

# Stabilizing selection for within-season flowering phenology confirms pollen limitation in a wind-pollinated tree

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## Summary

1. We examined the fitness consequences of pollen limitation in the valley oak (*Quercus lobata* Née, Fagaceae), a wind-pollinated, predominantly outcrossing tree endemic to California, by examining the relationship between within-year phenology and acorn production over an 8 year period.
2. We predicted that pollen limitation should result in trees flowering relatively early and late in the season, when fewer trees are in flower, to experience reduced reproductive success compared to trees flowering during the middle of the season.
3. Despite considerable variation in acorn production from year to year, analyses confirmed this prediction and indicated that there was significant overall stabilizing selection on budburst date consistent with the pollen limitation hypothesis.
4. Analyses including herbivory and pre-budburst temperatures at individual trees revealed significant correlations with acorn production, but we still found significant stabilizing selection on budburst date even when considering these variables.
5. *Synthesis.* Pollen limitation, as indicated by stabilizing selection on within-year flowering phenology, significantly affects acorn production by individual trees in *Q. lobata* and has the potential to influence other key life-history features including masting behaviour and spatial synchrony.

**Key-words:** acorn production, herbivory, mast-fruiting, phenology, pollen limitation, *Quercus lobata*, reproductive ecology, wind-pollination

## Introduction

The temporal pattern of life cycle events within populations has important consequences on plant fitness. Although such phenological patterns have been investigated in a variety of contexts (Rathcke & Lacey 1985), work has generally been focused on the relationship between leaf phenology and herbivory in deciduous trees (Crawley 1985; Crawley & Akhteruzzaman 1988; Aizen & Patterson 1995; Mopper & Simberloff 1995; Mopper *et al.* 2000; Tikkanen & Julkunen-Tiitto 2003) and the selective effects of flowering phenology in insect-pollinated plants (Schemske 1977; Augspurger 1981; English-Loeb & Karban 1992; Pilson 2000).

In contrast, little is known about the relationship between flowering phenology and fitness in wind-pollinated species, where, unlike in insect-pollinated systems (Ashman *et al.* 2004; Knight *et al.* 2005), it has often been assumed that pollen is abundant and able to travel long distances (Koenig & Ashley 2003; Davis *et al.* 2004; Friedman & Barrett 2009). Challenging this view has been considerable empirical and theoretical work indicating that pollen limitation may play an important role in mast-seeding (Janzen 1976; Norton & Kelly 1988; Smith, Hamrick & Kramer 1990; Kelly, Hart & Allen 2001; Satake & Iwasa 2002a), as well as recent work on two species of oaks (genus *Quercus*) suggesting both that pollen is limited and that pollen dispersal is far more restricted than previously suspected (Knapp, Goedde & Rice 2001; Sork *et al.* 2002a). Although the limited extent of pollen dispersal in oaks is

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debatable (Abraham *et al.* 2011), pollen limitation clearly has the potential to have important effects on seed production and fitness in these wind-pollinated, largely self-incompatible trees.

Here, we investigate such effects in the valley oak, *Quercus lobata* Née, a widespread species endemic to the foothill and valley regions of California and threatened due to poor recruitment, land-use practices and global climate change (Sork *et al.* 2002a; Kueppers *et al.* 2005; Tyler, Kuhn & Davis 2006). Valley oaks, like other species in this widespread genus, are wind pollinated, largely self-incompatible (Cottam, Tucker & Santamour 1982; Sork *et al.* 2002b) and rarely hybridize with the closely related and often sympatric blue oak *Quercus douglasii* Hook. & Arn. (Craft, Ashley & Koenig 2002). The possibility of pollen limitation is of particular interest because acorn production in this species, as in other congeneric species, is highly variable and synchronized (Koenig *et al.* 1994a). Such 'mast-seeding' or 'masting' behaviour is of widespread ecological and evolutionary interest (Koenig & Knops 2000; Kelly & Sork 2002).

