Notes

Pollen limitation and flower abortion in a wind-pollinated, masting tree

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Abstract. Pollen limitation is a key assumption of theories that explain mast seeding, which is common among wind-pollinated and woody plants. In particular, the pollen coupling hypothesis and pollination Moran effect hypothesis assume pollen limitation as a factor that synchronizes seed crops across individuals. The existence of pollen limitation has not, however, been unambiguously demonstrated in wind-pollinated, masting trees. We conducted a two-year pollen supplementation experiment on a masting oak species, *Quercus lobata*. Supplemental pollen increased acorn set in one year but not in the other, supporting the importance of pollen coupling and pollination Moran effect models of mast seeding. We also tracked the fate of female flowers over five years and found that the vast majority of flowers were aborted for reasons unrelated to pollination, even in the presence of excess pollen. Pollen limitation can reduce annual seed set in a wind-pollinated tree, but factors other than pollen limitation cause the majority of flower abortion.

Key words: anemophily; flower abortion; perennial plants; pollen; seed set; wind pollination.

Introduction

Pollen limitation, the production of less than the maximum seed potential due to inadequate pollen receipt by ovules, is common among animal-pollinated plants but has received little attention in wind-pollinated plants (Koenig and Ashley 2003, Ashman et al. 2004, Knight et al. 2006). Despite this, pollen limitation has become central to the theoretical mechanisms regarding masting, the synchronous and intermittent production of seeds. Theories to explain masting generally rely on pollen limitation to explain the within-population synchrony of seed set (Satake and Iwasa 2000, 2002, Koenig et al. 2014). In addition, pollen limititation is often considered a negative consequence of small population sizes or fragmentation (Knapp et al. 2001, Wilcock and Neiland 2002, Jump and Peñuelas 2006). Surprisingly, however, pollen limitation has rarely been experimentally demonstrated in natural populations of wind-pollinated plants (Koenig and Ashley 2003).

Mast seeding is common among both insect- and wind-pollinated plants (Kelly 1994, Kelly and Sork 2002) and is particularly important to populations of

seed predators. The resource pulses generated by masting events can also have a cascading effect through food webs such that even those organisms that do not directly rely on mast seeds as a resource are still affected by the variability in seed set (Jones et al. 1998).

Two often cited drivers of masting are the internal resource dynamics of plants and pollination success (Isagi et al. 1997, Satake and Iwasa 2000, Rees et al. 2002, Koenig et al. 2014). Resource dynamics are central to many theories of masting (Isagi et al. 1997, Rees et al. 2002). Their importance is supported by numerous studies that have reported mast years being followed by a year of particularly poor seed set (Sork et al. 1993, Pearse et al. 2014), a trend typically attributed to resource limitation in nonmast years. Resource dynamics alone, however, cannot account for the high synchrony in seed set among plants within a region, since each plant could presumably maintain its own unique schedule of high and low seed production (Satake and Iwasa 2000).

Pollen limitation is one factor that could maintain synchrony in seed set. There are two key mechanistic hypotheses that link pollination success to masting (Satake and Iwasa 2000, Koenig et al. 2014). First, the pollen coupling hypothesis suggests that pollen could synchronize seed crops between individuals because plants that flower in synchrony with conspecifics will all produce a larger seed crop in that year. In turn,

depleted resources from that masting event will limit flower production for the entire population in the following year (Satake and Iwasa 2000). Second, the pollination Moran effect hypothesis suggests that weather events in some years will limit pollination and result in a poor seed set, and, in other years, resource availability may limit seed set (Koenig et al. 2014). Both of these hypotheses predict pollen limitation in masting plants in some years and resource limitation in others.

We tested for pollen limitation in valley oak (*Quercus lobata*), a masting, wind-pollinated tree, using pollen supplementation experiments in two consecutive years. In addition, we followed the fate of female flowers over five years and related this to the interannual variation in seed crops. The pollen limitation hypothesis predicts that pollen supplementation will enhance reproduction, but not necessarily in all years. Pollen limitation also predicts that the total seed crop of a given year will be more closely related to the successful maturation of flowers into fruits than to the initial abundance of flowers, so the size of a seed crop in a given year may be unrelated to the abundance of female flowers in that year.

