

Masting promotes individual- and population-level reproduction by increasing pollination efficiency

XOAQUÍN MOREIRA,^{1,2} LUIS ABDALA-ROBERTS,¹ YAN B. LINHART,³ AND KAILEN A. MOONEY^{1,4}

¹Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92697 USA

²Misión Biológica de Galicia (MBG-CSIC), Apdo. 28, 36080 Pontevedra, Galicia, Spain

³Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309 USA

Abstract. Masting is a reproductive strategy defined as the intermittent and synchronized production of large seed crops by a plant population. The pollination efficiency hypothesis proposes that masting increases pollination success in plants. Despite its general appeal, no previous studies have used long-term data together with population- and individual-level analyses to assess pollination efficiency between mast and non-mast events. Here we rigorously tested the pollination efficiency hypothesis in ponderosa pine (*Pinus ponderosa*), a long-lived monoecious, wind-pollinated species, using a data set on 217 trees monitored annually for 20 years. Relative investment in male and female function by individual trees did not vary between mast and non-mast years. At both the population and individual level, the rate of production of mature female cones relative to male strobili production was higher in mast than non-mast years, consistent with the predicted benefit of reproductive synchrony on reproductive success. In addition, at the individual level we found a higher conversion of unfertilized female conelets into mature female cones during a mast year compared to a non-mast year. Collectively, parallel results at the population and individual tree level provide robust evidence for the ecological, and potentially also evolutionary, benefits of masting through increased pollination efficiency.

Key words: Boulder Canyon, Colorado, USA; masting; *Pinus ponderosa*; pollen; pollination success; seed cones; sex allocation; synchrony; trade-off; wind pollination.

INTRODUCTION

Mast seeding (“masting”) is a reproductive phenomenon defined as the synchronous and intermittent production of seed by a population of perennial plants (Silvertown 1980, Kelly 1994, Kelly and Sork 2002). Three main hypotheses have been put forward to explain the evolutionary fitness advantages of masting events. First, the “predator satiation hypothesis” states that masting reduces the negative effects of attack by seed predators on plant fitness through predator satiation (Janzen 1971, Silvertown 1980, Kelly and Sullivan 1997, Elzinga et al. 2007). Second, the “animal dispersal hypothesis” states that masting improves seed dispersal through greater attraction of animal seed dispersers (Norton and Kelly 1988, Kelly 1994). Third, the “pollination efficiency hypothesis” states that masting increases pollination success through synchronized flowering effort (Norton and Kelly 1988, Kelly 1994, Kelly et al. 2001, Kelly and Sork 2002, Kon et al. 2005). Additionally, these predictions about masting behavior are also likely to be influenced by resource allocation and physiological costs of reproduction (e.g., Satake and

Iwasa 2000, Crone et al. 2009, Rossi et al. 2012), as well as variation in environmental factors influencing resource allocation constraints (e.g., Koenig and Knops 1998, Inouye et al. 2002, Crone and Lesica 2006).

The pollination efficiency hypothesis assumes that flowering and fruiting are synchronous among individuals at the population level, and that male and female functions are also produced synchronously at the individual plant level, with both of these conditions maximizing reproductive success (Smith et al. 1990, Kelly et al. 2001, Rapp et al. 2013). Nonetheless, there may be other dynamics that constrain synchrony. In monoecious species (e.g., oaks and many conifers), where pollen and ovules are produced by different structures (Koenig et al. 2003), relative allocation to male and female functions at the individual level might be influenced by trade-offs between the sexes (i.e., sex allocation constraints; Charnov 1982, Campbell 2000, Parachnowitsch and Elle 2004). Such constraints may influence sex ratios at both the individual and population level, which could in turn determine the degree of pollen limitation (e.g., Freeman et al. 1980). Relative allocation to female function may be especially low during mast years because these structures are energetically more costly to produce (Charnov 1982, Campbell 2000). Such a scenario is more likely for wind-pollinated species (a common pollination syndrome in masting species) than for animal-pollinated plants, because high

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⁴ Corresponding author. E-mail: mooneyk@uci.edu

flowering synchrony may decrease reproductive success due to stronger competition for pollinators in animal-pollinated species (i.e., pollinator satiation; Rathke 1983, Kelly et al. 2001).

