

# Trade-offs between vegetative growth and acorn production in *Quercus lobata* during a mast year: the relevance of crop size and hierarchical level within the canopy

Belén Sánchez-Humanes · Victoria L. Sork ·  
Josep Maria Espelta

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**Abstract** The concept of trade-offs between reproduction and other fitness traits is a fundamental principle of life history theory. For many plant species, the cost of sexual reproduction affects vegetative growth in years of high seed production through the allocation of resources to reproduction at different hierarchical levels of canopy organization. We have examined these tradeoffs at the shoot and branch level in an endemic California oak, *Quercus lobata*, during a mast year. To determine whether acorn production caused a reduction in vegetative growth, we studied trees that were high and low acorn producers, respectively. We observed that in both low and high acorn producers, shoots without acorns located adjacent to reproductive shoots showed reduced vegetative growth but that reduced branch-level growth on acorn-bearing branches occurred only in low acorn producers. The availability of local resources, measured as previous year growth, was the main factor determining acorn biomass. These findings show that the costs of reproduction varied among hierarchical levels, suggesting some degree of physiological autonomy of shoots in terms of acorn production. Costs also differed among trees with different acorn crops, suggesting that trees with large acorn crops had more available resources to allocate for

growth and acorn production and to compensate for immediate local costs of seed production. These findings provide new insight into the proximate mechanisms for mast-seeding as a reproductive strategy.

**Keywords** Cost of reproduction · Growth · Mast-seeding · Modular organization · Valley oak

## Introduction

A fundamental tenet of life history theory is that reproduction comes at a cost, resulting in trade-offs with other fitness traits (Williams 1966; Roff 1992; Obeso 2002). Trade-offs between reproduction and growth in plants have been shown in herbaceous species, conifers, and angiosperm tree species (Morris 1951; Gross 1972; Abrahamson 1975; El Kassaby and Barclay 1992; Obeso 1993). No phenomenon is likely to illustrate the potential costs of reproduction more dramatically than mast-seeding in perennial plant species (Kelly 1994; Koenig and Knops 1998; Kelly and Sork 2002; Monks and Kelly 2006; Sork 1993; Sork and Bramble 1993; Yasumura 2006). Mast-seeding is a reproductive strategy that results in the synchronized production of large crops during some years and small or negligible crops during other years (Janzen 1971; Silvertown 1980; Norton and Kelly 1988; Sork et al. 1993; Kelly and Sork 2002). Because of the large year-to-year variation in seed production, one would expect trade-offs between seed production and growth, especially during years of large crop production when resources are limiting (Tuomi et al. 1983). The trade-off hypothesis has also been referred to as the resource switching hypothesis because it proposes that resources are differentially allocated to developing fruits by shifting them from vegetative growth (Norton and Kelly

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B. Sánchez-Humanes (✉) · J. M. Espelta  
Centre for Ecological Research and Forestry Applications  
(CREAF), Autonomous University of Barcelona,  
08193 Bellaterra, Spain  
e-mail: belen.sanchez@creaf.uab.es

V. L. Sork  
Department of Ecology and Evolutionary Biology and Institute  
of the Environment, University of California, Box 951786,  
Los Angeles, CA 90095-1786, USA

1988; Kelly and Sork 2002; Obeso 2002; Monks and Kelly 2006). However, the evidence for trade-offs between seed production and vegetative growth is not universal (Nienstaedt 1985; Dick et al. 1990b; Cremer 1992; Despland and Houle 1997; Alley 1998; Snook et al. 2005; Yasumura 2006). Moreover, this correlation may be the indirect outcome of other factors affecting tree growth, rather than evidence for the cost of reproduction. For example, Knops et al. (2007) reanalyzed their previous data from several California oak species (Koenig and Knops 1998) and concluded that the observed oscillations in tree ring growth were due to rainfall and that once this effect was removed, no trade-offs were evident in overall growth measured in the trunk. This finding highlights the need to search for costs at other locations of the plant.

Investment in reproduction is a hierarchical process (Obeso 2004a). Competition for local resources could be most intense between shoots (where fruits usually grow) or branches, if they are autonomous to some extent from other parts of the tree's canopy (Dick et al. 1990a; Despland and Houle 1997; Obeso 1997; Yasumura 2006). Therefore, the trade-off between growth and reproduction may be more apparent within a shoot of a branch or among branches than in the trunk because the overall cost of reproductive modules could be compensated by the growth of vegetative ones elsewhere (Watson and Casper 1984; Obeso 1997). Although the costs of reproduction are often studied at the population or whole-plant level, to understand how the process works, we should measure those costs at different hierarchical levels by documenting growth and reproduction at various levels within a tree (Henriksson and Ruohomaki 2000; Suzuki 2000, 2005; Hasegawa et al. 2003; Obeso 2004b; Kawamura and Takeda 2006).