Methods

Study system and site

We conducted our study at Hastings Reservation, located 40 km southeast of Monterey in central coastal California. Pollination supplementation experiments were conducted on Haystack Hill (36.385114° N, −121.561906° W) within the reserve. This site is a patchwork of native and nonnative grassland, oak savanna, and chaparral (Griffin 1990). Three oak species, *Quercus lobata*, *Q. douglasii*, and *Q. agrifolia* are common; all are wind pollinated. Two of those species (*Q. lobata* and *Q. douglasii*) can hybridize, but hybrids constitute a small percentage of trees in the area (Abraham et al. 2011).

We used valley oak (*Q. lobata*) to experimentally test for pollen limitation. As a masting species, *Q. lobata* exhibits high interannual variation in seed set and high synchrony in seed set over large areas (Koenig et al. 1994, Koenig and Knops 2013). Interannual variation in acorn crop is correlated with spring temperatures (Koenig et al. 1996), suggesting that pollination, which happens in spring, is involved in masting dynamics. Likewise, trees that flower outside of the population mean flowering time tend to produce fewer acorns than those that flower synchronously with other trees (Koenig et al. 2012). This leads to a trend where years with low synchrony in flowering have low acorn crops (Koenig et al. 2014).

Pollen supplementation experiments

We chose 30 mature *Q. lobata* individuals within our study site based on size (>25 cm diameter at breast height) and accessibility. Pollen supplementation experiments were conducted in 2012 and 2013. In each year, pollen-supplemented and control (open-pollinated) branches were compared within trees.

Within-plant comparisons may lead to overestimation of pollen limitation when pollen-supplemented flowers compete for resources with control flowers (Knight et al. 2006) We attempted to minimize this effect by choosing branches that were separated by at least 5 m of vascular tissue. Because trees are often modular in their carbohydrate use (Hoch 2005), these distant branches were unlikely to compete for resources in the same way as neighboring flowers on smaller plants.

Prior to leaf set, we chose two branches of roughly equal size on each tree and randomly assigned one branch to each treatment (control or pollen supplementation). Each branch had 100–1000 leaves. We counted the number of female flowers and leaves present on each branch in late spring (May–June) and counted acorns on each branch the following September. From this, we calculated the number of acorns and flowers per 100 leaves, as an estimate of acorn density (APL) and flower density (FPL) on each branch. As female flowers develop from leaf axils in oaks (Sharp and Sprague 1967), standardization of flowers and acorns to the number of leaves accounts for differences in branch size and architecture.

We added conspecific pollen to branches in slightly different ways in 2012 and 2013. In 2012, we tied a plastic mesh bag with 3-cm mesh size around pollination and control branches. Each week, starting at the first week of flowering, we collected bulk *Q. lobata* catkins from trees outside of the experimental population. Each pollen collection contained pollen from at least five individuals, but the identity of those individuals changed throughout the season as different individuals began and ceased flowering. Each week those bulk-collected catkins were divided evenly into 30 aliquots each containing ~20 catkins, and those catkins were placed on the pollen supplementation bagged branch. The control branch received no catkins.

In a subset of supplementation and control treatments ($N = 9$ of each), we assayed pollen receipt during the preflowering period of the branches by taping a microscope slide with a thin layer of vacuum grease to pollen supplementation and control branches and then recording the pollen caught in the grease. Grease slides were left in trees for one week, during which time, the ones on pollen supplementation branches received one application of catkins. We also included a third treatment (pollen exclusion) on a third randomly chosen branch on each tree by placing a cotton pollen-exclusion bag over the branch and taping the bag onto the main stem of the branch in order to limit air and pollen flow into the bag. All bags (mesh bags and pollen exclusion

bags) were removed in June, one month after trees had stopped flowering.

