RESEARCH ARTICLE

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Evolutionary drivers of mast-seeding in a long-lived desert shrub[1]

Susan E. Meyer[2,4] and Burton K. Pendleton[3]

PREMISE OF THE STUDY: The evolutionary drivers and proximal regulators of mast-seeding are well understood for species of mesic environments, but how these regulators interact with high spatial and interannual variability in growing-season precipitation for a masting species in a desert environment has never been examined.

METHOD: We followed flowering and seed production in 16 populations of the North American desert shrub blackbrush (*Coleogyne ramosissima*) from contrasting environments across its range over an 11-year period to determine patterns of interannual reproductive output variation.

KEY RESULT: Patterns of reproductive output in blackbrush did not track current growing season precipitation, but instead were regulated by prior-year weather cues. The strength of the response to the masting cue depended on habitat quality, with higher mean reproductive output, shorter intervals between years of high seed production, and lower CVp at more favorable sites. Wind pollination efficiency was demonstrated to be an important evolutionary driver of masting in blackbrush, and satiation of heteromyid seed predator-dispersers was supported as an evolutionary driver based on earlier studies.

CONCLUSIONS: Both the evolutionary drivers and proximal regulators of masting in blackbrush are similar to those demonstrated for masting species of mesic environments. Relatively low synchrony across populations in response to regional masting cues occurs at least partly because prior-year environmental cues can trigger masting efforts in years with resource limitation due to suboptimal precipitation, especially in more xeric low-elevation habitats.

KEY WORDS blackbrush; *Coleogyne ramosissima*; mass flowering; predator satiation; resource matching; wind pollination efficiency

Masting—defined most broadly as high and synchronous interannual variation in seed production in a population of perennial plants—is a well-known phenomenon that has been investigated empirically for a wide range of species, particularly species of more mesic environments (Kelly and Sork, 2002). Several alternative, but not necessarily exclusive, hypotheses have been proposed to address both the proximal regulation of masting and the selective forces that act to shape it as an adaptive response. In this study, we first establish that blackbrush (*Coleogyne ramosissima* Torr. [Rosaceae]), a regionally dominant shrub in the transition zone between warm and cold deserts in western North America, exhibits masting. We then address both the proximal regulators and the evolutionary drivers that have shaped the masting response in this species.

The resource-matching hypothesis proposes that flower and seed production are a direct response to resources available in the current year (Kelly, 1994). Although it is rarely couched in these terms, resource matching has commonly been invoked to explain high interannual variation in productivity in deserts, and specifically in reproductive output of desert shrubs (Beatley, 1974). The positive correlation between current-year precipitation and reproductive output has been clearly demonstrated for desert shrubs of western Australia (Davies, 1976; Davies and Kenny, 2013). Many desert shrubs may be considered masting species according to the broad definition above, because high interannual variation in precipitation directly drives high interannual variation in growth, flowering, and seed production.

The question of resource matching is often approached by quantitatively examining whether there is a positive relationship between growth and reproduction across years within individual plants. A positive relationship would indicate a direct positive response to current resource conditions rather than a trade-off between reproduction and growth caused by switching resources to reproduction in mast years. This type of positive relationship is

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[2] US Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory, 735 N 500 E, Provo, Utah 84606; and

[3] US Forest Service, Rocky Mountain Research Station, 333 Broadway SE, Albuquerque, New Mexico 87102

[4] Author for correspondence (e-mail: semeyer@xmission.com;smeyer@fs.fed.us)

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apparently uncommon in masting species of mesic environments (Monks and Kelly, 2006). In contrast, in desert environments the positive relationship between growth and reproduction across years within individual plants is usually obvious, although little quantitative information exists to support this observation. Interannual variation in environmental drivers, especially precipitation, is more extreme in deserts, making current-year drivers likely to be more important.

