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BRIEF COMMUNICATION

Mast years increase wind pollination and reduce seed predation in sugar maple (*Acer saccharum*)

Elizabeth E. Crone[1] | **Joshua M. Rapp**[2]

[1]Department of Evolution & Ecology, University of California, Davis, CA 95616, USA

[2]Mass Audubon, Lincoln, MA 01773, USA

Correspondence

Elizabeth E. Crone, Department of Evolution & Ecology, University of California, 1 Shields Avenue, Davis CA 95616 USA.
Email: ecrone@ucdavis.edu

Abstract

Premise: In general, mast seeding (intermittent and synchronous seed production) increases plant fitness through economies of scale in which reproduction is more successful in high-seed years. These benefits have been most studied in wind-pollinated trees. Increased pollination success in mast years has been considered more important for wind- than animal-pollinated species, although this assumption is rarely explicitly tested.

Methods: In this study, we documented patterns of reproduction in *Acer saccharum* in central Massachusetts, United States over 15 years. We used pollinator exclusion experiments conducted over 6 years to test whether high-flowering and high-seed years lead to more successful wind pollination, more successful insect pollination, and lower predispersal seed predation. *Acer saccharum* is both insect- and wind-pollinated, allowing us to compare the strength of these two benefits.

Results: At our study site, *A. saccharum* was strongly alternate-bearing, meaning that trees alternated synchronously between high-flowering, high-seed years and low-flowering, low-seed years. Wind pollination was higher and predispersal seed predation lower in mast years, but insect pollination was similar in all years.

Conclusions: We showed geographic variation in patterns of *A. saccharum* seed production in comparison to past research. We also showed that synchronous flowering increases wind pollination more than insect pollination and that it decreases seed predation. *Acer saccharum* is dichogamous; protogynous trees were more likely to flower in mast years, and protandrous trees experienced larger benefits from wind-pollination in mast years. These results highlight masting trees as interesting study systems for future research on sex allocation.

KEYWORDS

alternate bearing, dichogamy, economy of scale, mast-seeding, masting, pollen limitation, pollination, predispersal seed predation, Sapindaceae, wind pollination

Mast seeding is a phenomenon in which plant reproduction is synchronized at the population level and highly variable among years (Kelly, 1994; Crone and Rapp, 2014). Because of these fluctuations in floral and seed resources, masting has the potential to have far-reaching effects on community and ecosystem dynamics (Janzen, 1976; Ostfeld and Keesing, 2000; Kelly and Sork, 2002; Inari et al., 2012). One of the primary reasons why mast-seeding occurs is that synchronous reproduction leads to "economies of scale" that increase reproductive success. Although various economies of scale have been proposed (Kelly, 1994), the two most commonly studied are increased pollination success and decreased seed predation in high seed years (Herrera et al., 1998; Kelly and Sork, 2002). Both benefits have considerable empirical support (Bogdziewicz et al., 2024), but there have been more experimental studies of the relationship between masting and seed predation (reviewed by Zwolak et al., 2022) than masting and pollination success.

In the absence of experiments, one line of inference for the pollination benefits of mast seeding comes from global patterns of variation in seed production. In the context of mast seeding, many ecologists have reasoned that the fitness benefits of synchrony should be stronger in wind-pollinated plants (Janzen, 1976; Herrera et al., 1998; Kelly and Sork, 2002; Pearse et al., 2020). In brief, the logic behind this expectation is that wind pollination is a mass action process that clearly increases in efficiency with increased density of reproductive plants (Smith et al., 1990; Kelly et al., 2001; Rapp et al., 2013). In contrast, animal-pollinated species could have specialist pollinators that are effective even at low flowering-plant densities and could even be satiated (and therefore less efficient) at high flower densities (Ashton et al., 1988; Żywiec et al., 2018). Consistent with this hypothesis, seed production tends to be more variable in wind- than animal-pollinated plant species (Herrera et al., 1998; Kelly and Sork, 2002; Pearse et al., 2020; Qiu et al., 2023). However, many animal-pollinated plant species experience more pollen limitation in smaller populations (Ghazoul, 2005), suggesting that both wind- and animal-pollinated species would experience pollination benefits from mast seeding. A few case studies have demonstrated higher pollination success of insect-pollinated plants in mast years (Forsyth, 2003; Crone and Lesica, 2006), but there is no consensus on whether this is a general benefit (see Żywiec et al., 2018; Ito and Kudo, 2022, for contrasting examples).

