

Lagged effects of early-season herbivores on valley oak fecundity

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Abstract The seasonal match between folivore and leaf phenology affects the annual success of arboreal folivore populations because many folivores exploit developing leaves, which are an ephemeral resource. One strategy for folivores to exploit early-season leaves is to anticipate their emergence. The consequence of this behavior for trees is that individuals that set leaves earlier may experience greater rates of folivore damage, with potential negative fitness consequences. To test this hypothesis, we surveyed the early-season phenology, insect folivore damage, and acorn crop of a population of valley oaks (*Quercus lobata*) over a 3-year period. We found that trees that set leaves earlier

experienced greater rates of folivore damage than trees that set leaves later in the season. In addition, we observed a lagged effect of folivore damage on acorn production, whereby trees with greater leaf damage produced fewer acorns in the subsequent year. These results indicate potential negative fitness consequences of earlier leaf phenology. Our study suggests that folivore pressure may be one factor that affects the optimal timing of leaf set in oaks.

Keywords Herbivory · Leaf set · Phenology · *Quercus* · *Chionodes*

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Introduction

The timing of early-season events is important for perennial plants and their folivores and has received considerable attention recently due to the effects of climate change (Parmesan 2007). Early-season phenology is often driven by the perception of photoperiod or climatic cues (Polgar and Primack 2011). However, optimal spring phenology is influenced by selection pressures imparted by both biotic and abiotic factors (Rathcke and Lacey 1985; Polgar and Primack 2011; Elzinga et al. 2007). For example, the phenology of plants and pollinators must be synchronized in order for successful pollination and mating to occur (Schemske 1977; Augspurger 1981), and spring phenology of folivores must match early-season plant development if the folivore exploits ephemeral plant tissues such as developing leaves or flowers (van Asch and Visser 2007; Singer and Parmesan 2010). Conversely, plants may avoid setting leaves, flowering, or pushing sap at times when the risk of herbivory is great (Aide 1993; Tikkanen and Julkunen-Tiitto 2003), and both plants and folivores may time their phenology so as to avoid deleterious

abiotic conditions such as frost or drought (Inouye 2008; Polgar and Primack 2011).

Directional selection for later leaf set is likely imparted by a variety of abiotic and biotic factors. For example, rare, late spring frost events could impose strong selection for later leaf set in plants and would be difficult to detect without long-term phenological studies (Augsburger 2009). Additionally, early-season biotic interactions such as colonization by pathogens and folivores might negatively affect long-term fitness by depleting resource stores, limiting growth, and limiting future seed set (Hunter 1992; van Asch and Visser 2007). Consequently, a variety of factors may exert conflicting selection pressures on leaf set phenology within a single population.

There are three hypotheses for how the life history of folivores may relate to their hosts (Fig. 1). First, according to the “phenological match” hypothesis, folivore development is expected to match the development of the plant tissues on which they feed (van Asch and Visser 2007; Singer and Parmesan 2010). Folivores are expected to synchronize their life histories to capitalize on leaf or flower set because plant tissues rapidly accumulate defenses that limit the growth of folivores, and, thus, there is only a short window of opportunity when many folivores can colonize a plant

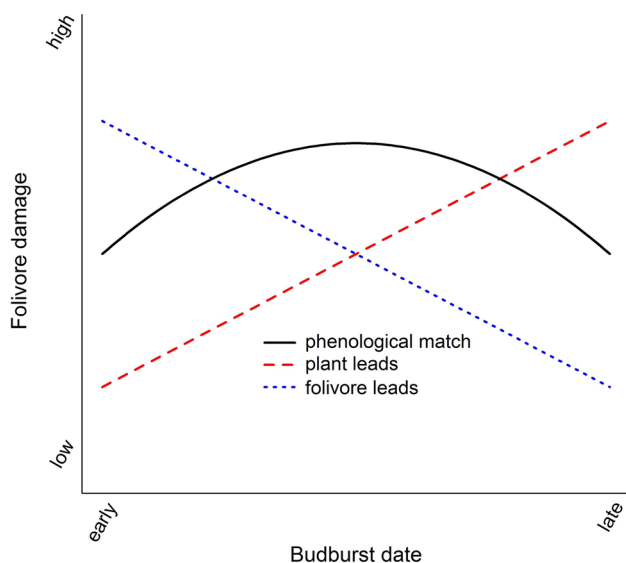


Fig. 1 Expected relationships between budburst phenology and folivores damage. The phenological match hypothesis predicts that folivores and leaves emerge synchronously, thus, those leaves emerging at the population mean will experience the highest herbivore damage. The folivore leads hypothesis predicts that because folivores emerge before the population mean of leaf set, leaves that develop earlier will be disproportionately colonized by folivores. The plant leads hypothesis suggests that early-season folivores emerge after the population mean of leaf set. If leaves quickly develop defenses after set, leaves that develop earlier may escape folivores because they are already defended by the time folivores emerge

(Feeny 1970; van Asch and Visser 2007). Thus, the phenological match hypothesis predicts that folivores are most likely to colonize trees that leaf out at the population peak.