We addressed the issue of pollen limitation by investigating how within-year flowering phenology in the population is related to acorn production by individual trees. Specifically, if pollen is limited, we predicted that trees flowering relatively early and late in the season would be subject to greater pollen limitation and thus experience poorer reproductive success than trees flowering during the middle of the season. In terms of selection pressure, there should be stabilizing selection on flowering date, with trees flowering near the mean date experiencing higher fitness than trees flowering before or after the mean. Although similar patterns have been observed in insect-pollinated systems (Schemske 1977; Augspurger 1981), such a relationship between flowering phenology and fitness has not previously been examined in a wind-pollinated system.

Two alternative selective factors potentially influencing leaf and flowering phenology in oaks are environmental conditions and herbivory, the latter of which is known to potentially influence acorn production in *Quercus robur* L. (Crawley 1985) and may play an important role in influencing leaf and flower phenology in tree communities (Murali & Sukumar 1993). Herbivory has previously been found to result in directional selection in several species, with early-flushing individuals sometimes suffering relatively high rates of defoliation (Varley & Gradwell 1968; Pilson 2000) or vice-versa (Murali & Sukumar 1993; Mopper & Simberloff 1995). Here, we analyse 2 years of data on leaf herbivory to test the alternative hypothesis that the observed relationship between phenology and fitness is due to the selective effects of herbivory rather than pollen limitation. We also use 2 years of temperature data recorded at individual trees to test whether micro-environmental conditions independent of phenology might be responsible for the observed pattern.

We first document variation in within-year flowering phenology over eight seasons, confirming that the number of trees flowering at any one time follows a normal distribution and that there is strong concordance in relative budburst date among individuals across years. We then perform phenotypic

selection analyses to test whether selection on phenology is consistent with pollen limitation and whether selection on herbivory or micro-environmental differences offer alternative explanations for the observed relationship between phenology and acorn production.

## Materials and methods

### FIELD METHODS

We studied a population of 84 *Q. lobata* at Hastings Reservation, Monterey County, central coastal California, between 2003 and 2010. Each spring starting on or before 1 March, we surveyed all trees weekly for budburst and flowering activity. Trees were examined with binoculars and scored on the following three scales:

- Budburst*: (0) < 5% green; (1) 5–25% green; (2) 25–75% green; (3) > 75% green, fully leafed out.
- Catkin stage*: (0) none seen; (1) present but closed; (2) expanded; (3) some brown and spent; (4) largely brown and spent.
- Catkin number*: (0) None seen; (1) a small number; (2) a fair number; (3) many catkins present.

For the analyses conducted here, the metric we used to assess phenology was the Julian date on which budburst (measure a) was first recorded as being in category 1. To estimate the proportion of trees shedding pollen on any 1 day, we determined trees for which the catkin stage (measure b) was recorded as being either category 2 or 3 for each day relative to the mean budburst date for that year. Thus, a tree with catkin stage 2 on the fifth day after the mean budburst date (and < 2 prior to that date) and a 3 on the twelfth day (and a 4 after that date) was assumed to have been potentially shedding pollen on each of days 5 through 12 relative to the mean budburst date. Weekly surveys were continued until all trees had fully leafed out and achieved budburst category 3.

We used acorn production as our measure of fitness. Acorn production of trees was determined each autumn in early- or mid-September by means of visual surveys in which two observers scanned different parts of the canopy and counted as many acorns as they could in 15 s (Koenig *et al.* 1994a,b). Counts were then added, yielding the number of acorns per 30 s (N30). For all analyses, values were log-transformed ( $\ln[N30 + 1] = \text{LN}30$ ) to reduce the correlation between the mean and the variance.

Herbivory was quantified during June–July of 2009 and 2010 by examination of intact leaves in the canopy of the trees. One hundred leaves were examined at each of 1–4 sites (mean = 3.8) for damage due to herbivorous insects. We recorded the estimated proportion of each leaf damaged or eaten as a result of herbivory, from which we calculated (i) the proportion of leaves for which the per cent of estimated area lost to herbivory was > 1%, and (ii) the overall estimated proportion of leaf area lost to herbivory. Both measures were square-root arcsin transformed for analysis.