Evidence for trade-offs is most likely to be found during a mast year in trees with large and small crops because the cost of reproduction may vary at this time among individuals with different levels of investment in acorn production (e.g. Isagi et al. 1997; Herrera et al. 1998; Sork et al. 1993). We focused on the following questions: Do trees that produce large fruit crops do so because they allocate more of their resources to reproduction than to vegetative growth? Alternatively, do such trees have an overall higher level of resource availability? Or do such trees have both more resources and more effective ways to allocate those resources to reproduction? In the study reported here, we assessed the trade-offs in vegetative growth and reproduction in a mast-seeding tree, *Quercus lobata* Née (California valley oak), during a mast year. Oaks are considered to be a classic masting species due to the phenomenon of periodic, synchronous acorn production in different populations and species (Sork et al. 1993; Koenig et al. 1994b; Kelly and Sork 2002 and references therein; Espelta et al. 2008), despite the fact that the year-to-year variation or population

synchrony varies greatly across species. We focused on the proximate costs of reproduction on vegetative growth at the canopy, branch, and shoot level as a basic step toward establishing evidence for trade-offs. Using sets of low- and high-acorn-producing trees during a year of high acorn production, we tested the hypotheses that (1) costs of reproduction will be more apparent in shoots and branches than at the whole-canopy level, (2) the potential costs will be more intense in trees with larger fruit crop sizes, and (3) the availability of local resources, as indicated by growth during the previous year, will strongly affect growth and acorn production.

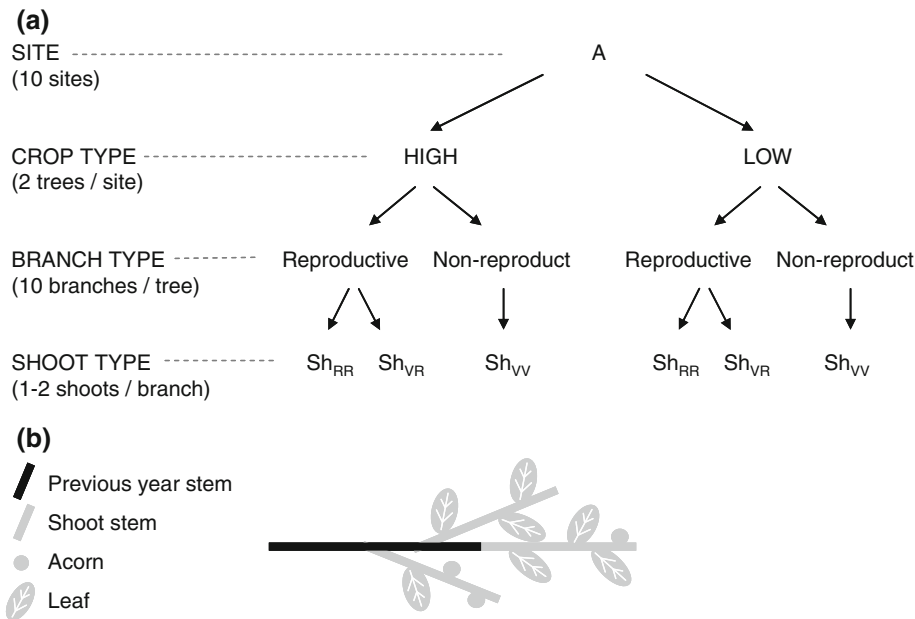
This investigation was carried out during a year of high acorn production by a specific *Q. lobata* population. In the first part of the paper, we examine the results of a split-plot nested experimental design at the tree, branch, and shoot level to see whether there are trade-offs between growth and reproduction on (1) trees with high versus low acorn production, (2) reproductive branches versus non-reproductive branches, and (3) shoots with acorns versus those without acorns on reproductive branches and non-reproductive branches. In the second part, we utilize a path analysis to interpret direct and indirect causal relationships among previous year biomass, shoot growth, and acorn production.

## Materials and methods

### Study species and study site

*Quercus lobata* Née (California valley oak) is endemic to California, where it occurs in savanna oak communities on deep loamy soils, principally below 600 m a.s.l. in the Central Valley, surrounding valleys, and foothills (Pavlik et al. 1991). *Q. lobata* is a diploid, wind-pollinated, monoecious, and predominantly outcrossing tree species (Sork et al. 2002). It flowers in March–April before leaves emerge, and each female flower develops into an acorn over the summer, maturing in late September to early October of the year of pollination.