In 2013, we collected pollen as in 2012. Instead of placing catkins in bags attached to experimental branches, we instead dried catkins for one week to induce dehiscence, placed aliquots of dried catkins into paper sacks, and then placed the paper sacks over pollen supplementation branches and agitated them. Pollen retains complete viability for over one month in several oak species (Gómez-Casero et al. 2004), so collected pollen was likely viable. As in 2012, we added pollen to the supplementation branches weekly over the flowering season. On a small number of trees ($N = 3$) outside of the main experiment, we assessed the efficacy of pollen addition with this method by supplementing pollen on flowering branches, counting pollen that was attached to the stigmas of 10 female flowers, and comparing this to pollen counts on 10 flowers on control (open-pollinated) branches from the same trees.

Flower and acorn surveys

We surveyed female flowers and acorns on marked branches of 83 Q. lobata individuals over 5 yr (2009–2013). Trees were located throughout Hastings Reservation and were chosen based on their inclusion in a long-term survey of acorn production (Koenig et al. 1994). In a few cases, branches were inaccessible leading to slightly different sample sizes each year.

Two branches on each tree were arbitrarily chosen and marked in each year. In late spring (May–June), we counted the number of female flowers per branch. The following September, we counted the number of acorns on the same branch. Counts were summed between branches. We calculated acorn and flower abundance per 100 leaves as a measure of acorn and flower density, and calculated the mean and standard error of acorn (mAPL) and flower density (mFPL) for the entire population in each year. From the results of the pollen supplementation studies in 2012 and 2013, we calculated alpha as the ratio of mAPL(supplemented)/mAPL(control). We then calculated the potential acorn crop for the population would be in each year in the absence of pollen limitation as alpha × mAPL(population).

Statistical analysis

We analyzed the pollen supplementation experiments in each year separately, using a mixed effects linear model where either acorn density (APL) or flower density (FPL) was a function of treatment (either supplemented or control). Tree was included as a random factor in all analyses. Pollen exclusion experiments were analyzed in the same way, comparing control (open-pollinated) and pollen-exclusion branches. Efficacy of the pollen supplementation experiments was analyzed with a linear model describing pollen counts per area or per stigma as a function of treatment (pollen supplementation or control). All statistics were calculated in R using the package nlme (Pinheiro et al. 2009, R Development Core Team 2012).

Results

Pollination experiments

Pollen supplementation increased the density of pollen near flowers in 2012 by 744% (control = 2.39 pollen grains/mm^2, supplemented = 20.2 pollen grains/mm^2, $F_{1,16} = 13.5$, $P = 0.002$). In 2013, pollen supplementation increased pollen receipt by oak stigmas by 357% (control = 12.6 pollen grains/stigma, supplemented = 56.4 pollen grains/stigma, $F_{1,4} = 7.81$, $P = 0.049$). Pollen exclusion decreased acorn density by 70% compared to open-pollinated controls ($F_{1,29} = 9.4$, $P = 0.004$; Appendix A: Fig. A1).

In 2012, acorn production by supplemented branches was 26% greater than open-pollinated control branches, a nonsignificant difference (mean control APL = 0.93, mean supplemented APL = 1.17, $F_{1,28} = 0.4$, $P = 0.53$; Fig. 1) In 2013, however, supplemental pollen significantly increased acorn density by 125% above open-pollinated branches ($F_{1,29} = 7.8$, $P = 0.009$; Fig. 1). Flower production (FPL) did not vary between control and pollen-supplemented branches in 2012 ($F_{1,28} = 0.2$, $P = 0.68$) or 2013 ($F_{1,29} = 3.1$, $P = 0.09$).

Flower and acorn surveys

Both acorn and flower density varied between years (flowers, $F_{4,336} = 12.0$, $P < 0.001$; acorns, $F_{4,336} = 8.1$, $P < 0.001$; Fig. 2). The yield of acorns per flower also varied between years ($F_{4,336} = 10.3$, $P < 0.001$), with a minimum of 4.5% of flowers producing acorns in 2010 and a maximum of 18.4% of flowers producing acorns in 2011.

Based on the experiments, we estimated the size of the acorn crop in each year in the absence of pollen limitation. In the pollen-limited year (2013), we estimated a population-wide density of 1.94 acorns per 100 leaves in the absence of pollen limitation. This suggests that in the absence of pollen limitation, 12.7% of female flowers would have developed into acorns compared to the observed value of 5.7% (Fig. 2).