Here, we evaluated patterns of flower and seed production and economies of scale in sugar maple, *Acer saccharum* Marsh (Sapindaceae). Sugar maple is widely considered to be a masting tree species (Houle, 1999; Rapp and Crone, 2015; Cleavitt and Fahey, 2017). Sugar maple is an especially interesting species in relation to masting and pollen limitation because its reproductive system includes both wind and insect pollination (Gabriel, 1968; Gabriel and Garrett, 1984). Plants are monecious, i.e., produce separate male and female flowers, and dichogamous, i.e., sequentially hermaphroditic with both protandrous (male-first) and protogynous (female-first) individuals (Gabriel, 1968). This mating system presumably minimizes self-pollination (Gabriel, 1967). We used these features of sugar maple biology to compare seed set in relation to wind and insect pollination in mast and non-mast years. We also quantified the amount of predispersal seed predation in mast and non-mast years.

Specifically, we, first, quantified patterns of flowering intensity and seed production of individual plants for 14 years using standard metrics of mast seeding. Using these data, we evaluated whether seed production was consistent with common definitions of masting (coefficient of variation (CV) > 1; Kelly et al., 2001) or with alternate bearing (CV = 1; see Appendix 1, supplemental: 1). Second, we tested for pollination economies of scale by monitoring pollination success of plants with and without pollinator exclusion for 6 years. If plants experienced an economy of scale due to wind pollination, we would expect to see more seeds produced by pollinator-excluded flowers in mast years. If plants experienced an economy of scale due to insect pollination, we would expect a larger difference between open-pollinated and bagged flowers in mast years. Third, we tested for a predispersal predation economy of scale by monitoring the proportion of predated seeds in the same 6 years and testing the expectation that seed predation would be lower in mast years. Together, these results contextualize generalizations about mast seeding that have, to date, been based largely on studies of wind-pollinated tree species.

MATERIALS AND METHODS

Study system

Acer saccharum is a tree species that can live hundreds of years and reaches reproductive maturity at 30–60 years (Godman et al., 1990; Houle, 1999). It flowers from late April through May, and flowers are visited by spring bees including andrenids and occasional *Bombus* queens (E. E. Crone and J. M. Rapp, unpublished data). Seeds mature in late summer (roughly, September) and are wind-dispersed during fall and winter. Seeds occur in paired samaras (winged seed pods), and usually one of the two is filled with a single seed, though it is possible for both to be filled or both to be empty (Godman et al., 1990). Past studies have reported peaks in sugar maple seed production every 2–7 years, with considerable geographic variation in mast intervals (Godman et al., 1990; Houle, 1999; Rapp and Crone, 2015; Cleavitt and Fahey, 2017). Sugar maple is the primary source of maple syrup, which is harvested in early spring when sap moves through the trees (Rapp et al., 2019).

Our study took place at Harvard Forest, a research center in Petersham, Massachusetts, United States (42°29′15″ N 72°11′15″ W), owned and operated by Harvard University. Our study is based on a set of 20 trees selected randomly (by mapping and numbering all trees, then selecting 20 random numbers) along Prospect Hill Road, an unpaved road that runs by a set of historic houses, currently used as dormitories for visiting researchers. Before establishment as a research forest in 1907, much of the land at Harvard Forest was farmed (Jenkins et al., 2008), including our immediate study area, and our focal trees were most likely planted during this period. We selected trees along this small road to facilitate tree canopy access for pollinator exclusion experiments. One tree in our data set that was monitored from 2011 to 2021 was cut down due to advanced decay and proximity to a building; it was replaced with another tree in 2022. Both of these trees are included in this study; results were nearly identical if the tree with only three years of data was excluded (E. E. Crone, unpublished analyses).