In the absence of over-riding selective forces involving "economies of scale," it would be adaptive for desert shrubs to always reproduce as early as possible by responding directly to current-year resource availability, i.e., through resource matching. The concept of economies of scale states that there is "greater reproductive efficiency at high reproductive effort" (Norton and Kelly, 1988) and that this more than compensates for the negative effect of lost opportunities for reproduction in low seed production years (Rees et al., 2002). High interannual variation in seed production in response to selection associated with economies of scale represents a narrower definition of masting that is applied "to cases where some evolutionary force is operating to exaggerate variation in seed crops" (Monks and Kelly, 2006). This narrow definition has been termed "normal" masting (Kelly, 1994), or "true" masting (Koenig and Knops, 2000). To our knowledge, masting in this narrow sense has never been demonstrated for a desert shrub.

One well-supported hypothesis for an economy of scale involved in the masting phenomenon is increased reproductive efficiency in wind-pollinated species at high reproductive effort, which proposes that if seed set is pollen-limited, individuals that flower synchronously will show higher seed set than individuals that flower asynchronously (Norton and Kelly, 1988; Smith et al., 1990; Kelly and Sullivan, 1997; Kon et al., 2005). The advantage for wind pollination efficiency hinges on synchronous flowering, but not necessarily on high interannual variation in flowering, if plants have sufficient resources to exhibit high reproductive effort in successive years (Kelly and Sullivan, 1997). A second hypothesis with strong support for an economy of scale involves seed predator satiation at high reproductive effort (Kelly and Sullivan, 1997). This hypothesis proposes that high interannual variation in seed production reduces losses to seed predators. Predator satiation is usually thought to operate through a predator numerical response, i.e., through limiting seed predator populations in low production years so that some seeds can escape predation in a subsequent high production year. An alternative mechanism is through predator functional response, i.e., the seed predators are unable to process all seeds in a high production year, permitting some seeds to escape, even though predator numbers are high. (Kelly, 1994).

For populations to take advantage of the economies of scale provided by masting, they must have some proximal means of synchronizing flowering among individuals within a population. A large body of research supports the hypothesis that this synchronization is achieved through response to environmental cues—usually cues that are received in the year or years immediately prior to the mast year (Kelly et al., 2013). These are usually weather cues, such as temperature variation, that are often experienced regionally, resulting in regional synchronization. A commonly observed pattern in forest trees is a mast year that follows an exceptionally warm growing season (summer) the previous year, especially if the summer two years previous was cooler than average. More recently, models that use temperature differentials, e.g., the temperature difference between the previous summer and the summer two years previous, have also been found to have strong predictive power (Kelly et al., 2013).

As blackbrush is both wind-pollinated (Pendleton and Pendleton, 1998) and subject to intense predation from vertebrate seed predators (Meyer and Pendleton, 2005, 2015), we asked whether masting in this species is selectively favored by forces involving economies of scale rather than maximization of yearly reproductive effort. We also examined whether flowering synchronization is achieved through prior-year environmental cues.

OBJECTIVES AND HYPOTHESES

Our first objective was to (1) document patterns of mass flowering and mast seeding in blackbrush using flowering and seed production data from 16 populations collected over an 11-year period, and (2) to test the preliminary hypothesis of resource matching as the explanation for high interannual variation in flowering intensity by directly examining the relationship between growing season precipitation and both flowering intensity and reproductive output.

We then sought to determine whether, over the range of environments occupied by blackbrush, there is variation in habitat quality that affects both mean reproductive output and the strength of the masting phenomenon. We hypothesized that higher-quality sites support blackbrush populations with higher reproductive output on average, and that higher reproductive output is associated with less interannual variation, i.e., that populations in more productive habitats mast less strongly than populations in less productive habitats (Kelly and Sork, 2002).

We also examined the role of wind pollination efficiency as a driving force behind masting in blackbrush by quantifying the relationship between flowering intensity and seed fill, which should be positively correlated if pollen limitation restricts seed fill at lower flowering intensities (Kelly et al., 2001). Lastly, we tested the hypothesis that environmental cues received in previous years operate to synchronize blackbrush masting (Kelly et al., 2013).