The study site is located in the Sedgwick Reserve, which is administered by the University of California at Santa Barbara as part of the University of California Natural Reserve System. The 2,380-ha reserve is 10 km northeast of Santa Ynez (Santa Barbara County, CA, USA). The study trees sampled for this study are located in the valley along Figueroa Creek (34°42'N, 120°02'W) with elevations ranging from 300 to 400 m a.s.l.. In this valley, stem density averages about 1.19 adult trees/ha (Sork et al. 2002); adult trees have breast height diameters >40 cm, and adult crown areas range from 64.5 to 581.9 m<sup>2</sup>, with a mean [ $\pm$ standard deviation (SD)] of 291.6  $\pm$  129 m<sup>2</sup> (Pluess et al. 2009). Data on acorn production of valley oak at this



**Fig. 1** **a** Schematic of sampling design: two trees were chosen from each of ten different sites (A–J) within Figueroa valley. One tree of each pair was designated a high acorn producer and the other, a low acorn producer (crop type: high vs. low). Within each tree, five reproductive and five non-reproductive branches were selected at random (branch type: reproductive vs. non-reproductive). The longest shoot

with and without acorns was registered for each branch (Shoot type:  $Sh_{RR}$  shoots with acorns,  $Sh_{VR}$  shoots without acorns from reproductive branches,  $Sh_{VV}$  shoots from non-reproductive branches). **b** Diagram of a sample reproductive branch. Previous year stem is represented in *black*; current year shoots (stem, leaves and acorns) are represented in *gray*

study site indicate strong year-to-year variation in crop size: the CVi (individual coefficient of variation) for 11 acorn-producing adults sampled at Sedgwick from 1994 to 2009 was 2.29 (W. Koenig and J. Knops, unpublished data). In their study as well as for the trees sampled in this study, the last year of large acorn production occurred in 2002 (V.L. Sork, unpublished data).

### Sampling design

To analyze the allocation of resources during a mast-fruiting year, we devised a split-plot nested design. We selected ten pairs of valley oak adults located in the vicinity of each other, with one tree in each pair being a high acorn producer and the second tree, a low acorn producer. These trees were part of a separate phenology study of flower and acorn development for 100 trees, in which we estimated acorn crop size during this same season (Lentz and Sork, unpublished data). For our study, high-acorn-producing trees came from the top 20 percentile of this sample, and low-acorn-producing trees came from the low 20 percentile, based on their ranks for acorn production measured by visual counts of acorns on each tree using the Koenig et al. (1994a) method.

Sampling was carried out during the last week of October 2007, when both the vegetative and reproductive growth seasons were finished, and the stems, leaves, and

acorns were at their maximum size. Within each tree, we randomly selected five reproductive and five non-reproductive 2-year-old branches (Fig. 1a) from a band of the canopy located 5–8 m from the ground, on the south side, where acorns were consistently most abundant. Using a large pruning pole, we cut each branch such that it included one stem that had developed during 2006 and all of its shoot stems with their leaves and acorns that had developed during the spring and summer of 2007 (Fig. 1b). Branches were tagged and kept in separate bags at 4°C until measurements were taken.

We assessed costs of reproduction in terms of biomass, size, and number of shoots and leaves in reproductive versus non-reproductive branches and shoots. To quantify the previous year's growth (2006), we measured the dry biomass of the last year's stem. To measure current (2007) growth in reproductive and non-reproductive branches, we measured the number of reproductive and vegetative shoots, leaves, acorns, and cupules for each branch. In reproductive branches, shoots and their leaves were separated into two groups: shoots with and without acorns, respectively. For each branch, either reproductive or non-reproductive, we measured the length, diameter, volume, number of leaves, and number of acorns found on the largest shoots with (if any) and without acorns. To measure the biomass of the various parts of the branches, we then dried all fractions in an oven at 70°C for 96 h and weighed the

dried sample to the nearest 0.001 g. Vegetative biomass of a branch was calculated as the sum of shoot stem and leaf biomass, and total biomass was the sum of shoot stems, leaves, and acorn biomass.

Some of the acorns were already dispersed at the time of sampling, which we ascertained because the cupules were still attached to the shoot. In these cases, the diameter of the cupule was measured. We estimated the biomass of these acorns using a regression approach that linked the diameter of the cupule [ $x$  (mm)] and dry mass of the acorns [ $y$  (g)] from a set of acorns randomly selected ( $y = 0.4192x - 3.8158$ ,  $r^2 = 0.70$ ,  $n = 75$ ).

### Data analysis

To identify the location of resource allocation from vegetative to reproductive growth, we analyzed growth in branches and shoots at three hierarchical levels of study (Fig. 1a): tree, branch, and shoot. At the tree level, we compared trees with high and low acorn production, and at the branch level, we compared two branch types, namely, those with acorns (reproductive branches) and those without acorns (non-reproductive branches). At the shoot level, we compared three shoot types: shoots with acorns ( $Sh_{RR}$ ), shoots without acorns from reproductive branches ( $Sh_{VR}$ ), and shoots from non-reproductive branches ( $Sh_{VV}$ ).