Starting in fall 2004, temperature experienced by individual trees was determined by small recorders (iButtons<sup>®</sup>; Maxim Integrated Products Inc., Sunnyvale, CA, USA) placed on the north side of the trunk of each tree 1.5 m above the ground. iButtons were programmed to record temperature at 4-h intervals; for the analyses performed here, we used the mean pre-budburst temperature recorded at each tree by averaging temperatures between 1 January and 14 February. Failures were common during the first years of the study, and thus, we restricted our analyses to 2009 and 2010, when data were available for all trees.

## DATA ANALYSIS

Concordance of budburst across years was examined with the mean ( $\pm$ SD) pairwise Pearson correlation coefficient ( $r$ -value) of budburst dates across all trees for each pair of years ( $N = 28$ ), as recommended by Buonaccorsi *et al.* (2003). The significance of mean maximum temperature to budburst date of individual trees was tested using Pearson correlations (individual years) and a mixed-effects model in which 'mean maximum temperature' (1 January to 14 February) and 'year' were independent variables, and 'tree' was included as a random effect.

The relationship between phenology (budburst date) and fitness, the latter estimated by the visual surveys, was assessed using two different mixed-effects models, in both cases including 'tree' as a random effect. First, we compared budburst relative to the annual mean (budburst of tree  $i$  in year  $x$  – mean budburst date for year  $x$ ) vs. the acorn crop of tree  $i$  in year  $x$ . Secondly, we compared standardized budburst date vs. standardized acorn crop ([budburst date or acorn crop of tree  $i$  in year  $x$  – mean budburst date or acorn crop of all trees in year  $x$ ]/SD of budburst date or acorn crop of all trees in year  $x$ ). We visualized the relationships between pairs of variables using locally weighted scatterplot smoothing ('loess' regression). We then calculated directional ( $\beta$ ) and stabilizing ( $\gamma$ ) selection coefficients on budburst date using each of the two models, reporting standardized coefficients (doubled for quadratic terms) for regressions of acorn productivity on the relevant measure of budburst date including both linear and quadratic terms (Lande & Arnold 1983; Stinchcombe *et al.* 2008).

To test whether observed patterns were potentially due to herbivory or micro-climatic temperature differences among trees rather than pollen limitation, we performed parallel selection analyses using the two measures of herbivory and mean pre-budburst temperatures as independent variables. We then conducted multiple regression analyses, again with 'tree' as a random effect, including as independent variables phenology (relative or standardized budburst date), herbivory (per cent leaves damaged or per cent herbivory on leaves), and mean pre-budburst temperatures, in all cases as both linear and quadratic terms. We sequentially dropped the least significant term until all remaining variables were statistically significant ( $P < 0.05$ ) to determine whether phenology remained an important selective factor when these alternative variables were considered. All statistical procedures were performed in R 2.12.2 (R Development Core Team 2011).

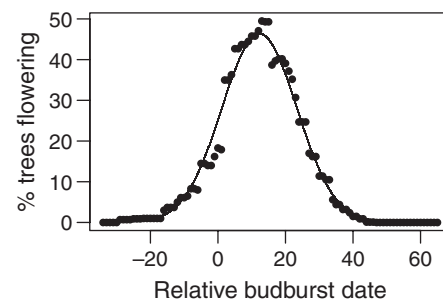
## Results

Across years, the earliest date of budburst ranged from 16 February (2010) to 5 March (2006 and 2007), the latest date from 2 April (2007) to 30 April (2006), and the mean date of from 12 March (2005) to 4 April (2006) (Table 1). However, despite this variation, budburst dates of individuals were highly correlated across all pairs of years (mean  $\pm$  SD  $r = 0.69 \pm 0.05$ , all 28 pairwise  $P$ -values  $< 0.001$ ). Thus, although there was considerable variation among years in phenology, with mean date of budburst differing by as much as 24 days in different years, the ranking of budburst across trees was similar from year to year.