MATERIALS AND METHODS

***The study system*—**Blackbrush is the dominant landscape shrub on over three million hectares in interior western North America. It occurs on shallow soils in the transition zone between warm and cold deserts at elevations of 950–2000 m (Meyer and Pendleton, 2005). Populations extend from southeastern California across the Mojave Desert and into the Colorado Plateau region (Richardson and Meyer, 2012). Blackbrush typically forms extensive monospecific stands between mixed desert shrub communities at lower elevations, and juniper-sagebrush communities at higher elevations (Bowns and West, 1976). Considerable ecotypic variation has been documented in this species, including variation in cold tolerance, germination syndrome, and plant growth characteristics (Pendleton and Meyer, 2004; Meyer and Pendleton, 2005; Richardson et al., 2014). Genetic analysis of 14 populations from across the range revealed the existence of two metapopulations corresponding to the Colorado Plateau and Mojave Desert regions (Richardson and Meyer, 2012).

As mentioned earlier, blackbrush is wind-pollinated and is also largely self-incompatible (Pendleton and Pendleton, 1998). The

flowers are borne in late spring on the ends of branchlets formed the previous growing season. The one-seeded achenes (hereafter referred to as seeds) are dispersed in early summer. Fallen seeds are quickly harvested by rodents or, in some areas, by large-bodied ants (Auger, 2005; Suazo et al., 2013; Meyer and Pendleton, 2015). Heteromyid rodent seed predators (kangaroo rats and pocket mice) play a vital role in blackbrush seedling establishment because they cache numerous seeds in shallow scatter hoards (Meyer and Pendleton, 2005, 2015; Auger, 2005). Seedlings that emerge from overlooked seeds in scatter hoards are more abundant following years with large seed crops (Meyer and Pendleton, 2015).

Flowering and fruiting field data collection—We followed flower and seed production of 16 blackbrush populations yearly from 1991 to 2000; flowering was also scored for a subset of populations in 2001 (Table 1). Four populations were in the central Mojave Desert (Clark County, Nevada [NV]), seven were in the eastern Mojave Desert (Washington County, Utah [UT]), and five were in southeastern Utah on the Colorado Plateau. Within each geographic area, we chose populations from across the elevational range of blackbrush.

Each year during fruiting, but prior to seed dispersal, flowering intensity of at least 100 mature clumps (crown diameter > 40 cm) was scored on an ordinal scale between 0 (no flowering) and 3 (profuse flowering). For each population each year, 10 branch samples were then collected at random from the area where flowering intensity had been scored. The same general area was sampled each year, but individual clumps were not followed through time. Flowers were removed from the branches and counted, and the single one-seeded achenes were removed from the enclosing sepals. The number of filled seeds was determined by cut test (Ooi et al., 2004), and fill proportion was calculated as the total number of filled seeds divided by the total number of flowers for each branch sample.

The flowering intensity score for each clump was converted to a quantitative estimate of number of flowers per unit of shrub surface area using a regression equation obtained by stripping and counting all flowers from 14 clumps of known surface area and flowering intensity (see Appendix S1, Supplemental Data with the online version of this article, for detailed explanation). Mean flowering intensity per population per year was then calculated. This mean flower-per-area value was then converted to a proportion of the maximum possible flower density (0.188 flowers per square centimeter of shrub surface area, i.e., all clumps rated in the highest category). Reproductive output (seed production per unit of shrub surface area) for each site and year was then calculated as a proportion of the maximum possible output by multiplying flowering intensity proportion by seed fill proportion. Expressing flowering intensity and reproductive output values as proportions of the maximum possible does not change the analysis relative to the use of absolute values, but provides a standardized and easily understood way of presenting the data.

Meteorological and climate data—Monthly temperature and precipitation data for each population were obtained for each year of the study using the PRISM Data Extractor, http://prismmap.nacse.org/nn/ (Prism Climate Group, 2013). The monthly data were used to calculate precipitation totals and mean temperatures for fall–winter (October–January), winter–spring (February–May) and summer (June–September) from 1989–2001. Mean values for these

TABLE 1. Location, climate information, and flowering intensity, seed fill, and reproductive output population coefficients of variation (CVp) for 16 sites included in the blackbrush masting study. Sites are listed from high to low elevation within each site group. (* = 2001 flowering data were collected at these sites.)