Patterns of flower and seed production

To evaluate whole-tree seed production, we made timed counts of seeds across the canopy using binoculars in late summer (Koenig et al., 1994). Seed counts were made every year from 2011 to 2024. We (Crone and Rapp) each counted the number of seed pairs observed in 15 s. The two counts were summed and used as a metric of seed production for that tree. To evaluate flowering, one of us (Rapp) visited each tree during peak flowering (late April through early May) and scored flowering intensity of each tree in one of four categories: none; low, <1000 flowering buds; medium, 1000–10,000 flowering buds; high, >10,000 flowering buds). Flowering intensity was scored from 2011 to 2024. During flower surveys and other spring fieldwork (see Economies of scale section below), we also evaluated whether trees had only male flowers or both male and female flowers, and if so, which sex matured first on each tree. First-sex data were collected from 2011 to 2017 (the years during which we were working in the tree canopy; see Economies of scale section).

We quantified variation in flowering intensity and seed production using the coefficient of variation (CV; defined as the ratio of the among-year standard deviation to the mean) and autocorrelation function (ACF; calculated at lags 1–6, i.e., the correlations between observations separated by 1–6 years). Mast-seeding is characterized by $CV > 1$ and a negative lag-1 ACF (Crone et al., 2011); alternate bearing is characterized by $CV = 1$ (see Appendix 1: Supplemental calculation 1) and an ACF that alternates between negative at odd lags and positive at even lags. Each metric was calculated at the population level (hereafter CVp and AC1p; Koenig et al., 2003) using the single time series for our site, and at the individual level (hereafter CVi and AC1i; Koenig et al., 2003) using the time series for each focal tree. We summarized individual-level metrics using the average and standard error across all individuals. We also calculated synchrony among trees (r, the average correlation between individual trees), corrected for sample size as described by Bjørnstad et al. (1999). In brief, this method involves recalculating the correlation over random pairs of trees so that each tree is used exactly once in each sample; our results are based on 50,000 bootstrapped data sets. All metrics were calculated for both flowering intensity and seed counts. For these analyses flowering intensity categories were converted to numbers: 0, 500, 5000, 25,000. This categorical index means that flowering intensity would not necessarily follow expected sampling distributions, and analyses should be interpreted in a descriptive way.

We evaluated relationships among various metrics (e.g., CVi vs. average seed production across trees) using simple Pearson correlations. We also evaluated flowering intensity as a predictor of seed production using negative binomial family, log-link generalized linear mixed models (GLMMs) with flowering intensity as a fixed-effect predictor and tree ID and year as random effects. In these and all other analyses, we followed the methods of Zuur et al. (2009) and evaluated models by, first, finding the best (lowest AIC) of all possible combinations of random effects using the saturated model with all fixed effects, and second, removing nonsignificant interactions from the full model with the best (based on AIC) combination of random effects.

Economies of scale

From 2012 to 2017, we quantified insect pollination by installing pollinator exclusion bags on three branches with female flowers of 3–5 trees each spring during flowering. Tree canopies were accessed via a mobile bucket truck. Female flower production in sugar maples tends to be in the upper part of the tree crown (Godman et al., 1990; J. M. Rapp, unpublished data for our study system). In the fall, we collected the bagged branches and nearby control branches (i.e., flowering branches marked in the spring, but not given pollination exclusion bags). Pollinator exclusion bags were 40.6 × 45.7 cm Delnet pollination bags with a 336 μm pore diameter; for reference, sugar maple pollen is ~25 μm in diameter; Philbrick and Bogle, 1981). Upon harvest, we categorized each seed pod as empty, containing a filled seed (recorded as filled, wrinkled or small in the Harvard Forest meta-data; as noted in the meta-data, wrinkled and small seeds appeared to be aborted, i.e., pollinated but not predated), or predated by insects (recorded as grub, exit hole, or moldy in the Harvard Forest meta-data; as noted in the meta-data, the term moldy refers to evidence of mold in the seed pod from insect frass, but we did not observe moldy but uneaten seeds). From 2012 to 2014, we collected data on fates of seeds on an additional 164 branches that did not receive pollen-exclusion treatments.