Alternatively, mismatches between leaf set and folivore colonization may result from variation in folivore foraging strategies and development combined with imperfect information concerning the environmental factors influencing leaf phenology (Singer and Parmesan 2010). If the cost experienced by a folivore that colonizes late and encounters a presumably better-defended plant is small compared to the risk of that folivore colonizing a plant too early and not having any resources at all, then folivores might adopt a conservative “plant leads” strategy whereby they colonize plants later in the season. As a potential consequence of this, the interannual variation in population sizes of late-colonizing Lepidopteran folivores is expected to be less than the variation in early-colonizing folivores, suggesting that early-colonizing folivores undertake a greater risk of failure due to asynchrony with their resource (Forkner et al. 2008).

If, however, folivores incur relatively few costs from emerging before their host plants set leaves, but high costs due to late season emergence, then folivores might adopt spring phenologies that precede their hosts—the “folivore leads” hypothesis. For example, the median hatch time of winter moth consistently precedes the median budburst of its *Quercus robur* host (van Asch et al. 2007), despite high mortality when the phenological mismatch with its host is too great (Tikkanen and Julkunen-Tiitto 2003). Each of the three scenarios that relate folivore emergence to leaf set lead to different relationships between the timing of leaf set of a given tree and the amount of damage it receives, where the match scenario predicts a hump-shaped relationship, the plant leads scenario predicts that late emerging leaves will be disproportionately colonized, and the folivore leads scenario predicts that earlier emerging leaves will be disproportionately colonized (Fig. 1).

There may be an advantage to plants that avoid development at times of year when the risk of herbivory is high. For example, some tropical trees set leaves during the dry season when there is less risk of herbivory (Aide 1993). Analogously, if the timing of folivore risk is consistent in temperate systems, and herbivory imparts a substantial fitness cost on the plant, then selection by folivores might influence the timing of leaf set. While the relationship between spring phenology and folivore abundance has received considerable attention in several systems (Crawley and Akhteruzzaman 1988; Hunter 1992; Chen et al. 2003; Pearse and Karban 2013), few studies have examined how this relationship affects plant fitness. In part, this is likely due to difficulties in measuring fitness in perennial plants. Non-outbreak levels of herbivory have been shown to reduce seed production or tree growth in some systems

(Crawley 1985; Marquis and Whelan 1994), but perennial plants may also forgo short-term reproduction or growth in favor of later growth or resource storage (Boege and Marquis 2005).

We related the early spring phenology (leaf set) of a population of valley oaks (*Quercus lobata*) to folivore damage and to subsequent secondary growth and acorn production in order to ask two questions: (1) Does early-season folivory to *Q. lobata* follow the plant leads, folivore leads, or phenological match hypothesis? (2) Does early-season folivore damage reduce *Q. lobata*'s subsequent reproduction or growth in the same year or in the year following? We used these relationships and the previously reported relationship between leaf set and acorn production (Koenig et al. 2012) to assess selection on the timing of leaf set imposed by herbivory.

Methods

Site and natural history

Our study was conducted at Hastings Natural History Reservation located in central coastal California. The climate at the site is Mediterranean, with hot, dry summers and cool, wet winters. The study site comprises oak forest and oak savannah habitats mixed with open grasslands and chaparral. The dominant trees at the site include *Q. lobata* (valley oak), *Q. agrifolia* (coast live oak), and *Q. douglasii* (blue oak). In portions of the study site, *Q. kelloggii* (black oak) and *Q. chrysolepis* (canyon live oak) occur, along with a small proportion of other hardwood species including madrone (*Arbutus menziesii*) and California bay (*Umbellularia californica*). Our study focused on *Q. lobata*, a deciduous oak endemic to California.