Code	Region/Site	Latitude	Longitude	Elev (m)	Annual Precip (mm)	Annual Temp (°C)	Flower Intensity CVp	Seed Fill CVp	Repro Output CVp
Central Mojave Desert									
PPS	Potosi Pass, NV	36°00′53″ N	115°29′58″ W	1667	353	12.4	1.44	1.09	1.52
LPT	Lower Potosi, NV	35°59′49″ N	115°28′19″ W	1451	314	13.9	0.76	0.84	1.36
RRO	Red Rocks Overlook, NV	36°06′59″ N	115°26′41″ W	1174	224	16.7	1.39	1.65	2.27
BDI	Blue Diamond Turnoff, NV	36°01′51″ N	115°23′08″ W	1041	178	17.9	0.98	0.84	1.00
Eastern Mojave Desert									
BDS	*Beaver Dam Summit, UT	37°06′01″ N	113°49′20″ W	1484	331	15.6	1.24	1.36	1.66
VYR	*Veyo Road, UT	37°16′24″ N	113°38′38″ W	1423	352	14.4	1.10	1.68	1.81
BRW	*Browse, UT	37°21′44″ N	113°15′52″ W	1295	359	14.4	0.90	0.90	0.99
WHL	*Winchester Hills, UT	37°13′25″ N	113°37′54″ W	1227	312	15.8	0.84	1.32	1.62
CCL	Castle Cliff, UT	37°04′23″ N	113°52′21″ W	1213	305	16.5	1.05	2.01	2.40
TOQ	*Toquerville Turnoff, UT	37°16′48″ N	113°18′41″ W	1164	322	15.9	0.82	0.96	1.08
LGR	*LeGrande, UT	37°10′33″ N	113°20′19″ W	985	280	16.7	1.09	1.41	1.77
Colorado Plateau									
LRK	*Little Rockies, UT	37°45′36″ N	110°39′06″ W	1700	230	12.1	1.28	1.86	2.08
DDT	*Dirty Devil Turnoff, UT	38°09′35″ N	110°37′15″ W	1500	177	11.7	1.20	1.03	1.67
SLV	*Salt Valley, UT	38°45′41″ N	109°36′02″ W	1497	242	12.1	0.97	0.77	1.16
NHK	North Hanksville, UT	38°47′36″ N	110°26′12″ W	1343	168	12.1	1.00	1.37	2.16
HITE	*Hite, UT	37°53′22″ N	110°24′51″ W	1232	227	14.2	0.92	1.28	1.61

parameters and also for mean annual temperature and precipitation were obtained from the long-term data set (1981–2010, also from the PRISM Data Extractor) for each site. Precipitation and mean temperature values were then converted to proportions of the long term means at each site for each four-month period and for the growing season (October–May; blackbrush is usually dormant under summer conditions). We also averaged growing season precipitation values for each year using data from the study sites in each region (Mojave Desert, n = 11 and Colorado Plateau, n = 5) to obtain relevant estimates of regional year quality to compare with regional patterns of flowering intensity. We supplemented the PRISM data set with observations from specific NOAA weather stations in each region to document the late spring frost event of 1995. We also used a mesicness index, defined as mean annual precipitation/mean annual temperature (P/T-ratio) as a weather variable in some analyses.

Statistical analyses—We plotted mean flowering intensity, reproductive output, and year quality (measured as mean growing season precipitation) each year for the Mojave Desert and the Colorado Plateau regional groups to examine patterns of flowering intensity, reproductive output, and year quality through time and to compare these patterns between regions. We then regressed mean flowering intensity and mean reproductive output on mean growing season precipitation to examine whether there was any obvious relationship between current year quality and either flowering intensity or reproductive output.

Coefficients of variation (CVs) were calculated for flowering intensity, seed fill, and reproductive output across years for each region. In addition, we examined the degree of regional synchrony in each reproductive measure using the mean pairwise correlation coefficient (r), which averages the correlations between each pair of sites in the region across years; high synchrony is indicated by a high mean value of r (Buonaccorsi et al., 2001, 2003).