To test the effects of crop type, branch type, and shoot type on vegetative growth, we performed mixed linear modeling (also known as hierarchical linear modeling) so that we could test the effect of both fixed and random factors while taking into account the hierarchical structure of the data (shoots within branches within trees within sites). We used two sets of model designs. The first one (referred to as Branch models) tested the effect of branch type and crop type on the vegetative and reproductive growth of the branch. For the Branch models, the dependent variables were total biomass, vegetative biomass, and number and biomass of shoot stems and leaves. Site (10 sites) and tree (20 trees) nested within site were random factors. Crop type (high or low production) and branch type (reproductive or non-reproductive branches) were fixed factors. To control for the effect of the previous year's growth on the current year's growth (Woollons and Norton 1990, Brien et al. 2006), the biomass of the last year's stem was introduced into the model as a covariate.

In the second set of models, we focused on the shoot level (referred to as Shoot models hereafter) and tested the effect of shoot type and crop type on the shoot growth variables. We were not able to incorporate shoot level into the previous hierarchical model because shoots with and without acorns could not be nested hierarchically into branches with and without acorns. Moreover, the type of measurements we made at the shoot level could not be made in a

manner that enabled comparison to those performed at the branch level. For the Shoot models, the dependent variables were length, diameter, volume, and number of leaves of the largest shoot stem of the branch both without and with acorns (if present). Site, tree nested within site, and branch (10 branches per tree) nested within Tree were random factors. Crop type (high or low production) and shoot type ( $Sh_{RR}$ ,  $Sh_{VR}$  and  $Sh_{VV}$  shoots) were fixed factors. Biomass of the previous year's stem was also considered as a covariate. For both sets of models, the variables were natural log or square-root transformed when necessary to meet the assumption of normality. These analyses were performed with SAS statistical software ver. 9.1 (SAS Institute, Cary, NC) by using the Mixed procedure.

To examine direct and indirect relationships between the previous year's growth and current growth of reproductive and vegetative shoot stems, leaves, and acorns, to eliminate spurious relationships among variables, and to construct a possible causal model among variables, we conducted a path analysis (Wright 1921; Mitchell 1992). Path coefficients (standardized regression coefficients) quantify direct effects of an independent variable on a dependent one (Mitchell 1992). We assumed unidirectional relationships when the directionality was clear and otherwise used bidirectional relationships when cause and effect were not apparent. Only the reproductive branches were included in this analysis (5 branches per tree and 20 trees). The branch, nested within tree, is the unit of the analysis. In our path model, previous year's growth, measured as the biomass of the 2006 stem, was introduced as the exogenous variable (variable with no explicit causes). Biomasses of vegetative and reproductive shoot stems of the branch, vegetative leaves (those from vegetative shoots) and reproductive leaves (those from reproductive shoots), and acorns were introduced as endogenous variables (variables that participate in the model as dependent and/or independent factors), but leaf biomass, given its high correlation with shoot stem biomass, was dropped from the model to avoid collinearity. Our model takes into account that previous year's biomass can directly affect the biomass of reproductive and vegetative shoot stems and that reproductive shoot stem biomass may affect acorn biomass. Moreover, if resources were to be reallocated from vegetative to reproductive shoots in a branch, this would be indicated by negative paths between vegetative and reproductive shoot stems. Path analysis was performed with the Mplus statistical software ver. 5 (Muthén & Muthén, Los Angeles, CA).

### Results

For all growth parameters, the biomass of vegetative growth in 2006 significantly covaried with the dependent

**Table 1** Results of separate Mixed linear models testing the effects of branch type (reproductive vs. non-reproductive), crop type (high vs. low acorn production), including their interactions and biomass in 2006 as a covariate ( $n = 200$ )

Source	<i>df</i>	Total biomass <sup>a</sup>	Vegetative biomass <sup>b</sup>	Shoot stem biomass <sup>b</sup>	Leaf biomass <sup>b</sup>	Number of shoots <sup>a</sup>	Number of leaves <sup>a</sup>
Branch type (BT)	1	391.50***	1.02	4.83	4.34*	0.02	0.79
Crop type (CT)	1	3.33	1.09	0.18	1.19	6.80*	7.34*
BT × CT	1	24.11***	10.57**	10.89**	8.24***	7.30**	10.94**
Biomass 2006	1	91.67***	174.18***	298.09***	104.63***	65.04***	94.61***
Error term	189						
Site, S (%)		11.72	21.43	17.49	19.84	6.93	10.74
Tree, T (%)		19.82	14.72	12.57	14.88	0.05	1.75

Values reported are *F* statistics and the percentage of covariance due to the random factors site (S) and tree (T), respectively, on six growth variables measured at the branch level

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$

<sup>a</sup> Ln transformed

<sup>b</sup> Square root transformed

**Table 2** Parameter estimates for the linear models in Table 1 for the six growth variables for crop type (high or low) and branch type (non-reproductive or reproductive)