We surveyed the early-season leaf phenology, leaf damage, acorn crop, and radial growth of 68 *Q. lobata* trees over the course of three years between 2009 and 2011, inclusive. Trees were located in an area covering 800 hectares, and ranged in elevation from 460 to 950 m and in diameter at breast height (DBH) from 34 to 193 cm.

Phenology and leaf damage assessment

We assessed early-season leaf phenology in 2009, 2010, and 2011 by visual estimation of leaf set of trees on a weekly basis starting in late February and continuing into May of each year (Koenig et al. 2012, 2015). At each survey, the degree of leaf set was assigned a categorical value, where 0—no leaves, 1—very few leaves present (<ca. 5%), 2—less than half of leaves present (>ca. 5%; <ca. 50%), 3—>ca. 50% leaves present, and 4—full leaf set. Bud burst (leaf set) was considered to have occurred when >5%

of buds on a tree had broken and green foliage was visible. Spring temperatures were recorded from an on-site weather station as the mean of daily maximum temperatures for the months of March and April. This aspect of climate has been shown to relate to acorn crops and leaf phenology of *Q. lobata* in other studies (Koenig et al. 1996, 2015).

In each of the three years, we measured leaf damage by examining 2–4 branches from each tree, where half of the branches were low (1.5–5 m) in the canopy and the other half were high (5–10 m) in the canopy. For the high branch sample, branches were destructively harvested using a ladder and pole pruners, and for the low sample, branches were harvested with a step ladder and pruning shears.

We conducted our damage estimates over the course of six weeks from early June through late July. From each branch, we randomly chose 100 leaves and visually assessed whether they had been damaged by folivores. A leaf was considered damaged if >5% of its area was removed. This excluded minor necrotic spots caused by small arthropods, such as thrips and aphids, but included most other herbivore damage. We then calculated the proportion of leaves damaged per branch (N leaves damaged/ N leaves assessed). The proportion of leaves with damage has been a preferable measure of folivore interactions with trees in many studies (Karban 2008), as it allows for high subsampling of potentially patchy patterns of folivore damage, which a thorough measure of leaf area damage to a few leaves does not (Rothrock and Sterling 1982).

In spring 2013, we collected 40 caterpillars from all surfaces of early-season leaves (i.e., prior to leaf set of all trees in our population) on *Q. lobata* within the study area in order to gain insight as to the folivores most likely involved. Caterpillars were reared to adults and identified to species by John DeBenedictis and ISP. Rearings of early-season caterpillars found a variety of leaf-tying microlepidopterans causing damage to valley oak leaves. The most abundant folivore was the gelechiid moth, *Chionodespowelli* Hodges, which represented over one third of all rearings. Additional folivores included the gelechiids, *Chionodesjohnstoni* Clarke, *Telphusedulitella* (Bsk.), and *Xenolechia "staspa"* Hodges MS, as well as tortricid moths, *Epinotiaemarginana* (Wlsm.) and *Arphips-argyrospila* (Walker). Also, leaf mines caused by *Stigmella* sp. and *Camerarialo batiella* Opler and Davis were found and scored as leaf damage. Most of these species of herbivores are oak (*Quercus*) oligophages whose hosts are confined to *Quercus* or a subset of species therein (Powell and Opler 2009).

Acorn crop and radial growth

We assessed acorn crops in late September of 2009–2012 using the visual survey method of Koenig et al. (1994a),

by which two observers using binoculars count acorns for 15 s in each tree. Timed acorn counts strongly correlate with comprehensive crop assessments from litter fall traps, but lack problems of canopy acorn removal (Koenig et al. 1994a). Our survey contained a subset of the trees whose patterns of acorn production are described and analyzed elsewhere (Koenig et al. 1994b; Pearse et al. 2014). Counts were added ($N30$) and log-transformed ($\ln[N30 + 1] = \text{LN}30$) prior to statistical analysis. Radial growth in 2009–2012 was measured using dendrometers on an annual basis (September–September) as the change in circumference (mm) per year (Cattellino et al. 1986; Knops et al. 2007). Reproduction and growth were measured for an additional year (2012) and compared to measures of herbivore damage because we were interested in the lagged effects of herbivores on growth and reproduction.

Statistical analysis

We used linear mixed models to analyze the relationships among leaf set, herbivory, radial growth, and acorn set. As the study was conducted over three years, we included "year" and "tree" as random intercepts to account for non-independence among samples. Model effects of a given predictor were determined using a likelihood ratio test against a null model lacking only that predictor. Key informative and null models are summarized in Supplementary Table S1. Model fitting was conducted using maximum likelihood for all likelihood ratio tests. The key analyses included the effect of timing of leaf set (day of year) explaining percent damaged leaves, and the effect of percent damaged leaves explaining reproduction or lagged reproduction (LN30 acorns) as well as growth or lagged growth ($\Delta\text{mm}/\text{year}$).