We quantified pollination success using the proportion of unfilled seeds, i.e., empty seed pods relative to the total number of seed pods (summed across all categories of seed pods), similar to the method of Gabriel and Garrett (1984). We analyzed the proportion of empty seeds on each tree in each year using binomial family, logit-link GLMMs with fixed effects of mast index (average seed production across trees in each year), mating status (protandrous or protogynous) of each tree in each year, and their interaction. Saturated models also included random effects of tree ID and year. This analysis used the 159 (75 exclusion and 84 control) branches from the pollinator-exclusion experiment. We quantified predation as the proportion of seeds with grubs or exit holes relative to all categories except empty samaras. We analyzed the proportion of predated seeds on each tree in each year using binomial family, logit-link GLMMs with fixed effects of mast index (average seed production across trees in each year), and random effects of tree ID and year. This analysis used 84 control branches from the pollination exclusion experiment, plus164 additional branches (248 total branches).

Software acknowledgements

All analyses were implemented using R version 4.4.1 (R Core Team, 2024). Mixed models were implemented using lme4::(g)lmer (Bates et al. 2015) and compared using bbmle::ICtab (Bolker, 2023). Negative binomial models without random effects were implemented using the MASS::glm.nb (Venables and Ripley, 2002). Data management and figures sometimes used from commands from the tidyverse (Wickham et al., 2019) and plotrix (Lemon 2006) packages.

Confidence bands for economy of scale figures were calculated using merTools::predictInterval (Knowles and Frederick, 2024), including only estimation error (option include.residual.var = F).

RESULTS

Patterns of flowering and seed production

Both flowering intensity and seed production (measured as seed count/30 s) tended to occur in alternate years (Figure 1A, B), as evidenced by significant negative lag-1 autocorrelations, and a generally alternating (negative/positive) pattern of the autocorrelation function (Figure 1C, D). The coefficient of variation for population-level fluctuations (CVp) was 1.13 for flowering intensity and 0.91 for seed production (Figure 1E, F). The average coefficient of variation for individual trees, CVi, was lower than the population-level CV, 0.85 ± 0.06 for flowering intensity and 0.64 ± 0.06 for seed production. Trees that produced more seeds were also the ones with stronger signals of mast-seeding at the individual level (correlation among individuals of mean vs. CVi ($r = 0.92$, df = 19, $P < 0.001$) and mean vs. lag-1 autocorrelation ($r = -0.87$, df = 19, $P < 0.001$).

Flowering intensity and seed production were both synchronous among individual trees ($r = 0.56$, bootstrap CI = 0.46–0.69, and $r = 0.55$, bootstrap CI = 0.43–0.67 for seed production; Figure 1E, F). Flowering intensity was strongly correlated with seed production ($r = 0.63$, df = 269 (based on tree × year combinations), $P < 0.001$). Flowering intensity was a significant predictor of seed production (GLMM: $\chi^2 = 57.37$, df = 1, $P < 0.001$, log-scale slope = 0.61 ± 0.08), even after accounting for individual differences among trees and years (log-scale random SD of 0.99 for trees and 1.06 for years).

Nineteen of 21 individual trees produced both male and female flowers during the study; the remaining two trees produced only male flowers. Only two of 19 trees with both flower types were both protogynous and protandrous during our 7 years of data collection in tree canopies. Of the remaining 16 trees, our data set included eight protogynous trees and eight protandrous trees. Protandrous trees were more likely to produce flowers every year than protogynous ones (% of years with no flowers for protandrous and protogynous, respectively: 5.4%, 95% CI [1.3–13.3%], 20.6%, 95% CI [10.2–31.7%]; binomial GLMM [with random effect of tree ID]: $\chi^2 = 5.18$, df = 1, $P = 0.023$). Seed counts did not differ between protandrous and protogynous trees (GLMM of seed count vs. sex expression: $\chi^2 = 1.11$, df = 1, $P = 0.293$, $N = 87$ tree × year combinations).