Despite the general appeal of the pollination efficiency hypothesis as an explanation for masting behavior in perennial plants (e.g., Nilsson and Wästljung 1987, Norton and Kelly 1988, Kelly 1994, Kelly et al. 2001, Kelly and Sork 2002, Rapp et al. 2013), few studies have provided robust tests of this hypothesis based on long-term data sets comparing multiple mast and non-mast events to assess the influence of this reproductive behavior on pollination success (but see Kon et al. 2005, Rossi et al. 2012). Likewise, even fewer studies have tested its predictions at both the population and individual plant level (but see Brys et al. 2008). It is important to analyze the predictions of the pollination efficiency hypothesis at both levels because the ecological effects of masting are best described at the population level (e.g., Kelly 1994, Kelly et al. 2001), whereas the evolutionary dynamics must be documented at the level of the individual (Yang et al. 2008).

The main goal of this study was to test the pollination efficiency hypothesis in ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson), a long-lived, monoecious, and wind-pollinated species, for which episodic mast seeding events are common (e.g., Linhart and Mitton 1985, Mooney et al. 2011). Here we used a long-term data set (20 years) on pollen and seed cone production from 217 pine trees to address the following: First, we evaluated whether there was a positive relationship between the production of male strobili (i.e., pollen cones) and female reproductive success the following year (female cones take two years to mature) at the levels of both the population and the individual tree. We expected that years when the population produced more pollen cones would be followed by years when mature female cone production (i.e., a direct measure of reproductive success) was higher. We also expected a similar positive relationship at the individual tree level. Second, we tested whether these relationships differed between years of low reproductive output (i.e., non-masting years) and years with high output (i.e., masting years). For both population- and individual-level analyses, we expected that the production of mature female cones relative to male strobili would be higher for mast than for non-mast years, consistent with the predicted benefit of reproductive synchrony on reproductive success via masting. Third, we tested whether female reproductive success relative to initial investment in female reproduction varied between mast and non-mast years. Here we expected that the rate of production of mature female cones relative to immature (unfertilized) female cones (hereafter, "conelets") would be higher during masting events. Finally, we tested for trade-offs between male and female investment as a potential source of variation in reproductive dynamics. These long-term data, spanning multiple mast and non-mast years at both the

population and individual level, thus provide an exceptionally robust test of the pollination efficiency hypothesis.

MATERIALS AND METHODS

Pine species, study area, and data collection

Ponderosa pine is a conifer native to western North America, where it is one of the most widely distributed pine species (Richardson 1998). Male strobili ("pollen cones," hereafter) are produced in early spring and mature within the same year. They are usually clustered near the tips of lower branches of the tree. Female cones ("seed cones," hereafter) are usually found on the upper branches and are produced in early spring and require two growing seasons after pollination to mature, reaching their full size by mid-summer. Several months later, during the fall, seed cones open and release their seeds.

We carried out a long-term field study (from 1977 to 1996, except in 1982 and 1985 for pollen cones) for which we monitored a population of 217 ponderosa pine individuals distributed over a 2-ha area on the south-facing slope of Boulder Canyon at an elevation of 1740 m in the Front Range of the Rocky Mountains (near the town of Boulder, Colorado, 40°00'48" N, 105°18'12" W; Linhart and Mitton 1985). The age of studied trees at 30–50 cm above ground level ranged from about 40 to over 280 years.

We monitored pollen and seed cone production during each year (between July and October) by counting the total number of branch tips with pollen cones (produced and matured during the current year) and number of mature seed cones (pollinated during the previous year and matured during the current year) throughout the crowns of all trees. In addition to this, we also monitored the number of branches with unfertilized female conelets in 1979 and 1980 (previous to a non-mast and a mast event, respectively). The number of unfertilized female conelets per branch was very similar among individual trees (always 6–8 conelets per branch; Y. Linhart, *personal observation*). In order to ensure the continuity and consistency of data collection, one or more of the authors was present during all of the surveys.