Fixed sampling dates for herbivore damage in studies that assess the relationship between phenology and herbivory may confound the timing of leaf set with the absolute amount of time that leaves are present in that season. We sampled leaf damage across different dates for different individuals, thus, giving us the opportunity to disentangle the timing of leaf set from the overall sampling period. An initial comparison of models that included either leaf set, sampling period, or both factors indicated that folivore damage was a function of leaf set rather than the length of time leaves had been on the tree prior to sampling (ΔAICc leaf set = 0, leaf set + sampling date = 6.8, sampling date = 8.5). In subsequent analyses, we therefore focused on leaf set as opposed to sampling period.

We treated leaf damage as a canopy-scale event by averaging leaf damage scored on separate branches by individual tree. As support for this approach, damage levels varied among tree individuals (comparing a random effect of tree individual to an uninformative model: $\Delta\text{AICc} = 86$).

Initially, we observed that leaves higher in the canopies of our trees consistently experienced greater proportional leaf damage than lower leaves (mixed effects model, $\Delta\text{AICc} = 19$). Because we sampled high and low branches of each tree, however, average height of sampling for each tree did not correlate with leaf damage at the tree level (Pearson's $r = -0.05$, $P = 0.49$). Averaged damage estimates were only included in analyses when all subsample (branch) measurements were present. Because of difficulties in accessing branches of some trees, folivore damage measurements could not be made on a few trees each year resulting in samples of 68 trees in 2009, 65 trees in 2010, and 55 trees in 2011. Likewise, a few radial growth estimates were missing from given years due to equipment malfunction.

Models conformed to mixed model assumptions. R^2 statistics were calculated based on likelihood ratios between informative and null models (Nakagawa and Schielzeth 2013). All statistics were calculated in R2.15.1 (R Core Development Team 2012) using package nlme (Pinheiro et al. 2009) for mixed models.

Results

Budburst and herbivory

Leaf-out (budburst) of *Q. lobata* began on 24 Feb., 14 Feb., and 6 March in 2009, 2010, and 2011, respectively (Fig. 2a). Leaf-out day varied consistently by both tree and year (where "tree" explained 59 % of the variation in leaf-out, and "year" explained 25 % of the variation in leaf-out). In all years, budburst had occurred in all trees by 15 April and peak budburst occurred in late March. The mean maximum daily spring temperatures (March–April) at the site were 17.2 °C in 2009, 16.1 °C in 2010, and 16.3 °C in 2011. The mean percentage of leaves damaged each year was 47.8 % in 2009, 59.1 % in 2010, and 40.2 % in 2011. Percent damaged leaves varied consistently by both tree and year (where "tree" explained 28 % of the variation in leaf damage, and "year" explained 16 % of the variation in leaf damage).

Trees with earlier budburst experienced greater folivore damage (mixed effects model, likelihood ratio [LR] = 6.71, $P = 0.009$, $R^2 = 0.10$, Fig. 2b). On average, trees had 0.26 % fewer damaged leaves with each day of delayed budbreak. Consequently, trees that broke bud in early March experienced 15 % more damaged leaves than trees that broke bud in April.

Herbivory and oak fitness components

Average timed acorn counts ($N30$) per year were for 2009: 30.2; for 2010: 2.8; and for 2011: 15.6 acorns per tree. Acorn crop varied consistently by both tree and year