The likelihood of high reproductive output in consecutive years was examined by plotting current-year reproductive output against previous-year reproductive output across all sites and years. The plot was divided into quadrants using the 0.05 of maximum reproductive output as the vertical and horizontal axes. We then counted the number of observations in each quadrant, and used a χ^2 test of independence to determine if the apparently low incidence of consecutive years with high reproductive output was statistically supported.

Regression analysis was used to examine the relationship between environmental variables (mean annual temperature and mean P/T-ratio) and reproductive output mean and coefficient of variation at the population level (CVp; Table 1), and to examine the relationship between reproductive output mean and CVp.

The conceptual model of Kelly et al. (2001) was used to test the wind pollination efficiency hypothesis by plotting seed fill against flowering intensity for the complete population-year data set. We then fit a sigmoidal curve to the data to determine the asymptotic value for seed fill and the value of seed fill at mean flowering intensity. The difference between these two seed fill values is an estimate of the selective advantage of masting for increasing wind pollination efficiency. One limitation of the data set was that it did not differentiate between pollination failure and ovule abortion, but we eliminated zero and near-zero fill values known to be due to density-independent effects such as late-season frost rather than pollination failure. We also examined the effect of current-year weather variation on seed fill using multiple regression (SAS 9.4 Proc Reg) with and without flowering intensity included in the model.

To ascertain the environmental cues that synchronize flowering, we first performed correlation analysis with flowering intensity and all precipitation and temperature variables described earlier. We then performed exploratory regression analysis with flowering intensity as the response variable using combinations of the subset of climate variables with significant simple correlation coefficients (data not shown). Based on these preliminary analyses, we focused on yearly growing season precipitation and mean growing season temperature for the main analysis. We included weather data for the current year, the previous year, and the year prior to the previous year. We also used the derived variables $\Delta T_{1\text{-}2}$ (previous-year growing season mean temperature minus two-years-previous growing season mean temperature) or $\Delta P_{1\text{-}2}$ (a similar index using growing season precipitation) as described by Kelly et al. (2013), to test the hypothesis that the masting cue was the difference in temperature or precipitation between the previous and two-year-previous growing seasons rather than their absolute values. We performed a parallel analysis using $\Delta T_{0\text{-}1}$ and $\Delta P_{0\text{-}1,}$ which represents the difference between current- and previous-year mean growing season temperature and precipitation, respectively. We assumed that flowering behavior in a population would be a response to deviation from mean conditions at its own site. For this reason, data presentation is based on analysis of weather variables expressed as proportions of site means; however, analysis was also performed on absolute values, with no substantial difference in outcome (data not shown). We tested the effect of current year, previous-year, and second-year-previous growing season precipitation and temperature on flowering intensity singly and in combination, and also examined the simple and combined effects of the derived Δ variables. We used regression (SAS 9.4 Proc Reg) to evaluate and rank all models that included single-year variables, all models that included derived Δ variables, and all models that used combinations of single-year and derived Δ variables. We used Akaike Information Criteria (AIC) to rank the resulting models and examined the slopes and significance of regressor variables in the highest-ranking models.

RESULTS

Masting patterns at the regional level—Regional patterns of flowering intensity and reproductive output across years showed reasonably high interannual variation (Table 2; Fig. 1). The years 1991, 1995, and 1997 exhibited relatively high mean flowering intensity values in both regions, whereas in 1994 and 1996, little or no flowering was seen in any population. In 2000, Mojave Desert populations—but not Colorado Plateau populations—flowered intensively, whereas the converse was true in 2001. Regional CVs were higher for reproductive output (near 1.00) than for either flowering intensity or seed fill (approximately 0.7–0.9; Table 2), whereas reproductive output CVp, that is, coefficient of variation at the population level, ranged from 1.00–2.40 (Table 1). Lower CV at the regional level was apparently due to relatively low synchrony among populations, with mean r values < +0.5 for all three reproductive measures (Table 2). This low synchrony was due to both variation in magnitude of response to the masting cue in years when most populations masted and also to occasional high reproductive output

TABLE 2. Regional coefficients of variation (CV) and mean correlation coefficients (r) calculated for flowering intensity, seed fill, and reproductive output for blackbrush population groups in the Mojave Desert and Colorado Plateau regions.