Based on the proportion of trees with potentially shedding catkins, pollen availability closely matched a normal distribution, with the maximum number of trees flowering occurring 12.3 days following the mean budburst date (Fig. 1). Rela-

**Table 1.** Summary of budburst phenology of *Quercus lobata* at Hastings Reservation, 2003–2010

Year	Earliest	Latest	Range (days)	Mean date
2003	28 February	16 April	48	16 March
2004	3 March	3 April	32	18 March
2005	27 February	10 April	43	12 March
2006	5 March	30 April	57	4 April
2007	5 March	2 April	29	18 March
2008	3 March	22 April	51	26 March
2009	25 February	21 April	56	23 March
2010	16 February	13 April	57	17 March

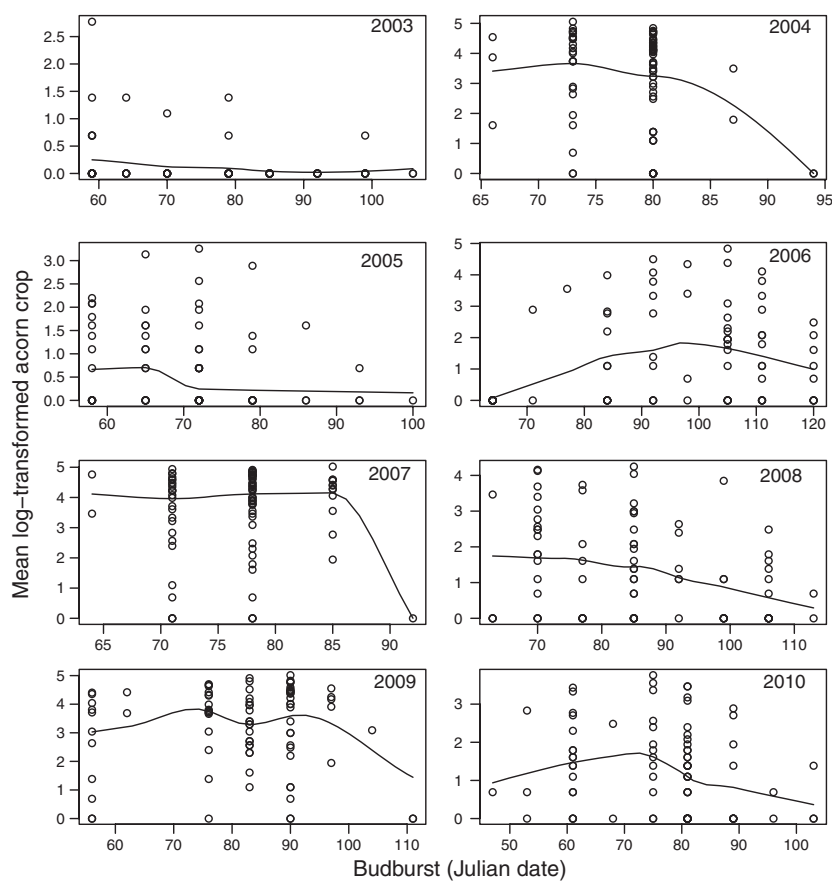


**Fig. 1.** Proportion of trees estimated to be shedding pollen on each day across all years relative to the mean budburst date. Curve is a normal distribution with mean  $\pm$  standard deviation =  $12.3 \pm 11.1$  days after the mean budburst date.

tively few trees shed pollen early and late in the season while nearly 50% of trees shed pollen 13–15 days after the mean budburst date. This supports the assumption that there is likely to be more pollen available to trees flowering during the middle of the season (i.e. trees whose phenology matched the mean budburst date) than for trees flowering either early or late relative to the mean budburst date.

The relationship between budburst and acorn production was highly variable among years (Fig. 2). We combined the 8 years of data in two ways differing in whether we standardized the acorn crop and budburst date (Table 2, Fig. 3). In both analyses, we detected strong stabilizing selection on budburst date ( $P \leq 0.003$ ). In addition, we found directional selection favouring earlier budburst in both analyses, although it was only significant when both the acorn crop and budburst date were standardized.

Mixed-effects models indicated significant linear, but not quadratic, effects of both herbivory and mean pre-budburst temperature on unstandardized acorn production. Specifically, increased acorn production was associated with less herbivory and higher mean pre-budburst temperatures, while neither variable was significantly associated with the standardized acorn crop (Table 2). In the multivariate analyses, the only term that remained in analyses of both the standardized and unstandardized acorn crop was stabilizing selection on phenology, while pre-budburst temperature exhibited directional selection when considering unstandardized acorn production (Table 3). Thus, neither herbivory nor environmental conditions appeared to



**Fig. 2.** Julian dates of budburst of individual trees plotted against the acorn crop of the trees for each year of the study. Curves drawn by 'loess' regression.