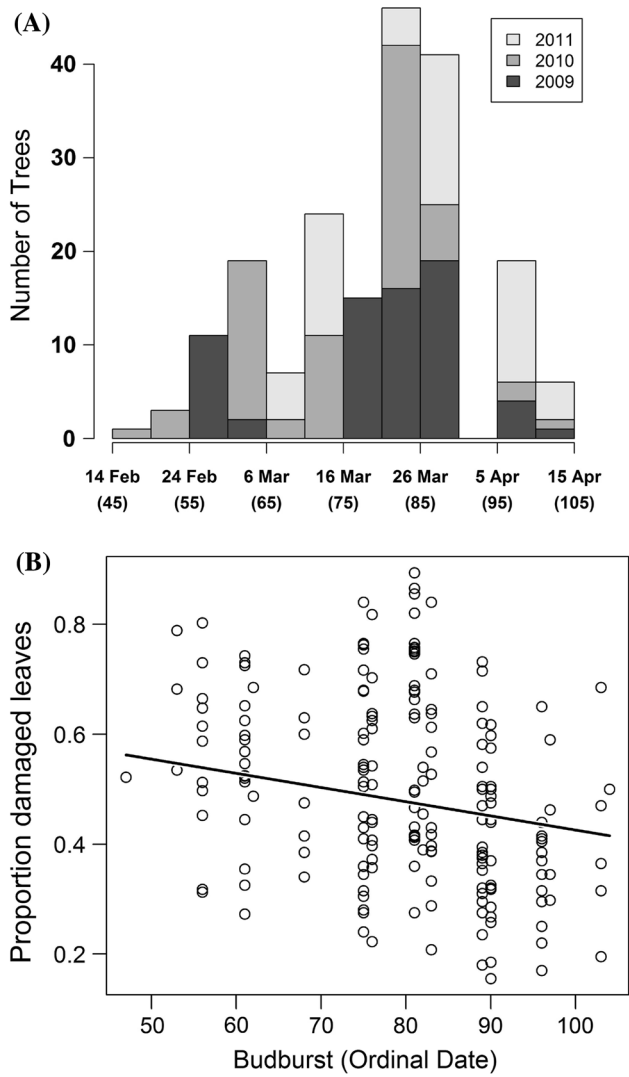


Fig. 2 Budburst and leaf damage in valley oak. **a** Histogram of budburst dates. *Shading* indicates year of sampling. Calendar date is shown as well as ordinal date (*in parentheses*). **b** A negative relationship between date of budburst and leaf damage. Leaf damage was measured as the proportion of leaves with >5 % visible leaf damage. *Points* represent one season of damage for an oak individual

(where "tree" explained 20 % of the variation in acorn crop and "year" explained 33 % of the variation in acorn crop). Greater leaf damage did not correlate with a reduced acorn crop in the same year (mixed effects model, likelihood ratio [LR] = 0.71, $P = 0.48$, $R^2 = 0.01$, Table 1). However, trees with greater leaf damage produced a smaller acorn crop the subsequent year (LR = 7.64, $df = 188$, $P = 0.006$; Table 1). Specifically, for every percent of leaves damaged, trees had on average 0.017 lower LN30 acorn counts.

Leaf damage did not relate to tree radial growth in the current year (LR = 0.71, $P = 0.40$). Likewise, leaf damage had no lagged effect on tree radial growth the subsequent year (LR = 0.79, $P = 0.38$). We found no evidence for a relationship between growth and acorn production in our dataset (LR = 0.58, $P = 0.44$).

Discussion

The prospect of a changing climate and alterations in plant phenology has highlighted the importance of the relationships that exist among plant phenology, folivore populations, and plant fitness (van Asch and Visser 2007; Singer and Parmesan 2010; Yang and Rudolf 2010; Polgar and Primack 2011). In particular, recent work has demonstrated that the match between folivore and plant phenology can lead to outbreaks of early-season folivores, which can result in forest defoliation events (van Asch and Visser 2007; Forkner et al. 2008). In addition, the emergence of early-season folivores can precede the leaf set of their hosts (the folivore leads scenario; Rehill and Schultz 2002; Tikkanen and Julkunen-Tiitto 2003), causing trees with early leaf phenology to experience greater folivore damage than those that leaf out later (Hunter 1992; Pearse and Karban 2013). Our study supports the folivore leads hypothesis for *Q. lobata* (Fig. 2b) and finds evidence that folivore damage has adverse fitness consequences for the affected trees (Table 1).

Table 1 The relationship between early-season folivore damage and *Q. lobata* growth and reproduction in the current year or one year later (lagged)

| Relationship analyzed (response–fixed effect) | Standardized β | R^2 | Likelihood ratio | P |
|-----------------------------------------------|----------------------|-------|------------------|-------|
| Growth–damage | 0.065 | 0.01 | 0.71 | 0.399 |
| Lagged growth–damage | –1.844 | 0.01 | 0.79 | 0.375 |
| Reproduction–damage | –0.048 | 0.01 | 0.51 | 0.477 |
| Lagged reproduction–damage | –1.704 | 0.10 | 7.23 | 0.007 |

Mixed model results with "year" and "tree" as random effects. Significant effects are bolded

The relationship between leaf set phenology and folivore damage is variable across systems. The folivore leads scenario, as supported here, has been found previously in oaks (Hunter 1992; Pearse and Karban 2013) and other temperate trees (Chen et al. 2003). However, a few studies have found no relationship between tree phenology and levels of folivore damage (Crawley and Akhteruzzaman 1988; Watt and McFarlane 1991; Pearse and Hipp 2009), and still others have found evidence for temperate trees with late leaf set experiencing greater leaf damage (Mopper and Simberloff 1995).