	Mojave Desert (n = 11)	Colorado Plateau (n = 5)
Regional CV		
Flowering Intensity	0.858	0.715
Seed Fill	0.877	0.837
Reproductive Output	1.036	0.969
Mean Correlation Coefficient		
Flowering Intensity	+0.401	−0.047
Seed Fill	+0.452	+0.498
Reproductive Output	+0.292	+0.410

that was out of synchrony, i.e., in a year when most populations had low reproductive output (Appendix S2 Tables S2a–S2c).

When mean regional flowering intensity was regressed on current-year growing season precipitation, the relationship was not significant, indicating that flowering intensity was largely uncoupled from current-year growing season precipitation on a range-wide scale ($R^2 = 0.0022$, n = 22, $P = 0.8358$; Fig. 1). The years with the highest flowering intensities varied in growing season precipitation from below average (1991 both regions, 2000 Mojave Desert), to near average (1997 both regions), to above average (1995 both regions, 2001 Colorado Plateau). The relationship between regional mean growing season precipitation and reproductive output was also not significant ($R^2 = 0.0665$, n = 20, $P = 0.2723$; Fig. 1). Reproductive output generally tracked flowering intensity except for 1995 in the Mojave region, when a late frost prevented seed set following mass flowering in many populations.

***Masting patterns at the population level*—**Flowering intensity, seed fill, and reproductive output varied dramatically from year to year at each study site (Appendix S2 Tables S2a–S2c). Coefficients of variation (CV) averaged 1.06 for flowering intensity, 1.27 for seed fill, and 1.63 for reproductive output (Table 1). Flowering intensity expressed as proportion of maximum varied from 0–0.78, seed fill varied from 0–0.78, and reproductive output varied from 0–0.51. Strict masting (i.e., no years of intermediate seed production; Kelly, 1994) was not observed. Flowering intensity and reproductive output varied over a range in each population, with years of no seed production, high seed production, and intermediate seed production (Appendix S2 Tables S2a-S2c). Flowering intensity was not always strongly linked to reproductive output, because there were many cases of medium to high flowering with little or no seed production. Flowering intensity tended to be somewhat synchronized among populations within a region (Table 2), but there were many exceptions. A common pattern was range-wide synchrony in low-flowering years (e.g., 1994, 1999) but more variable flowering response among populations in relatively high-flowering years (e.g., 1991, 1995, 1997; (Appendix S2 Tables S2a–S2c).

There was a strong negative relationship between reproductive output in a given year and reproductive output in the subsequent year ($\chi^2 = 8.45$, df = 1, $P = 0.0036$; Fig. 2). The reverse L shape of this plot indicates that years of high seed production were almost always followed by years of low seed production, while years of low seed production were followed by years of either low or high seed production.

***Masting variation among populations*—**Mean reproductive output at the population level decreased both above and below an optimum mean annual temperature near 15°C (Fig. 3A). This relationship was significant even with the inclusion of an outlier (Veyo Road), which had low reproductive output in spite of a mean annual temperature near the optimum. When population reproductive output was plotted as a function of P/T-ratio, reproductive output generally increased with increasing P/T-ratio, but the Potosi Pass and Veyo Road populations were outliers that showed low reproductive output in spite of occupying two of the most mesic sites (Fig. 3B). When these populations were included in the regression, the relationship between