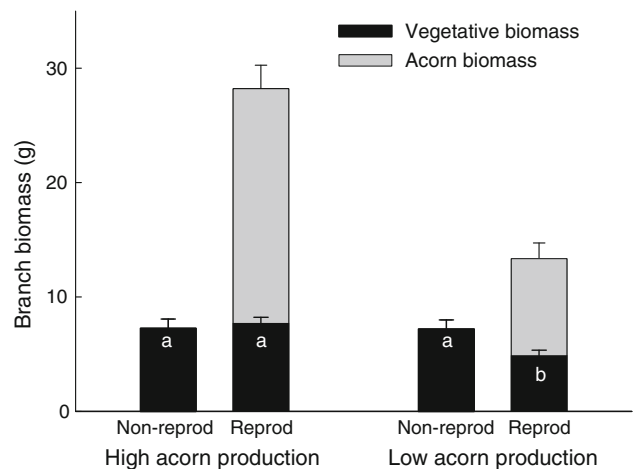
Crop type	Branch type	<i>n</i>	Total biomass <sup>a</sup>	Vegetative biomass <sup>b</sup>	Shoot stem biomass <sup>b</sup>	Leaf biomass <sup>b</sup>	Number of shoots <sup>a</sup>	Number of leaves <sup>a</sup>
High	Non-reproductive	50	1.64 ± 0.12	2.44 ± 0.14	1.10 ± 0.07	2.16 ± 0.13	1.63 ± 0.08	3.43 ± 0.10
High	Reproductive	50	3.25 ± 0.12	2.60 ± 0.14	1.32 ± 0.07	2.21 ± 0.13	1.81 ± 0.08	3.61 ± 0.10
Low	Non-reproductive	50	1.72 ± 0.12	2.53 ± 0.14	1.20 ± 0.07	2.22 ± 0.13	1.63 ± 0.08	3.45 ± 0.10
Low	Reproductive	50	2.69 ± 0.12	2.22 ± 0.14	1.16 ± 0.07	1.89 ± 0.13	1.42 ± 0.09	3.13 ± 0.10

Values are estimates of the mean ± standard error (SE)

<sup>a</sup> Ln transformed

<sup>b</sup> Square root transformed

variables (Table 1). In other words, for all trees, branch growth was positively correlated with how much the branch grew during the previous year. The model with total biomass showed no significant difference between type of tree, but it did show a dramatic difference between reproductive and non-reproductive branches, and leaf biomass also showed a modest, but significant effect (Table 1). During this mast year, reproductive branches produced more total biomass than non-reproductive branches due to the high mass of the acorns compared to stems and leaves (Fig. 2). The main effects in these models did not show a consistently strong effect for the rest of growth variables. However, as seen in Fig. 2 for vegetative branch biomass, the Mixed model results for all growth variables showed a highly significant interaction between crop type and branch type (Table 1). In the high-acorn-producing trees, the vegetative biomass did not differ between reproductive and non-reproductive branches, but in low-acorn-producing trees, the reproductive branches had a lower vegetative biomass than the non-reproductive branches (Fig. 2). The number of shoot stems and leaves and the leaf biomass were also lower in the reproductive branches of trees with a small crop (see the parameter estimates in Table 2). These results



**Fig. 2** Total branch biomass (g) [(mean + standard error (SE))] produced in 2007 by non-reproductive and reproductive branches in high- and low-acorn-producing trees ( $n = 200$ ). Total biomass is partitioned into vegetative [stems and leaves (black)] and acorn biomass (gray). Vegetative biomass bars with the same letter are not significantly different based on a posteriori tests of means at  $P < 0.05$

provide support for a trade-off between vegetative branch growth and acorn production that is exclusive to trees having a small crop.

**Table 3** Results of four separate mixed linear models testing the differences among four growth variables measured on shoots with acorns, shoots without acorns from reproductive branches, and shoots from non-reproductive branches (shoot type) in high and low acorn producers (crop type)