Discussion

We found experimental evidence for pollen limitation in Q. lobata, a wind-pollinated, outcrossing, mast-fruiting oak. Pollen supplementation affected acorn set in one of two years, suggesting considerable interannual variability in pollen limitation in natural populations of wind-pollinated plants. We also found that exclusion of nonself pollen dramatically reduced seed set, consistent with other oak species that show a high degree of outcrossing due to self-incompatibility (Boavida et al. 2001, Wright and Dodd 2013).
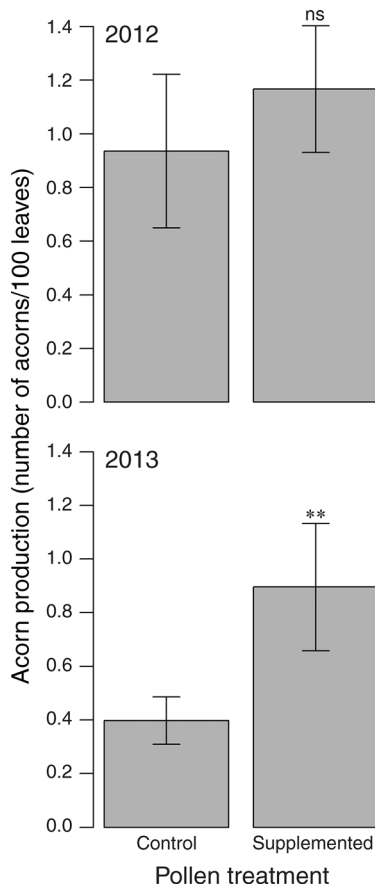
Fig. 1. The effects of supplemented pollen on acorn production. Acorns on paired open (control) branches and pollinated branches on 30 *Quercus lobata* trees were counted. Acorns are reported per 100 leaves to control for branch size. Bars show mean ± SE, and ns indicates nonsignificant.
** $P < 0.01$

Despite strong evidence for pollen limitation in *Q. lobata*, we found that most female flowers aborted even when supplied with surplus pollen. This suggests that processes other than a lack of pollination contribute to interannual variability in seed set. One likely possibility is resource limitation, an idea consistent with current theoretical considerations of masting (Satake and Iwasa 2000, 2002).

Pollen limitation has only rarely been documented for wind-pollinated plants, and most evidence suggesting pollen limitation in these plants is correlative (Koenig and Ashley 2003). Correlative evidence has suggested pollen limitation in at least two tree species, however. In whitebark pine (*Pinus albicaulis*), correlations between seed set and male reproductive allocation are consistent with pollen limitation (Rapp et al. 2013). In *Q. lobata*, individuals that flower either during the population mean-flowering time in a given year or in years with more synchronous flowering tend to produce larger

acorn crops than those that flower at the phenological extremes or in desynchronized years (Koenig et al. 2012, Koenig et al. 2014). Pollen limitation has also been experimentally documented in some populations of wind-pollinated herbs, grasses, and montane shrubs. Pollen limitation reduced seed set in *Spartina alterniflora*, an invasive marsh grass, when its populations were small (Davis et al. 2004). Likewise, when in low-density populations, the wind-pollinated herb *Mercurialis annua*, was pollen limited, though this was only the case for nonhermaphroditic individuals (Hesse and Pannell 2011). Pollen supplementation increased seed set in a montane *Betula* species, but had no effect on seed set in coastal populations (Holm 1994).