Economies of scale

In the pollination experiment, sugar maples had a higher proportion of filled seeds (i.e., less pollen limitation) in higher seed years (GLMM, main effect of mast index, $\chi^2 = 4.38$, df = 1, $P = 0.036$, $N = 154$, logit-scale slope = 0.010 ± 0.005, Figure 3A)

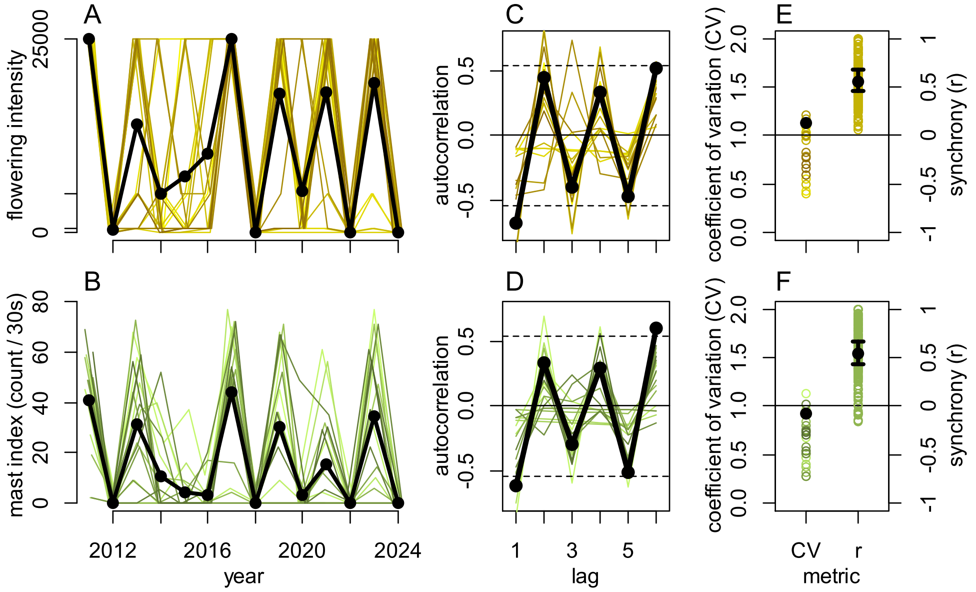

FIGURE 1 Descriptive metrics of mast seeding for *Acer saccharum* at Harvard Forest. (A, B) Time series of (A) flowering intensity, measured on a four-category scale, and (B) an index of seed production, the count of seeds per 30 s. In these panels, different colored lines represent trajectories of individual trees, and the population average is indicated by the thick black line with dots. (C, D) Autocorrelation function (ACF) for (C) flowering intensity and (D) seed production index. Here, colored lines represent the ACF for individual trees (ACF_i) and the solid line represents the ACF of average seed production at the population level (ACF_p), i.e., the ACF associated with the black line in panels A and B. (E, F) coefficient of variation (CV) and synchrony for (E) flowering intensity and (F) seed production index. For the CV, open circles represent the CV of individual trees (CV_i), and the black dot represents the CV of the population average (CV_p), i.e., the black line in panels A and B. For synchrony, open dots represent all possible pairs of plants, and the dark circle is the average across pairs, with error bars calculated based on bootstrapped subsets including each tree only once (see Materials and Methods).

and in the presence of insect pollinators (main effect of treatment: $\chi^2 = 7.11$, df = 1, $P = 0.008$; back-transformed proportions and 95% CIs: 0.409 [0.364, 0.455] and 0.470 [0.428, 0.512] for bagged and open pollinated flowers, respectively). Average seed set did not differ between protandrous and protogynous trees (main effect of first sex: $\chi^2 = 0.43$, df = 1, $P = 0.512$). However, there was a significant interaction between first sex and mast index ($\chi^2 = 6.42$, df = 1, $P < 0.011$), in which the effect of mast index was much stronger for protandrous than protogynous trees (Figure 2A, B). The proportion of filled seeds also differed among years (random effect SD: 0.141). No other effects in the original model were statistically supported, including the interaction of pollinator exclusion and mast index that would have indicated an insect pollination economy of scale ($\chi^2 < 0.1$, df = 1, $P = 0.842$), and the random effect of individual tree (DAIC = 1.8.)