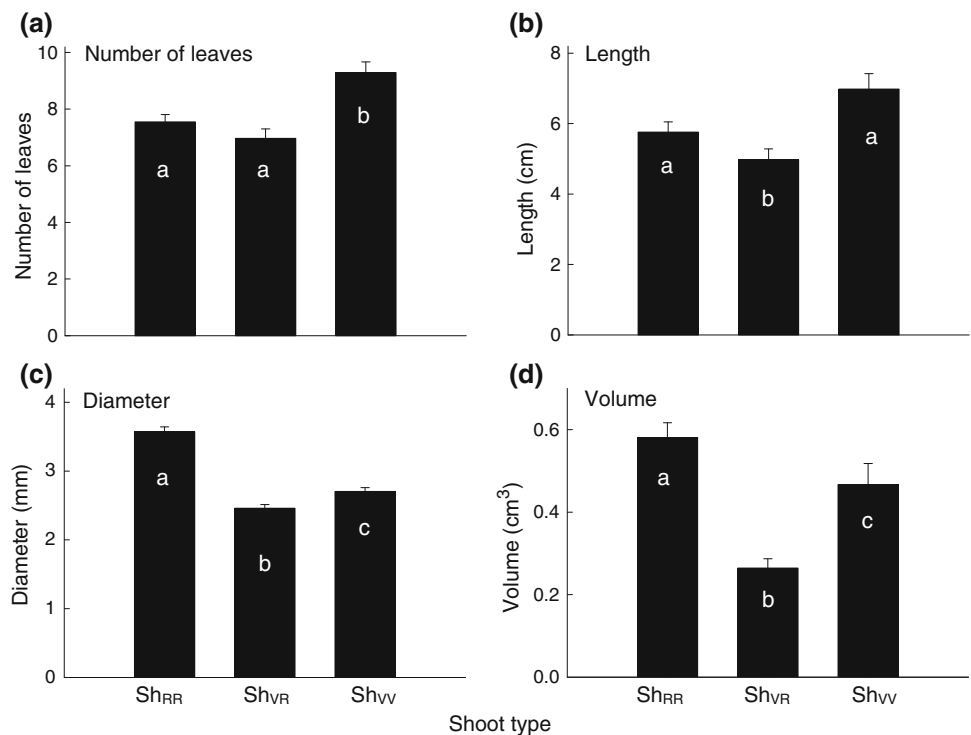
Source	<i>df</i>	Length <sup>a</sup>	Diameter <sup>a</sup>	Volume <sup>a</sup>	Number of leaves <sup>a</sup>
Shoot type (ST)	2	13.39***	120.85***	43.76***	18.21***
Crop type (CT)	1	3.65	3.20	0.81	2.61
ST × CT	2	1.36	2.46	0.36	1.19
Biomass 2006	1	1.16	0.21	0.29	0.33
Error term	288				
Site, S (%)		19.36	<0.01	16.58	8.62
Tree, T (%)		10.98	21.05	5.93	13.98
Branch, B (%)		31.33	<0.01	15.91	12.34

Values reported are *F* statistics and the percentage of covariance due to the random factors site (S), tree (T), and branch (B), respectively. Biomass in 2006 is included as a covariate ( $n = 300$ )

\*\*\*  $P < 0.001$

<sup>a</sup> Square root transformed

**Fig. 3** Differences among shoot types: **a** number of leaves, **b** length, **c** diameter, **d** volume of shoot. Shoot types:  $Sh_{RR}$  shoots with acorns from reproductive branches,  $Sh_{VR}$  shoots without acorns from reproductive branches,  $Sh_{VV}$  shoots from non-reproductive branches. Bars Mean + SE,  $n = 300$ . Bars with the same letter are not significantly different based on a posteriori tests of means at  $P < 0.05$

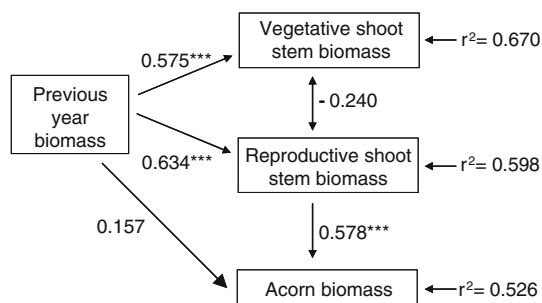


At the shoot level, we observed a very different pattern of evidence for the costs of reproduction. The mean shoot size did not differ significantly between trees with a large and small crop, respectively, for the four shoot variables (Table 3). However, we found significant differences among shoot types (Table 3). The cause of these differences is that (1) shoots on non-reproductive branches were the longest and showed the higher number of leaves (Fig. 3a, b); (2) shoots with acorns on reproductive branches had a higher diameter and volume than shoots without acorns or shoots on non-reproductive branches (Fig. 3c, d). Interestingly, shoots without acorns on reproductive branches

showed the lowest values for all growth measures. Thus, the shoots which were close to shoots with acorns showed reduced growth, suggesting a local vegetative cost of the adjacent reproduction.

To view the relationships among the vegetative growth and reproduction, we used a path model (Fig. 4). The model explained 53% of the variation in acorn production. The previous year's biomass had a strong positive effect on both reproductive and vegetative shoot stem biomass, as expected, and only a slight direct effect on acorn biomass (Fig. 4). However, acorn biomass was highly enhanced by reproductive shoot stem biomass and indirectly by the





**Fig. 4** Path diagram showing the standardized partial correlation coefficients between biomass of branches (2006), vegetative shoot stems (2007), reproductive shoot stems (2007), and acorns from reproductive branches ( $n = 100$ ). The estimate of  $r^2$  is given for each variable. Variables are square root transformed to achieve normality. Significance: \*\*\* $P < 0.001$

previous's year biomass through its effect on reproductive shoot stem biomass. The slightly negative trend between the biomass of vegetative versus reproductive shoots ( $P < 0.10$ ) suggests the existence of a cost of reproduction within branches that is consistent with the reduction in biomass shown by  $Sh_{VR}$  (shoots without acorns from reproductive branches) in the Mixed model. The same path model was performed including leaf biomass instead of shoot stem biomass, and the results were essentially the same (data not shown). Thus, the path model patterns indicate that the proximate mechanism for producing large acorn crops is to produce large numbers of reproductive shoots and, overall, that this increased production of many reproductive shoots comes at a marginal cost to vegetative shoots.