Data analysis

Defining mast and non-mast years.—Masting years are qualitatively defined by some as years when a heavy seed crop is produced (Silvertown 1980). As in past studies, we defined masting events quantitatively as those years when seed cone production by the population exceeded the mean by a designated amount, measured in standard deviations (LaMontagne and Boutin 2007). Specifically, we calculated the population deviation of the long-term mean in standard deviations for each year as $SD_t = (\bar{x}_t - \bar{x}_p)/SD_p$, where SD_t and \bar{x}_t are the standard deviation and mean for year t , and \bar{x}_p and SD_p are the standard deviation and mean for the population across all 20

years. Mast years were defined as those where $SD_t \geq 1.0$ (LaMontagne and Boutin 2007). This classification resulted in two mast years (1981, 1984) and 18 non-mast years (Appendix).

Evaluation of pollination efficiency test assumption.—Our tests of the pollination efficiency hypothesis (at both the population and individual level) are based upon regressing mature seed cone production onto pollen cone production, and testing the prediction that the slope of this relationship (i.e., seed cones per pollen-bearing branch tip) is steeper in mast than in non-mast years. However, the validity of this test assumes that relative investment in male (pollen) and female (unfertilized conelets) reproduction is unchanged between mast and non-mast years (Smith et al. 1990). For instance, if relative investment in female reproduction (i.e., unfertilized conelet production) were increased during mast years, this might result in more mature seed cones relative to pollen production without a change in pollination efficiency. To test this assumption, we regressed the number of conelets (i.e., unfertilized female cones) per tree onto the number of pollen-bearing branch tips for the one mast and non-mast year for which we recorded both variables, and tested whether the slope of this regression differs by year type. We did so using a generalized linear mixed model (GLMM) with the GLIMMIX procedure in SAS (SAS 9.2, SAS Institute, Cary, North Carolina, USA) specifying a Poisson distribution (i.e., log link function) and adjusting for overdispersion (Littell et al. 2006). The model tested for the effect of year type (mast or non-mast year, fixed effect), number of pollen branch tips, and their interaction (i.e., test of difference in slopes) as predictors of the number of conelets. Tree identity was included as a random factor to account for nonindependence of data from multiple years originating from the same individual.

Test of pollination efficiency.—Simple linear regressions were used to assess the relationship between male cone production (year t) and mature seed cone production (year $t + 1$ because female cones take two years to mature) at the population and individual tree level.

First, we performed a population-level regression between overall pollen (in year t) and mature seed cone (in year $t + 1$) production across the entire sampling period (P_p and S_p , respectively). Variables used in this regression were log-transformed means of each type of cone produced each year summed across all trees ($N = 18$ years for pollen cones and $N = 20$ years for seed cones). We also tested whether this relationship differed between non-mast ($N = 15$) and mast ($N = 2$) years by calculating the 95% confidence interval for the slope of the regression for non-mast years alone. If the two mast years are outside the confidence interval, this demonstrates that mast years differ from non-mast years.

Second, we performed an individual-level regression ($N = 217$), separately for mast and non-mast years,

between total pollen (year t) and mature seed cone (year $t + 1$) production (P_i and S_i , respectively), calculated as mean number of cones of each type produced per tree across all years. Using a GLMM and specifying a Poisson distribution (GLIMMIX Procedure in SAS 9.2), we tested for the effects of year type, number of pollen cones, and their interaction on the production of mature seed cones. The interaction term tested for a difference in the slope of the relationship between pollen and mature seed cone production across mast and non-mast years. Tree identity was included as a random factor to account for nonindependence of data from multiple years originating from the same individual. Our prediction was that, both at the population and individual level, the relationship would be steeper (i.e., greater ratio of mature seed cone to pollen cone production) for mast years.