The proportion of seeds with evidence of predispersal predation was lower in years with higher seed production (main effect of mast index: $\chi^2 = 180.9$, df = 1, $P < 0.001$, $N = 248$ branches, logit-scale slope = -0.09 ± 0.01; Figure 3). Seed predation varied among individual trees (random effects SD = 0.777), but did not differ substantially among individual trees (DAIC = 0.1, random effects SD = 0.252).

DISCUSSION

At our field site, sugar maple seed and flower production showed a strong pattern of alternate bearing, with individual trees alternating synchronously between years with high and low reproduction. We observed fitness benefits typical of patterns in masting tree species, including a seed predation economy of scale and a wind pollination economy of scale, but no economy of scale from insect pollination. This pattern broadly corroborates the expectation that wind pollination is a stronger economy of scale than animal pollination, which has previously been speculated (Herrera et al., 1998; Kelly and Sork, 2002; Pearse et al., 2020; Qiu et al., 2023), but never explicitly evaluated in a common

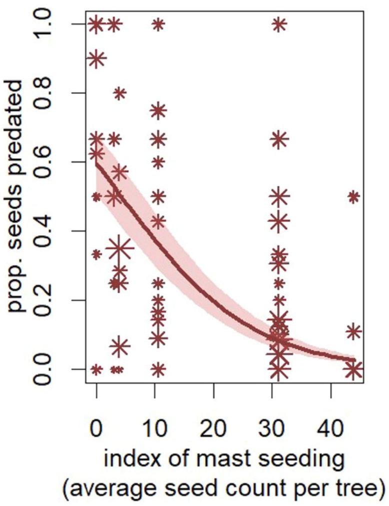

FIGURE 3 Predispersal seed predation, estimated as the proportion of filled seed pods with evidence of insect predation, including exit holes, the presence of grubs, or the presence of mold from insect frass.

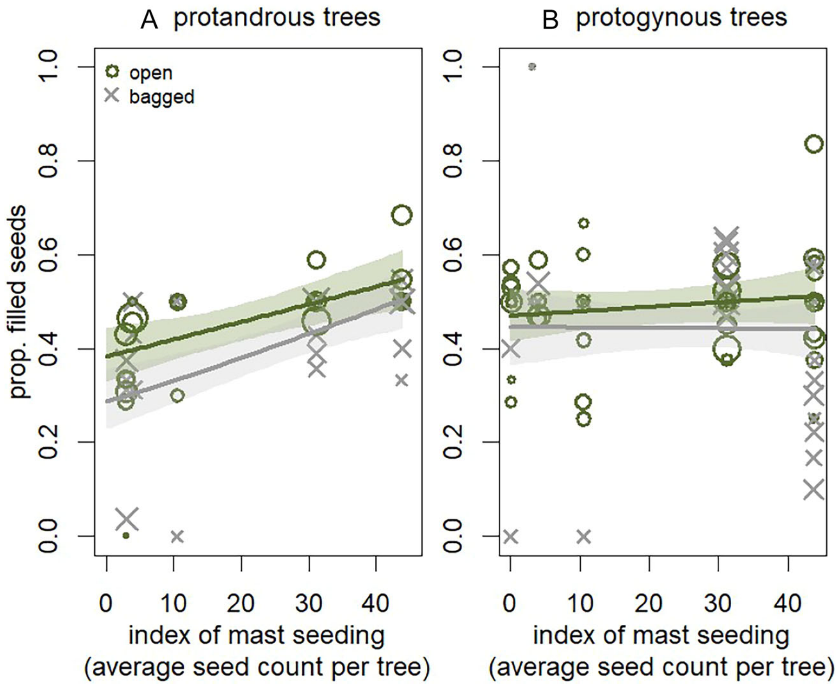

FIGURE 2 Pollination success, estimated as the proportion of filled seed pods (samaras) in (A) protandrous and (B) protogynous trees, in relation to average annual seed production. In both panels, ○ indicates open pollinated branches and × indicates branches with pollinator exclusion bags that allowed for wind pollination only.