## Discussion

This study provides two valuable insights into the trade-offs between growth and reproduction during a mast-seeding year of *Quercus lobata*. The first is that *hierarchy counts*; in other words, costs differ at the different canopy levels (tree canopy, branch, and shoot). The second is that the *costs of reproduction are not universal in a population*; consequently, costs may vary among trees with high versus low seed production.

*At what hierarchical level do costs of reproduction occur?* Our comparison of biomass allocation associated with growth and reproduction indicates different patterns for branch- versus shoot-level analysis. At the branch level, branches with acorns showed a reduction in allocation to vegetative growth only within trees with small crops. The reduction in leaf biomass is especially important because as leaves can photosynthesize, this reduction implies not only a reduction in leaf biomass but also in the growth that leaves can provide. Thus, it appears that the branch is an

important level at which to observe trade-offs. Conversely, at the shoot level, no differences were noticeable between high and low acorn producers; however, we did observe a difference in the size of shoots with and without acorns, respectively, in both types of trees: shoots with acorns were not the longest, but they were the largest in terms of diameter and volume. This difference in size may reflect a physiological constraint because a thicker stem or larger volume might facilitate the transport of resources (Zimmermann 1983), resulting in the presence of acorns on the larger shoots. An alternative explanation is that shoots with acorns were bigger because they are sinks of resources from adjacent shoots or branches (Wardlaw 1990; Newell 1991; Obeso 2004a). We can distinguish between these two hypotheses by looking at the rankings of diameters and volumes across types of shoot. We found: *shoots with acorns > shoots from non-reproductive branches > shoots without acorns from reproductive branches*. For the first hypothesis, we should not see any difference in size between shoots from non-reproductive branches and those without acorns on reproductive branches. The finding that shoots without acorns from reproductive branches were much smaller than shoots on non-reproductive branches supports previous evidence that shoots with fruits obtain their resources from their adjacent shoots without fruits (Miyazaki et al. 2007). Acorns seem to have a high sink strength (Wardlaw 1990; Obeso 2002). Thus, allocation of resources to different kinds of shoots is likely to be the outcome of source/sink processes within branches.

Our study demonstrates that costs of reproduction differ at different hierarchical levels, as we hypothesized. At the shoot level, we observed trade-offs between growth and reproduction in all types of trees. At the branch level, contrary to our hypothesis, we found such trade-offs only for the low-acorn-producing trees. This finding suggests that all trees in this population might be responding to some cue to produce acorns in the same year, but that the resources to produce acorn crops are more limited in the low-acorn-producing trees than in the high acorn producers. In the latter, acorn production reduces local shoot growth, but among branches it is not necessary to transfer resources from vegetative growth to reproductive growth, possibly due to the reduced growth of vegetative shoots being compensated by the increased growth of reproductive shoots of the same branch. The fact that some studies did not observe trade-offs across years of high and low seed production on trunk growth (Knops et al. 2007) can be explained in the same way, namely, the impact of seed production is not experienced strongly at the scale of the whole tree. Our findings suggest that the autonomy of shoots and branches can mitigate the overall costs of reproduction. Moreover, trunk growth in Mediterranean-type oaks exhibits a wider temporal window than tree reproduction: growth can well occur

before acorn development begins—and even after acorn dispersal (B. Sánchez-Humanes, unpublished data). Thus, the results of our study support the suggestions of others that the costs of reproduction are more likely to be detected at lower levels (Lovett Doust and Lovett Doust 1988; Obeso 1997).

*Why aren't the costs of reproduction universal?* We found differential evidence for the costs of reproduction at the branch level in high- versus low-acorn-producing trees. The lack of a trade-off in trees with a large crop could be explained by a wealth of resources (Reznick et al. 2000; Sgro and Hoffmann 2004), either due to increased photosynthesis (Newell 1991; Hasegawa et al. 2003; Ichie et al. 2005) or/and stored resources (Newell 1991; Miyazaki et al. 2002; Yasumura 2006), or by delayed costs of reproduction. Indeed, our study reveals that a major determinant of current growth and acorn production was branch biomass from the previous year (Fig. 4), which we interpret as an indicator of tree growth rate. The relationship between last year's and this year's growth has been shown by others (Woollons and Norton 1990; Fox et al. 2001; Brienen et al. 2006). The high acorn producers were able to allocate resources to both growth and acorn production. What we cannot determine, however, is whether these trees both grow and produce acorns well because (1) they are in good locations for growth, (2) they are in the stage of their life span for optimal growth (Bullock et al. 2004; Vieira et al. 2009), (3) they are genetically good seed-producing trees (Reznick et al. 2000), (4) they respond better to the potential cues that trigger synchronic massive seed production, and/or (5) they are depleting accumulated resources, which would result in a reduction of vegetative growth or reproduction in the future. On the other hand, low-acorn-producing trees do show that there is a cost to reproduction, expressed in terms of local vegetative growth (Fig. 2). Given the energy one would expect to be required for the maturation of acorns, we had anticipated that at the local scale, allocation of resources to the developing acorns would involve a depletion of resources for growth in a mast year if resources were to be limiting. The finding that the costs of reproduction were not uniform across trees points to the importance of resource accumulation during the intervening years, but it also indicates that resource accumulation alone is not the causal mechanism.