Evolutionary theory predicts that pollen limitation should be rare in wind-pollinated species, because wind pollination may be a reproductive strategy to avoid the risk of pollen limitation due to a lack of pollinating animals (Culley et al. 2002) and in plants with costly seeds compared to flowers (Rosenheim et al. 2014). Oaks fall into both of these categories. Moreover, estimates of average distance to paternal parents of acorns vary wildly but can be high (Sork et al. 2002, Abraham et al. 2011). However, wind pollination does not appear to eliminate the risks of pollen limitation. First, small population sizes may lead to a scarcity of pollen and pollen limitation, as has been found in wind-pollinated herbaceous plants (Davis et al. 2004, Hesse and Pannell 2011). Abiotic conditions that are unfavorable to airborne pollen, such as low wind and precipitation can reduce pollen flow (D'Amato et al. 2007), potentially resulting in pollen limitation in wind-pollinated species. Phenological asynchrony in flowering may lead to pollen limitation in wind-pollinated plants, just as it frequently does in animal-pollinated species (Augspurger 1981, Koenig et al. 2012). Finally, synchronous interannual variation in flowering could lead to pollen limitation in those years where few members of a population flower (Satake and Iwasa 2000). As a possible example, the abundance of pollen from wind-pollinated tree species in the genera *Abies*, *Carpinus*, *Fagus*, *Larix*, and *Picea* all showed high interannual variability across central Europe (Geburek et al. 2012).

Pollen limitation is central to current models of masting that rely on pollen limitation to drive population-wide synchrony in seed crops (Satake and Iwasa 2000, Kelly et al. 2001, Koenig et al. 2014). Each of these theories predict pollen limitation of seed crops in some years but limitation due to other factors, such as resources or flower crops, in others. Interestingly, masting plants are disproportionately wind pollinated (Herrera et al. 1998), and thus models of masting predicated on pollen limitation are incompatible with the notion that wind-pollinated plants are rarely pollen limited. It is worth noting that pollen limitation over a single season, as would be predicted for masting species,
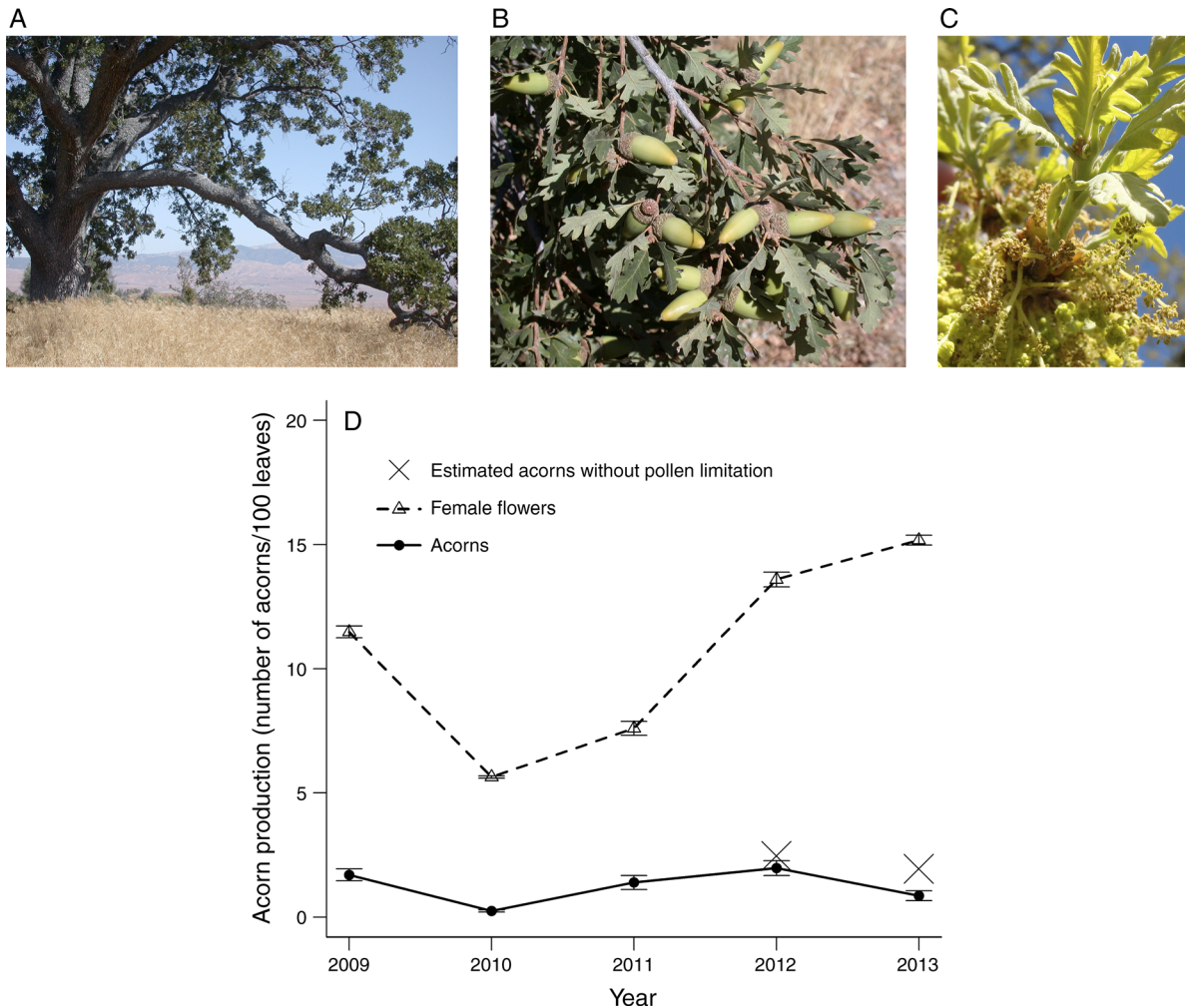
FIG. 2. Reproduction of *Quercus lobata* (valley oak). (A) A valley oak tree at Liebre Mountain, Los Angeles county, California, United States, (B) valley oak acorns, (C) valley oak flowers: large male catkins and minute female flowers. Photography by W. D. Koenig. (D) Surveys of female flowers and acorns on marked branches of 83 oak individuals over five years. Using the results of the pollen supplementation experiments, we calculated the acorn production in those two years in the absence of pollen limitation. Acorns are reported per 100 leaves to control for branch size. Bars show mean ± SE.