study system. This pattern is notable because it occurred even though this sugar maple population did not have the high coefficient of variation in seed production associated with mast seeding (CV > 1). Instead, patterns in our study were more consistent with alternate bearing, a phenomenon widely reported in crop plants but less well studied in wild plants (Goldschmidt and Sadka, 2021). Similarly, in an across-species comparison of alternate bearing crop plants, Garcia et al. (2021) reported higher CVs in wind- than animal-pollinated species, suggesting that fitness benefits of mast seeding for pollination extend to alternate-bearing crop plants. It is less clear whether fitness benefits of predator satiation would generally extend from mast seeding to alternate-bearing plants, which would be an interesting area for future research.

Some past studies of sugar maples have shown higher variation in seed production, and seed production at less regular intervals than our observations. For example, at Hubbard Brook, a site ~200 km north of Harvard Forest, sugar maple masting was more variable (CV = 1.47) and occurred at less regular intervals, with 1–4 years between peaks (Cleavitt and Fahey, 2017). Farther north, in the Canadian province of Quebec, sugar maple seed production was less variable (CV = 0.72) than we observed, at least over 7 years (Houle, 1999). In general, the intermast interval of sugar maples appears to be highly variable (Godman et al., 1990). One possible explanation for these differences in CV is methodology. In our study, use of timed seed counts probably led to underestimation of variation. In the highest seed production years, we were counting seeds continuously for the whole interval, so we did not quantify differences at the highest end of seed production.

In a more general sense, however, species that transition between alternate bearing and intermittent masting may not be surprising. The proximate mechanisms thought to cause mast seeding are consistent with the idea that both alternate bearing and erratic reproduction may occur on a continuum. For example, one theoretical model of mast seeding is the resource budget model (Isagi et al., 1997), which predicts that populations should undergo a transition from constant seed production to alternate bearing to mathematically chaotic patterns, depending on the costs of seed production relative to annual resource gain (Isagi et al., 1997; Satake and Iwasa, 2000). Sugar maple seed production is also correlated with the temperature differential between successive years (Cleavitt and Fahey, 2017), a common cue for mast seeding (Kelley et al., 2013), which can also shift from approximately alternate bearing to less-predictable intermast intervals, depending on the value of the difference needed for seed production (see Appendix 1: Supplemental calculation 2).

Although increased insect pollination is not an economy of scale, insect pollination appears to contribute to pollination of about 10% of all sugar maple seeds in both high and low flowering years. This work contrasts with one previous pollinator exclusion study in sugar maple (Gabriel and Garrett, 1984) that found no effect of pollinator exclusion. One possible explanation for this discrepancy is methodological; although the 336-μm pores in our pollinator exclusion bags are >10× the size of sugar maple pollen grains (see Materials and Methods), they could have inhibited pollen flow more than the nylon mesh bags with 1-mm^2 pores used by Gabriel and Garrett (1984). Another possible explanation is ecological; although the importance of insect pollination did not vary systematically with plant density, we observed substantial among-year variation in the contribution of insect pollination to seed set (Figure 2), which could indicate fluctuations in insect abundance (Inari et al., 2012; Crone, 2013). Finally, it may be that insects were consistently successful at pollinating sugar maple flowers simply because there are few other species flowering in our study region at this time of year. Unlike some other forests in the northeastern United States, there are few flowering understory plants in at Harvard Forest during early spring (Jenkins et al., 2008), and sugar maples are an important resource for spring bees (Urban-Mead et al., 2021).