Our study measured the cost of reproduction in terms of biomass, size, number of shoots, and leaves. Other currencies that have been employed to measure the costs of reproduction are carbon, nitrogen, and phosphorus (Reekie and Bazzaz 1987b; Chapin 1989; Obeso 2002 and references therein; Korner 2003). Korner (2003) states that growth seems not to be limited by carbon supply, even during mast-seeding years. The costs of reproduction might also be measured taking into account photosynthesis, respiration,

and resorption (Reekie and Bazzaz 1987a; Ashman 1994), all of which better reflect the true physiological cost of reproduction (Ashman 1994). However, a knowledge of the hierarchy-dependent costs of reproduction for vegetative biomass in *Q. lobata* will provide logistical support for analyses that can address the costs of reproduction in terms of nutrient allocation, growth, and reproduction processes.

#### Implications for masting hypotheses

This study provides some information that will facilitate answers to questions on the mechanisms of masting in tree populations. It has been hypothesized that the production of large crops is possible because (1) plants match their reproductive output to the variable resources available (resource matching hypothesis; see Monks and Kelly 2006), (2) resources are accumulated since the previous mast episode (resource accumulation hypothesis; see Sork et al. 1993), or (3) resources are shifted from vegetative growth to reproduction via trade-offs (resource switching hypothesis; see Norton and Kelly 1988).

The first two hypotheses do not necessarily lead to the expectation that trade-offs actually do exist. The resource matching hypothesis proposes that mast years are simply a reflection of year-to-year variation in the amount of resources produced as a consequence of environmental variation (Kelly 1994; Kelly and Sork 2002) and has rarely been proved (but see Despland and Houle 1997). The resource accumulation hypothesis proposes that mast years are possible when resources have been a priori accumulated. The accumulation of resources could diminish immediate trade-offs if sufficient resources are available for both seed production and vegetative growth. The resource switching hypothesis predicts a trade-off between growth and seed production because resources are reallocated from vegetative growth to developing fruits (Norton and Kelly 1988; Kelly and Sork 2002; Obeso 2002; Monks and Kelly 2006).

Among those alternative scenarios, defined by previous studies explaining the relationship between resource allocation and the production of large crops, we discard the resource matching hypothesis (Kelly 1994; Kelly and Sork 2002) because our trees produced acorns even at a cost to growth; this was especially true for low-acorn-producing trees. We cannot dismiss the resource accumulation hypothesis since some trees do seem to have sufficient stored reserves to produce large acorn crops without a great deal of immediate cost to vegetative growth. However, the measure of biomass as the currency for the costs of reproduction does not allow us to distinguish between no costs and the use of stored reserves. Our data are also consistent with resource switching at the lower hierarchical levels of the canopy because all trees showed a cost of reproduction



in terms of shoot growth when acorns were present, with the low acorn producers showing reduced growth in branches with acorns. Moreover, the fact that even trees with low biomass production produced acorns in this mast year suggests that all of the trees must be responding to a cue that triggers synchronous production (Kelly and Sork 2002). This single season study was not designed to directly test existing hypotheses on the evolution of masting because multiple years of data would be needed, such as that reported in other studies (Sork et al. 1993; Kelly and Sork 2002; Buonaccorsi et al. 2003; Koenig et al. 2003; Liebhold et al. 2004; Knops et al. 2007). Nonetheless, our results support that the one proximate mechanism that allows the production of large acorn crops is the reallocation of resources from vegetative to reproductive structures at the lower hierarchical levels of the tree.

In conclusion, our data indicate that large acorn crops cannot be the result of matching seed production to current resource availability (e.g., Despland and Houle 1997; Snook et al. 2005), resource accumulation alone (e.g., Sork et al. 1993; Yasumura 2006), or trade-offs at the level of the whole tree (e.g., Eis et al. 1965; Koenig and Knops 1998; Monks and Kelly 2006). Rather, our findings demonstrate that a combination of resource accumulation and trade-offs at low hierarchical levels of the canopy may be acting together to maximize acorn production during a mast year. The notion that the answer varies across trees and across hierarchical levels, together with the finding that the costs of reproduction are not in the reproductive modules but in their adjacent modules, adds new information that needs to be taken into consideration in discussions on the mechanisms of mast fruiting.

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