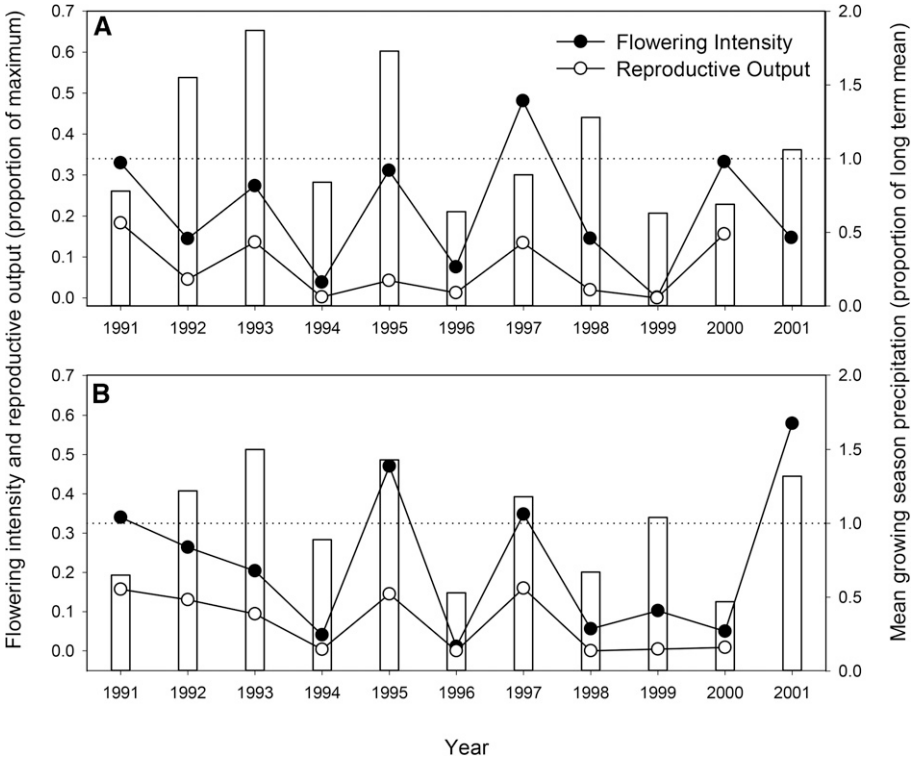

FIGURE 1 Regional mean flowering intensity and regional mean reproductive output expressed as proportion of maximum possible, plotted as a function of year over the period 1991-2001 (left axis) for (A) 11 blackbrush populations in the Mojave Desert and (B) 5 blackbrush populations on the Colorado Plateau. A subset of populations in each region was scored in 2001 for flowering intensity but not reproductive output (Table 1). Regional mean growing season precipitation each year of the study (vertical bars) is represented as proportion of the long term mean (right axis; horizontal dashed line at 1 = mean). There was no significant relationship between regional growing season precipitation and regional mean flowering intensity ($R^2 = 0.0022$, n = 22, $P = 0.8358$) or regional mean reproductive output ($R^2 = 0.0665$, n = 20, $P = 0.7806$).

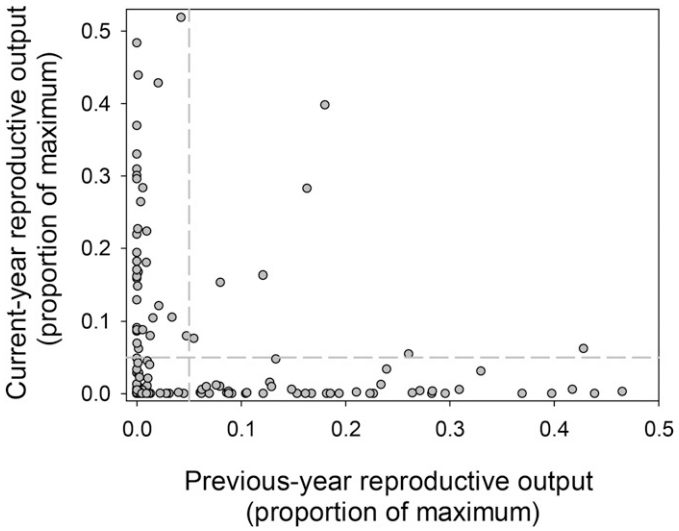

FIGURE 2 Reproductive output in 16 blackbrush populations over a 10-year period plotted over 2 consecutive years, i.e., with current year reproductive output (as proportion of maximum possible) plotted as a function of previous-year reproductive output (n = 144). Dashed lines divide the plot into four quadrants using 0.05 of maximum output as the coordinates. The null hypothesis of independence was rejected ($\chi^2 = 8.45$, df = 1, $P = 0.0036$).

P/T-ratio and mean reproductive output was no longer significant ($R^2 = 0.099$, n = 16, $P = 0.235$).