**Table 2.** Directional ( $\beta$ ) and stabilizing ( $\gamma$ ) selection coefficients ( $P$ -value) for budburst, two measures of leaf herbivory, and mean pre-budburst temperature of individual trees for *Quercus lobata* at Hastings Reservation based on mixed-effects models with fitness measured by annual or mean (log-transformed) acorn production

Dependent variable	Independent variable	$\beta \pm SE$	$P$ -value	$\gamma \pm SE$	$P$ -value
Relationship of budburst to acorn production					
Annual acorn crop	Relative budburst date	$-0.147 \pm 0.076$	0.056	$-0.780 \pm 0.090$	< 0.0001
Standardized acorn crop	Standardized budburst date	$-0.121 \pm 0.049$	0.012	$-0.055 \pm 0.019$	0.003
Relationship of herbivory to acorn production					
Annual acorn crop	Per cent leaves damaged	$-0.779 \pm 0.125$	< 0.001	$-0.107 \pm 0.194$	0.58
Annual acorn crop	Per cent herbivory on leaves	$-0.641 \pm 0.132$	< 0.001	$-0.177 \pm 0.210$	0.40
Standardized acorn crop	Per cent leaves damaged	$-0.059 \pm 0.078$	0.46	$-0.095 \pm 0.117$	0.42
Standardized acorn crop	Per cent herbivory on leaves	$-0.073 \pm 0.080$	0.37	$-0.127 \pm 0.121$	0.30
Relationship of mean pre-budburst temperature to acorn production					
Annual acorn crop	Mean temperature	$0.994 \pm 0.082$	< 0.001	$-0.168 \pm 0.337$	0.62
Standardized acorn crop	Mean temperature	$0.024 \pm 0.062$	0.70	$-0.223 \pm 0.255$	0.38

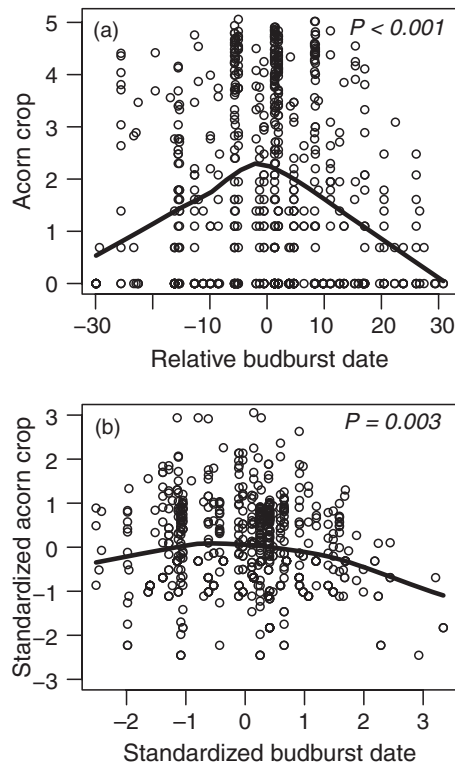
For description of variables, see text.  $N$  observations ( $N$  trees) = 677 (85) for budburst; 123 (69) for herbivory; 168 (84) for temperature.

be confounding the relationship between phenology and acorn production.

## Discussion

Recent re-evaluation of the importance of pollen limitation in wind-pollinated species has been spurred by experimental

studies of herbs and grasses (Davis *et al.* 2004; Friedman & Barrett 2009), theoretical work linking pollen limitation to mating behaviour and spatial synchrony (Satake & Iwasa 2000, 2002a,b), and studies on wind-pollinated trees suggesting strikingly short-distance pollen flow (Sork *et al.* 2002a) and a relationship between local pollen abundance and reproductive success (Knapp, Goedde & Rice 2001). We measured variation



**Fig. 3.** Relationship between budburst and acorn production by individual trees. (a) Budburst date relative to the annual mean vs. the acorn crop of tree  $i$  in year  $x$ . (b) Standardized budburst date vs. standardized acorn crop. All acorn crop data log-transformed; curves drawn by 'loess' regression. For statistics, see Table 2.

in budburst in a population of *Q. lobata* in California over a period of 8 years and examined phenological selection occurring on budburst date to test the importance of pollen limitation to a key fitness character (acorn production) in this wind-pollinated species.