Third, as an additional test of the individual-level reproductive advantage of masting, we assessed whether year type, number of conelets (year t), and their interaction were predictors of the number of mature female cones (year $t + 1$). The interaction tested whether the slope of the relationship between production of mature female cones and the production of conelets differed across the mast and non-mast years (for which we recorded conelets). In this case, we used a fixed-effects generalized linear model with the GENMOD procedure (SAS 9.2 System, SAS Institute, Cary, North Carolina, USA) specifying a Poisson distribution and controlling for overdispersion (Littell et al. 2006). Tree identity was included to account for nonindependence of data from multiple years originating from the same individual. In contrast with other analyses, tree identity was treated as a fixed effect because the random-effects model (using GLIMMIX) did not converge. Following the pollination efficiency hypothesis, we expected that the slope of the relationship between the number of conelets and the number of mature female cones would be steeper (i.e., greater ratio of mature female cones to conelets) for mast years.

RESULTS

In total, 462 511 branch tips with pollen cones and 102 264 seed cones were produced at the study site over the 18 and 20 years of sampling, respectively. The population-level mean annual reproductive output was $25\,695 \pm 2030$ pollen-bearing branch tips and 5113 ± 714 mature seed cones per year (mean \pm SE). Interannual production of pollen and seed cones varied extensively at the tree level, ranging from 68 to 106 101 pollen cones and 205 to 25 842 mature seed cones produced per tree across years, throughout the 18-year and 20-year period, respectively.

In addressing the main assumption of our test of the pollination efficiency hypothesis, we found a significant positive relationship between the number of pollen cones at the individual tree level (P_i) in a given year and the number of branches with unfertilized female conelets in

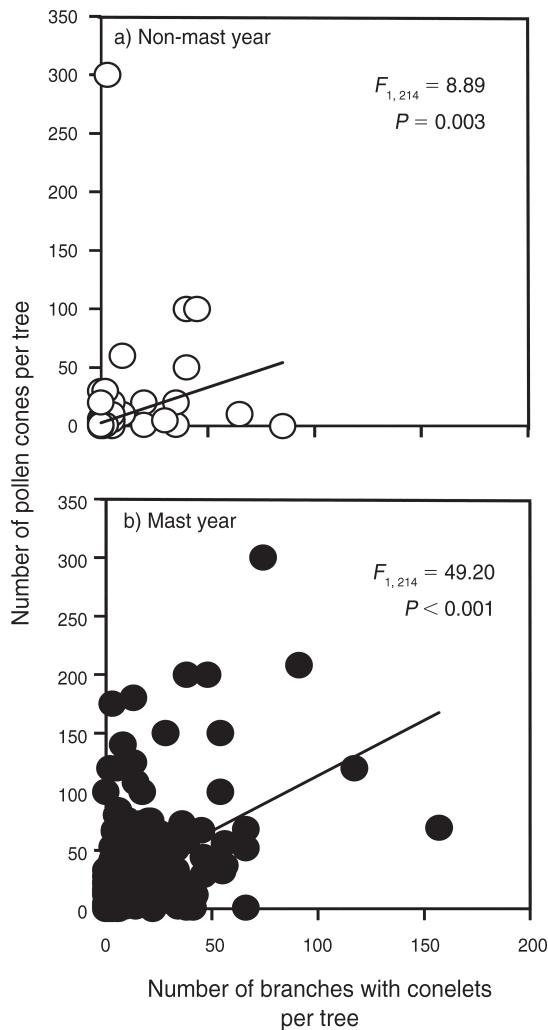


FIG. 1. *Pinus ponderosa* pollen cone production at the individual tree level in a given year as a function of unfertilized female conelet production in the same year (number of branches with conelets) during (a) the non-mast year (open circles), and (b) the mast year (solid circles). Each point represents an individual pine tree ($N = 217$ trees). The reported F and P values for the relationship are based upon a generalized linear mixed model (GLMM). The slope of this relationship was not different between the mast and non-mast year ($F_{1,213} = 2.01$, $P = 0.16$).

the same year for both the mast and non-mast year (Fig. 1). The GLMM revealed that the slope of this relationship did not differ between the targeted mast and non-mast year ($F_{1,213} = 2.01$, $P = 0.158$; Fig. 1).

