate was found in 2005 in *Q. ilex* (2004, 4.3 shoots year^{-1}; 2005, 0.8 shoots year^{-1}; 2006, 2.5 shoots year^{-1}; 2007, 0.9 shoots year^{-1}; and 2008, 1.2 shoots year^{-1}) ($F = 6.90$, $P < 0.001$) whereas in *Q. faginea* it was the highest (2004, 2.1 shoots year^{-1}; 2005, 3.3 shoots year^{-1}; 2006, 1.9 shoots year^{-1}; 2007, 1.5 shoots year^{-1}; and 2008 1.2 shoots year^{-1}) ($F = 50.23$, $P < 0.001$).

Discussion

Bud size and position effects on bud fate

The two studied oak species presented different strategies for bud production and survival that could be related to their contrasting leaf phenology and crown types. The evergreen oak species (*Q. ilex*) produced smaller buds with longer lifespans but higher mortality rates than the deciduous oak species (*Q. faginea*). Our results indicate that, in both species, larger buds displayed higher chances of

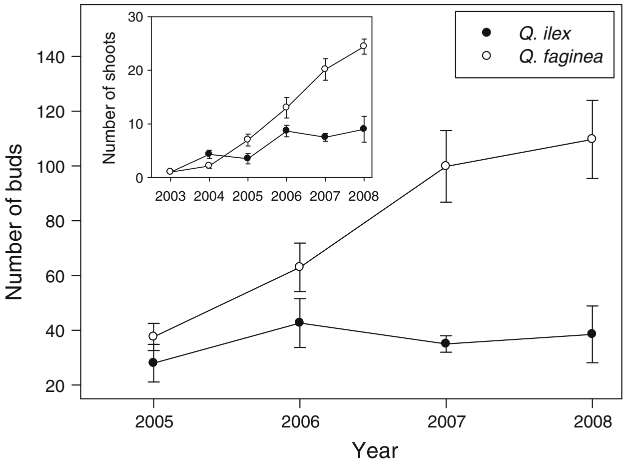


Fig. 6 Number of current-year buds and shoots per branch measured for each study year (mean ± SE). Data belong to branches sampled in 2009 at the end of the study

Table 3 Summary statistics for binomial GLMMs on the effect of bud position and bud size and sampling year on bud fate in the two study species

Factor	*Q. ilex*		*Q. faginea*	
	Z value	*P* value	*Z* value	*P* value
Year 2006	−9.11	<0.001	−7.45	<0.001
Year 2007	−4.43	<0.001	−7.09	<0.001
Shoot length	3.05	0.002	4.93	<0.001
Apical position × bud length	17.10	<0.001	16.92	<0.001
Non-apical position × bud length	15.44	<0.001	13.73	<0.001

Z values along with *P* values are shown for each fixed factor and species. For the categorical factor "Year" the analysis is shown in comparison with the first category (Year 2005). Other interactions were not considered due to collinearity issues (see text for further details)

bursting than smaller ones, irrespective of their position along the parent shoot. We assume that larger buds will contain more leaf primordia and will have therefore a higher probability to burst than smaller buds. Therefore, we regard bud size as a proxy of bud vitality. Previous studies (Gill 1971; Kozlowski et al. 1973; Sabatier and Barthélémy 2001; Montserrat-Martí et al. 2009) emphasize the strong influence of bud size and their position along the parent shoot on the shoot length formed by that bud. Consequently, it can be hypothesised that larger buds will have a greater impact on the expansion of the tree canopy than smaller ones if bud size determines the shoot length produced in the following year. Such allometric relationships between bud and shoot size may explain the skewed distribution towards short shoot lengths which was also observed in temperate oak species (Buck-Sorlin and Bell 2000) probably due to the high frequency of small buds.

Although larger buds had higher chances to burst than smaller ones, bud position was also relevant since, in both species, apical buds were larger and displayed a higher probability to burst than axillary ones. Bud size depends on the resource supply they require during the period of their development (Little 1970) and nutrients move preferentially to regions of high auxin concentrations (Phillips 1975). Consequently, the observed gradient in bud size along the parent shoot could be ultimately caused by auxin concentrations, which depend on the synthesis in young expanding leaves at the shoot apex, being later transported basipetally along the stem and inhibiting the growth of axillary buds (Cline 1997; Ljung et al. 2001; Tanaka et al. 2006; Shimizu-Sato et al. 2009). The higher likelihood for apical buds to burst or persist to the next year (the latter was observed only in the case of *Q. ilex*), agrees with previous studies on bud demography on temperate trees (Maillette 1982a; Jones and Harper 1987), possibly due to their priority over axillary buds for the use of water and nutrients. Due to the tendency of apical buds to be more important sinks for resources and water than axillary buds, we expected that the first would be larger than the second ones during dry years (which was the case in *Q. ilex*). On the other side, we found, during wet years, that axillary buds reached their maximum development and similar sizes to apical buds, probably because water deficit did not impair their enlargement (Alla et al. 2013). This may also explain why the apical buds of *Q. faginea*, which in the study area is close to its xeric limit of distribution, reached their maximum development only in moist years.