As found previously in *Q. robur* (Crawley & Akhteruzzaman 1988), there was considerable variability in phenology among years, with the date of earliest budburst varying by 18 days and the date of mean budburst varying by 24 days. Also as in *Q. robur*, there was significant concordance of

budburst among years; that is, the ranking of budburst among individuals in the population was generally similar from year to year. The main difference observed between these two populations was the range in budburst dates, which was constant at 25 days in *Q. robur* and varied nearly twofold (from 29 to 57 days) in *Q. lobata*.

Our primary goal was to determine the relationship between phenology and fitness, the latter estimated by visual estimates of acorn production conducted in the autumn. Although the relationship between these two factors was variable across years (Fig. 2), when data for years were combined, we found highly significant stabilizing selection centred almost precisely at the mean budburst date (Fig. 3) along with evidence for directional selection favouring earlier budburst.

A significant relationship between budburst and acorn production as found here could be due to several factors. First, as proposed above, budburst could correlate with pollen availability, which could translate into greater or lesser fertilization success and acorn production. Alternatively, environmental conditions, either directly or as a proxy for some unmeasured variable, could be correlated with both phenology and acorn production. A third possibility is that budburst correlates with herbivory, which could then affect acorn production and fitness. We tested for the effects of pre-budburst temperatures and herbivory on individual trees and found evidence that both factors affected acorn production. Multivariate analyses, however, indicated that there was still significant stabilizing selection on phenology even when including these potentially confounding variables. Thus, as found in at least two insect-pollinated systems (Schemske 1977; Pilsen 2000), our results demonstrate significant stabilizing selection on budburst date in *Q. lobata* that is consistent with the hypothesis that pollen limitation is important in this system.

A wide variety of selective factors are known to influence phenological timing and patterns in plants, while pollen limitation has long been recognized as being important in insect-pollinated systems. Our results confirm that pollen limitation can be a key selective influence in natural wind-pollinated systems as well. Such limitation is a prerequisite for the hypothesized importance of 'pollen coupling' to variability in

**Table 3.** Results of analyses to determine directional ( $\beta$ ) and stabilizing ( $\gamma$ ) selection for budburst date, leaf herbivory and mean pre-budburst temperature of individual trees for *Quercus lobata* at Hastings Reservation based on mixed-effects models with fitness measured by annual or standardized (log-transformed) acorn production

Dependent variable	Independent variable	$\beta \pm SE$	$P$ -value	$\gamma \pm SE$	$P$ -value
Relative budburst date, leaf herbivory and mean pre-budburst temperature on the annual acorn crop	Annual acorn crop				
	Relative budburst date	–	–	$-0.400 \pm 0.13$	0.003
	Mean pre-budburst temperature	$1.011 \pm 0.081$	< 0.001	–	–
Relative budburst date, leaf herbivory and mean pre-budburst temperature on the standardized acorn crop	Standardized acorn crop				
	Relative budburst date	–	–	$-0.062 \pm 0.18$	0.001

Analyses started with all variables in both linear and quadratic forms; the least significant variable was then dropped sequentially until only statistically significant variables remained. Results were identical using either of two measures of herbivory (per cent leaves damaged or mean per cent herbivory), but neither measure was significant in any analysis and thus is not reported. Mean pre-budburst temperature was only significant in the analysis of the annual acorn crop. Data for 2009 and 2010;  $N$  observations ( $N$  trees) = 168 (84) for temperature.

seed production (Satake & Iwasa 2000). Pollen limitation thus may play a key role not only in individual variability in seed production, as shown here, but as a factor driving both spatial synchrony (Liebhold, Koenig & Bjørnstad 2004) and variability in annual seed production in this and other masting species.

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