We found a significant positive relationship between the number of pollen cones at the population level (P_p) in a given year and the number of mature seed cones (S_p) in the following year (Fig. 2). Findings at the population level offered partial support of the pollination efficiency hypothesis. The mean value for one (but not both) of the mast years was outside and above the upper 95% confidence interval for the non-mast year regression, indicating that the rate of production of mature female

cones was higher relative to pollen production in that year (Fig. 2). In a similar way, for both mast and non-mast years the number of mature seed cones at the individual tree level (S_i) in a given year was positively predicted by the number of pollen cones (P_i) in the previous year (Fig. 3). In accordance with the pollination efficiency hypothesis, the slope of this relationship differed between mast and non-mast years ($F_{1,214} = 13.25$, $P < 0.001$), with the ratio of mature seed cones to pollen-bearing branch tips being significantly greater (2.75-fold) in mast years (Fig. 3). Furthermore, although the number of branches with unfertilized female conelets (year t) and the number of mature seed cones (year $t+1$) were positively related at the individual level, S_i (Fig. 4), the slope of this relationship differed between mast and non-mast years ($F_{1,213} = 79.49$, $P < 0.001$). Specifically, the ratio of mature seed cones to branches with unfertilized female conelets was greater (2.11-fold) in the mast year (Fig. 4), providing further support of the pollination efficiency hypothesis.

DISCUSSION

Results from this study provide strong support for the pollination efficiency hypothesis at the levels of both the population and the individual tree. We found a positive relationship between the production of mature female cones and pollen cones (from the previous year), and this relationship was stronger in mast than in non-mast

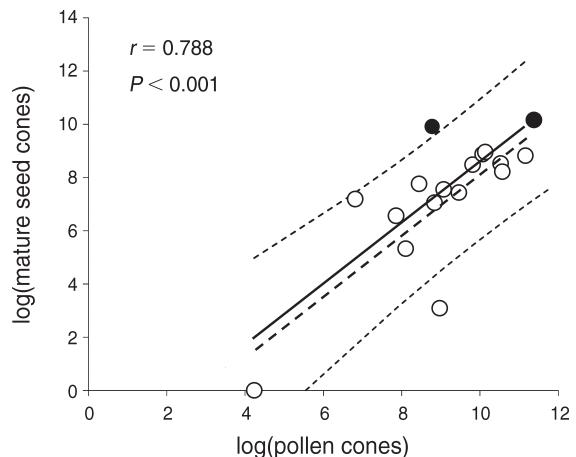


FIG. 2. *Pinus ponderosa* mature seed cone production at the population level in year $t + 1$ as a function of pollen cone production in year t (open circles correspond to non-mast years and solid circles to mast years). Points represent log-transformed mean values for each year ($N = 17$ years). The solid line represents the relationship predicted by the regression model for all years (mast and non-mast). The heavy middle dashed line represents the relationship predicted by the regression model for the non-mast years alone, accompanied by its 95% confidence interval (flanking dashed lines). One of the two mast years is outside the upper limit of the confidence interval, indicating that the rate of production of mature female cones was higher relative to pollen production in mast than non-mast years. Pearson r correlation coefficient and corresponding P value for overall regression are shown.