One unexpected result of our study was that the tendency toward masting depended on sex expression, associated with negative frequency dependence in reproductive success. Protandrous trees had higher proportions of filled seeds in mast years, when protogynous trees were more likely to flower, and protogynous trees had a higher proportion of filled seeds in non-mast years, when these trees were relatively unlikely to flower. In many plant species, individuals with fewer resources tend to be male, and individuals with more resources tend to be female (e.g., Bierzychudek, 1982). It may be that protogynous sugar maples tend to flower only when they have higher levels of stored resources, compared to protandrous ones. If so, these patterns are broadly consistent with the hypothesis that individual plants have more stored resources in mast years, a hypothesis that has generally been proposed for masting plant species (Isagi et al., 1997; Crone and Rapp, 2014; Bogdziewicz et al., 2020) and specifically for sugar maple (Rapp and Crone, 2015). More generally, our data point to an undertapped potential for mast-seeding plants as interesting models for testing sex allocation in relation to plant resource status (Rapp et al., 2013; Venner et al., 2016), complementing the longstanding body of work evaluating benefits of mast seeding for reproductive success.

AUTHOR CONTRIBUTIONS

This project was conceived by E.E.C., with input from J.M.R. during the planning and design phase. J.M.R. led all aspects of field implementation and data collection, including collecting nearly all of the data. E.E.C. consulted on fieldwork, co-led annual seed counts, and led data analysis and writing, with input and editing from J.M.R. Both authors agree on the final content of this manuscript.

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DATA AVAILABILITY STATEMENT

All data in this paper are original and have not been previously published. Raw data and meta-data are permanently archived in the Harvard Forest Data Archive, data set HF285 (https://harvardforest.fas.harvard.edu/data-archive). The R code and data file versions used in this manuscript are archived on Zenodo (Crone and Rapp, 2025).

ORCID

Elizabeth E. Crone https://orcid.org/0000-0002-5287-221X

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APPENDIX 1

Supplemental calculation 1. The coefficient of variation, CV, is the ratio of the standard deviation, σ, to the mean, μ.

$$\mathrm{CV} = \frac{\sigma}{\mu}$$

For exact alternate bearing, $\mu = 0.5X$, where X is seed production in "on" years, and seed production in "off" years is 0. For exact alternate bearing, the variance, i.e., the average squared deviation, is $0.25X^2$, noting that both "on" and "off" years would have a deviation of $0.5X$ from the average value of $0.5X$. Therefore, the standard deviation is $0.5X$ and the CV is one. This relationship is clearly independent of the value of X, as long as a species is strictly alternate bearing. See Crone et al. (2011) for further discussion of the relationship between the frequency of "on" years and the expected value of the CV.

Supplemental calculation 2. In some plant species, the temperature differential (or "delta-T") between two successive years is a cue for mast seeding. For a time series of uncorrelated random numbers, the time series of differences is negatively autocorrelated. To show this, consider a random number with mean 0 and standard deviation σ. For a time series of observations of this number, x_{i-1}, x_i, x_{i+1}, etc., the time series of differences is $x_i - x_{i-1}, x_{i+1} - x_i, x_{i+2} - x_{i+1}$, etc. The lag-1 covariance (i.e., covariance between two successive observations) in the time series of differences is $E[(x_i - x_{i-1})(x_{i+1} - x_i)]$, noting that the expected value of the difference is 0. This expands to $E[x_i x_{i+1} - x_i^2 - x_{i-1}x_{i+1} + x_{i-1}x_i]$. For independent random numbers, $E[XY] = E[X]E[Y]$, so (because the mean of the time series is 0), all of the terms drop out except $-x_i^2$, i.e., the expected value of the lag-1 covariance of differences is $-E[x_i^2] = -\sigma^2$, and (because the mean of the time series of differences is also 0), the time series of differences tends to alternate between positive and negative. If the threshold temperature differential for seed production were any positive number, then seed production would tend to occur in alternate years, i.e., alternate bearing. If the threshold temperature differential were a higher positive number, then seed production could occur at longer and less regular intervals, similar to mast seeding.