need not limit the overall fitness of an individual, as perennial plants may store resources that were not spent on seeds in a year of limiting pollination and use them for future reproduction.

In addition, although our results support prior work indicating that pollen limitation can be important in wind-pollinated species, several studies have failed to find pollen limitation in various animal and wind-pollinated masting plants (Tamura and Hiura 1998, Pias and Guitián 2006, Brookes and Jesson 2007). Our results support the conclusion that pollen limitation is only significant in some years, although it is also likely that not all wind-pollinated species may be pollen limited under any conditions. In these cases, masting may be caused by factors independent of pollination. For example, weather appeared to act as a synchroni-

zation cue for a variety of masting New Zealand plant species, as opposed to a factor that limits pollen (Kelly et al. 2013).

A previous experimental example of pollen limitation in a masting species comes from the insect-pollinated legume *Astragalus scaphoides* (Crone and Lesica 2006). In this species, individuals that flower in nonmast years are pollen limited (Crone and Lesica 2006). The high interannual variation in flowering in this species is thought to be driven by resource dynamics, where those plants with a high seed set invest in few flowers the following year (Crone et al. 2009). We propose a slightly different mechanism to be at play in *Q. lobata*, given that pollen limitation is significant in some years but not others (Fig. 2), and pollen limitation was not greater in years with fewer flowers, as there was greater floral

investment in the pollen limited year (Fig. 2). Instead, we suggest that differences in abiotic conditions and phenological synchrony of flowering between years drive pollen limitation in *Q. lobata* (Koenig et al. 2012, Koenig et al. 2014).

In summary, we experimentally confirmed that pollen limitation occurs in a wind-pollinated masting tree, but only in one of two years. Our results are broadly consistent with models of mast seeding that implicate pollen limitation as a factor that synchronizes seed set. We also found that *Q. lobata* invests in far more flowers than it matures into seeds, even in the absence of pollen limitation. This is also consistent the pollination Moran effect model of mast seeding, as this model predicts resource limitation either of flowers or fruits, while the pollen coupling hypothesis relies on resource limitation of flowers only. While wind pollination bypasses potentially unreliable animal pollinators, wind pollination does not eliminate the potential for pollen limitation playing a key role in reproduction. More work will be necessary in order to determine how pollen limitation varies from year to year and the extent to which wind pollination is in fact more reliable than animal pollinators.

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