Contrary to our second hypothesis, we did not find an absolute threshold of bud size below which budburst could be impaired. Even the shortest buds could produce new shoots, perhaps under conditions of low competition with neighbouring buds. However, we observed a relative threshold of budburst since larger buds had higher possibilities to burst than smaller ones. This relative threshold varied over years depending on environmental conditions, as did the mean and maximum bud lengths. For example, both species presented in 2006 the highest mean and maximum bud lengths as compared to the other years, in response to minimum and maximum temperatures occurring during the maximum bud growth rate (Alla et al. 2013).

Implications for tree architecture

In the evergreen species we observed many old buds and even four-year-old buds were still viable whereas in the deciduous one almost all bursting buds were one-year-old. Therefore, our results suggest that *Q. ilex* is able to form a bud bank with buds of different ages which are able to burst over the next years. Contrastingly, the crown development of *Q. faginea* depends entirely on the production and survival of current-year buds, whose amount in the studied branches increased through time. Such contrasting patterns in bud production and longevity allow describing two different strategies for canopy development in the studied species. *Q. ilex* may accumulate viable buds during several years to produce many shoots in those years with favourable climatic conditions (e.g., wet and mild springs) or to replace shoots damaged due to biotic or abiotic factors (Nitta and Ohsawa 1998). Contrastingly, *Q. faginea* relies on the abundant production of large current-year buds. This observation may be related to the higher inter-annual variation of shoot production as described for *Q. ilex* with respect to *Q. faginea* in the same study area (Montserrat-Martí et al. 2009). In the deciduous species, the whole foliage must be renewed each spring, which requires developing a large number of buds. Contrarily, *Q. ilex* is an evergreen that has 3-4 cohorts of leaves, and by preserving a viable old bud bank can tolerate a significant annual oscillation of shoot production. The strategy of *Q. faginea* allows this species to respond vigorously to favourable climatic conditions and reach taller canopy heights than *Q. ilex*. However, bud formation and crown development of the deciduous species seem to be more vulnerable to the dry Mediterranean conditions than that of the evergreen (Montserrat-Martí et al. 2009; Sanz-Pérez and Castro-Díez 2010). As a result of all these factors, in the studied area *Q. faginea* trees tend to be taller than similarly-aged *Q. ilex* trees, which could be due to the numerous shoots derived from large apical buds in the former. On the contrary, multi-stemmed *Q. ilex* trees develop their crown more horizontally than *Q. faginea* trees because of the bursting of non-apical and older buds, achieving the former a more “shrubby-type” development than the latter. These strategies seem to be important to explain the differences in the crown architecture of both species, although other factors should also be considered, such as differences in bud and shoot orientation, shoot length distribution and subsequent direction of growth of produced branches (tropism), etc. (Buck-Sorlin and Bell 2000).

In conclusion, bud size and position are important determinants of the fate of buds, i.e. the probability to survive and/or burst, in both studied oak species. Apical buds have higher chances of bursting into new shoots than axillary buds, since more than 50 % of apical buds produced new shoots whereas only 30 % of axillary buds did, being the latter percentage even lower in the evergreen (*Q. ilex*) than in the deciduous (*Q. faginea*) oak species. Large buds, irrespective of the position along the parent shoot, have higher probability to burst and produce new shoots than smaller ones. However, all buds, independently of their position and length, may eventually burst into new shoots. The observed differences in the bud longevity of both study species could help to explain their different crown architectures and abilities to respond to biotic and abiotic shoot damage: *Q. ilex* seems to rely on a larger and longer-lived bud bank comprised of smaller buds which determine a higher ability to resprout after damage but a lower ability to expand the canopy in height, whereas *Q. faginea* growth depends on an abundant production of large, short-lived current-year buds, that enable performing a large vertical expansion of the canopy.

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