We found evidence that early-season folivore damage had an impact on oak fitness in terms of reduced acorn production in the year following the damage. However, folivore damage did not correlate with either acorn production in the same year or with radial growth of the tree. While folivores often consume a relatively small proportion of tree leaf material, experimental removal of folivores has been found to affect acorn set in *Q. robur* (Crawley 1985) and growth in *Q. alba* (Marquis and Whelan 1994). In the current study, we found that the negative fitness consequence of herbivory was manifest after a 1-year lag (Table 1). This is consistent with the complex system of between-year resource allocation found in many trees (Sala et al. 2012; Barringer et al. 2013). For example, several studies have found a lag-1 autocorrelation in acorn set, suggesting that resource depletion due to a high acorn crop results in a low crop the following year (Sork et al. 1993; Pearse et al. 2014). In this case, we do not know the mechanism of resource storage and interannual allocation, but in other trees nitrogen, carbohydrates, or phosphorous become depleted in some seasons and appear to limit future seed set (Miyazaki 2013; Ichie and Nakagawa 2013; Sala et al. 2012).

Our data support the hypothesis that folivores may select for later leaf set in *Q. lobata*. We observed a weak but significant negative relationship between folivore damage and fecundity in the following year (Table 1). Likewise, the relationship between phenology and herbivore damage was weak, but significant (Fig. 2). Based on this, the selection pressure of herbivores on timing of leaf set is probably weak in any given year. However, when taken over the lifespan of a long-lived tree, or many generations thereof, the fitness consequences of early-season herbivory may be substantial. Moreover, leaf set phenology is typically under strong genetic control, with an average of heritability estimates for various phenological events in plants at 0.18 (Geber and Griffen 2003), and estimates of leaf set heritability in *Q. lobata* seedlings ranging from 0.2 to 0.5 (Pearse et al. 2015).

A previous 9-year study at the same site found evidence for stabilizing selection in leaf set date, with trees that set leaves near the median leaf set date producing greater acorn

crops (Koenig et al. 2012). The trend towards stabilizing selection around the median leaf set date is consistent with expectations based on oaks outcrossing and flowering at the same time as they set leaves (Sork et al. 1993) such that greater pollination is likely when flowering at the same time as other trees (Augspurger 1981). Our results here suggest that a lagged effect of folivore damage caused by early leaf set may be one factor opposing stabilizing selection due to reproductive synchrony (Koenig et al. 2012). This highlights the need to account for longer timescales and lagged effects when assessing selection pressures on long-lived trees such as oaks.

Many other biotic and abiotic factors could also influence selection pressure on the timing of oak leaf set, but may not be observed within a single season. Rare early-season frost events might have a large and long-lasting fitness consequence in trees. For example, an unusual weather pattern in Illinois in 2007 caused substantial frost damage to trees that set leaves early in that year (Augspurger 2009), and this damage affected tree growth, mortality, and reproduction for several growing seasons (Augspurger 2011). Alternatively, some unmeasured correlate of folivore damage could cause the lagged reduction in the acorn crop. Nevertheless, this study supports the hypothesis that a reduction in fitness due to early-season leaf damage in oaks is an important factor selecting for later leaf set.

The relationship between plant phenology and folivore interactions is becoming increasingly important as a warming climate shifts the phenology of plants and their folivores (Singer and Parmesan 2010; Yang and Rudolf 2010). In general, the success of folivores in future climates will depend upon the degree to which their phenology continues to match that of their host (van Asch et al. 2007; Singer and Parmesan 2010). Here we show that the match between folivore and host phenology may not be exact, as trees that set leaves earlier than the population mean may experience greater folivore damage.

Past studies have shown that folivores may benefit from emerging slightly before all of their hosts set leaves (Tikkanen and Julkunen-Tiitto 2003). Our results indicate that trees may benefit from setting leaves after folivores have already colonized a different tree, although the negative consequences of herbivory may only be apparent in subsequent years. Thus, as climate alters the phenologies of oak trees and their folivores, the resulting phenological mismatch may have fitness consequences for both parties.

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