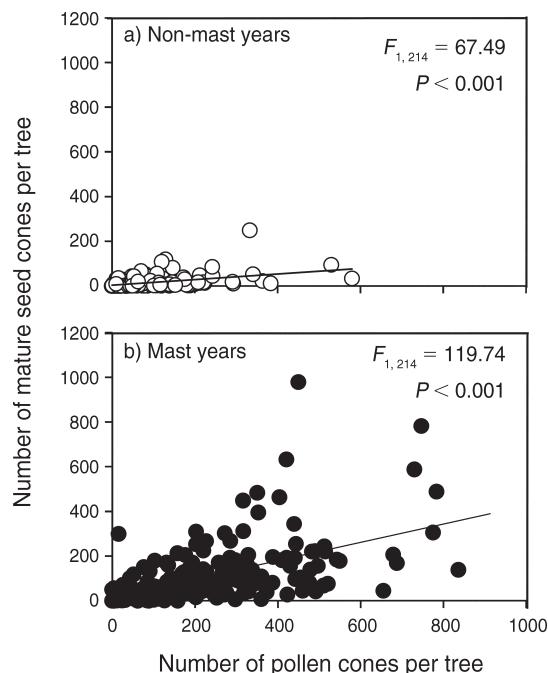


FIG. 3. *Pinus ponderosa* mature seed cone production at the individual tree level in year $t + 1$ as a function of pollen cone production in year t during (a) non-mast years (open circles), and (b) mast years (solid circles). Each point represents an individual pine tree ($N = 217$ trees for $N = 2$ mast years and $N = 16$ non-mast years). The reported F and P values for the relationship are based upon a generalized linear mixed model (GLMM). The slope of this relationship differed between mast and non-mast years ($F_{1,214} = 13.25$, $P < 0.001$), with the seed cone : pollen cone ratio being significantly greater in mast years.

years at both the individual and population levels. Importantly, our study suggests that these results were not influenced by shifts in investment in female and male fitness between mast and non-mast years, because the relative allocation to pollen cones and unfertilized female conelets was constant across year types for a sample of mast and non-mast years. We also found that the production of mature seed cones relative to unfertilized female conelets (from the previous year) was significantly greater during a mast than a non-mast year. Collectively, these results provide a robust test of the pollination efficiency hypothesis based on a long-term data set allowing for comparison of multiple mast and non-mast events.

Although our results contribute to a growing literature supporting pollination efficiency as an important driver of masting behavior (e.g., Norton and Kelly 1988, Kelly 1994, Kelly et al. 2001, Kelly and Sork 2002, Kon et al. 2005, Rapp et al. 2013), other mechanisms could also explain this reproductive strategy. Most notably, the predator satiation hypothesis states that masting allows escape from local seed predators through herbivore satiation (Janzen 1971, Silvertown 1980). Indeed, an independent analysis based on the same data set used in the present study provides strong support for

this hypothesis at both the individual and population levels (Linhart et al. 2014). The pollination efficiency and predator satiation hypotheses are based on an economy of scale, where perennial plants benefit from larger and less frequent reproductive efforts instead of more frequent and smaller ones (Norton and Kelly 1988, Rossi et al. 2012). Although both hypotheses have been well-studied and discussed in a diverse array of plant species (Silvertown 1980, Kelly 1994, Kelly and Sork 2002), comparisons of their relative importance and concurrent effects are still lacking. One exception is a study by Kon et al. (2005), who compared the relative influence of both mechanisms on annual fluctuations in reproductive success in the long-lived tree *Fagus crenata*, observing that predator satiation was more important than pollination efficiency. Similarly, Rossi et al. (2012) demonstrated that both mechanisms act as agents of natural selection on plant reproductive synchrony, and synergistically influence seeding dynamics of the conifer *Abies balsamea*. Our findings with ponderosa pine, together with results from these two studies, underscore

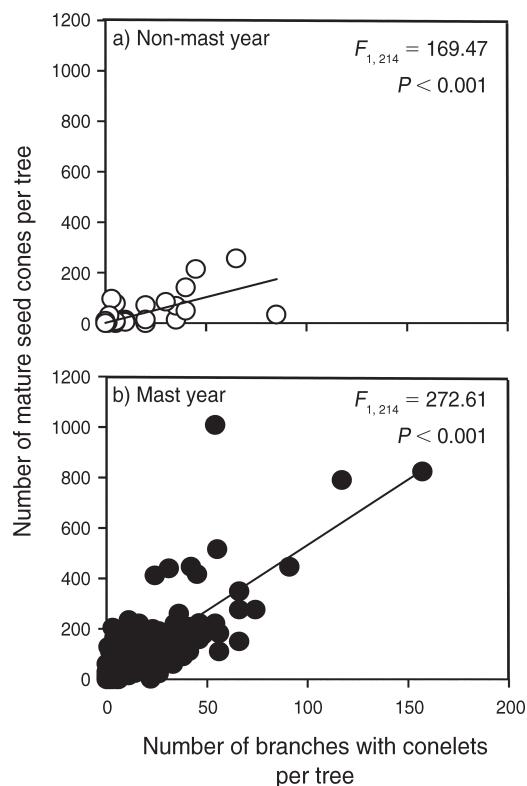


FIG. 4. *Pinus ponderosa* mature seed cone production at the individual tree level in a given year as a function of unfertilized female conelet production in the previous year during (a) one non-mast year (open circles), and (b) one mast year (solid circles). Each point represents an individual pine tree ($N = 217$). The reported F and P values for the relationship are based upon a generalized linear model (GLM). The slope of this relationship differed between the mast and non-mast year ($F_{1,213} = 79.49$, $P < 0.001$), with the mature cone : unfertilized female conelet ratio being significantly greater in the mast year.

the need to simultaneously assess the influence of multiple factors in order to fully understand the ecology and evolution of masting in plants.

Masting is also predicted to occur independent of any benefit of increased pollination or predator satiation entirely via so-called “pollen coupling” models (Satake and Iwasa 2000, 2002). Under such models, depletion of stored resources for seed production exceeds resource gain via nutrient uptake (Isagi et al. 1997), and these resource allocation constraints result in independent chaotic patterns of reproductive investment for both female and male function. Chance co-occurrence of male and female investment in turn increases physiological costs due to increased seed set, entraining otherwise independent patterns of variation in male and female investment into synchrony. Alternatively, Rossi et al. (2012) proposed that masting may evolve specifically as a mechanism to avoid self-pollination and associated seed abortion (Nilsson and Wästljung 1987) and inbreeding depression during early life stages (Greene et al. 1999). Importantly, these (and other) neutral explanations for masting are not mutually exclusive with the deterministic explanations delineated by the pollination efficiency (or predator satiation) hypothesis.

In testing for the pollination efficiency hypothesis, particularly in monoecious species, a fundamental assumption is that there is no within-tree variation across mast and non-mast years in relative allocation between male and female sexual functions (i.e., due to reproductive trade-offs; Charnov 1982, Campbell 2000, Parachnowitsch and Elle 2004). These sex allocation constraints may complicate the detection of predicted patterns; relative investment in the female function, for example, may decrease under low resource availability because female structures are energetically more costly to produce (Charnov 1982, Campbell 2000). Such a situation is more likely to occur during periods of high reproductive output (e.g., masting events) due to limited resources and resource allocation constraints favoring male over female investment (Knops and Koenig 2012; but see Burd and Allen 1988). To test this, we regressed the production of male cones with the number of unfertilized female conelets at the individual tree level and found that the slope of this relationship did not change between a mast and a non-mast year. Consequently, the greater ratio of mature seed cone to pollen cone number for mast years was due to increased pollination efficiency, and not due to altered patterns of sex allocation investment (i.e., higher relative allocation to female function) between mast and non-mast years. This finding agrees with previous work, which reported no change in relative allocation between sexes across varying (environmental, reproductive) conditions (Knops and Koenig 2012, Rapp et al. 2013). Collectively, these findings are consistent with the idea that reproductive trade-offs are weak because resources within an individual are mobile, i.e., stored reserves

from non-mast years can be allocated to reproduction during mast years (Isagi et al. 1997).

In summary, our findings provide multiple lines of support for the pollination efficiency hypothesis. Synchronous male and female reproduction within individual trees, together with high population-level reproductive synchrony, probably has been selected to increase reproductive success in ponderosa pines. Parallel results at both levels demonstrate the ecological (population level) and evolutionary (individual tree level) benefits of masting in tree species. Finally, our present findings, in combination with previous assessments of this same population (Mooney et al. 2011; Linhart et al. 2014), indicate that masting behavior has in all likelihood evolved as a response to multiple selective forces, including both pollen limitation and herbivory (Rossi et al. 2012).

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SUPPLEMENTAL MATERIAL

Appendix

Classification of mast and non-mast years by using the number of standardized deviations of the annual cone production from the long-term mean seed production ([Ecological Archives E095-067-A1](#)).