The strength of masting, measured as reproductive output CV, was negatively correlated with mean reproductive output, indicating that populations at more favorable sites (i.e., high mean reproductive output) masted less strongly than populations at less favorable sites (i.e., low mean reproductive output, Fig. 4A). The Blue Diamond population, an extreme outlier with both the lowest reproductive output and the lowest CV, was excluded from the regression as presented. However, even with this population included, the regression was significant ($R^2 = 0.280$, n = 16, $P = 0.035$). Reproductive output CV was also negatively correlated with site quality as indicated by P/T-ratio, with lower CV at more favorable mesic sites (Fig. 4B). The Blue Diamond population, which occupies the most xeric site in the study, was again the outlier. Plants in this population rarely flowered or produced seed at all, resulting in a low mean with little variance. When this population was included in the regression in Fig. 4B, the results were no longer significant ($R^2 = 0.055$, n = 16, $P = 0.235$). The upper elevation outlier populations in Fig. 3B (Potosi Pass and Veyo Road) had higher CVs than other mesic sites (Fig. 4B), but were included in the plotted regression.

Flowering intensity and seed fill—Seed fill generally increased with increasing flowering intensity, although there was considerable variation in seed fill at higher flowering intensities (Fig. 5). When the sigmoidal model of Kelly et al. (2001) was fit to the data, the regression was highly significant ($R^2 = 0.5844$, n = 152, $P < 0.0001$). The predicted seed fill value was 0.329 at the mean flowering intensity of 0.206, while the asymptotic value for seed fill was 0.463. The intersection of mean flowering intensity with the fitted curve was in the upper half of the steep part of the curve, with a 41% increase in seed fill at the asymptote over the fill value at mean flowering intensity. This means that plants that concentrate their flowering effort in

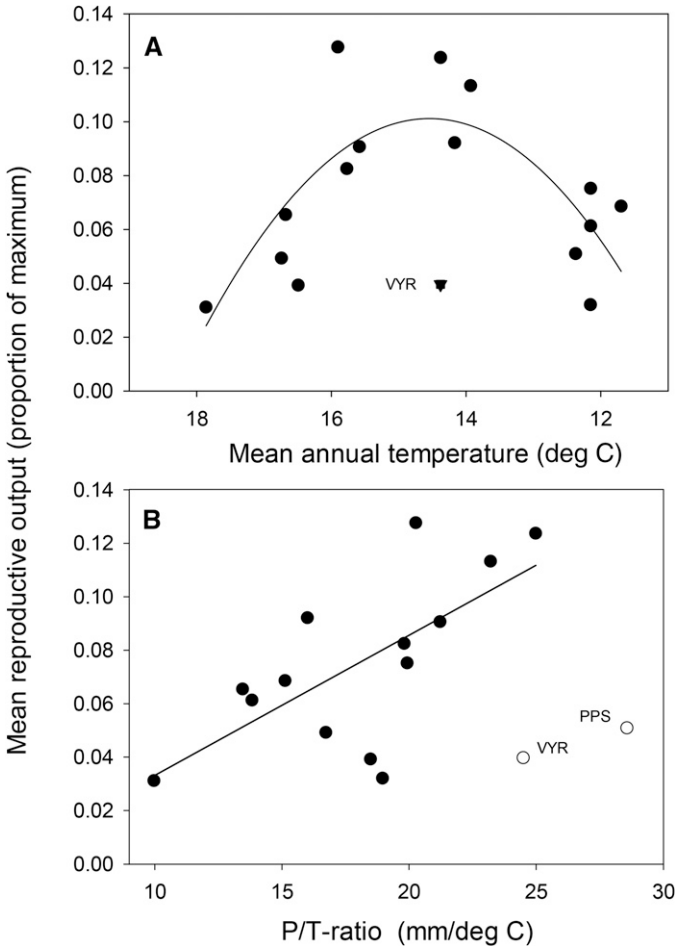

FIGURE 3 (A) The relationship between mean annual temperature and mean reproductive output for 16 blackbrush populations. Reproductive output decreases when temperature either increases above the optimum or decreases below the optimum. The data were fit with a quadratic equation: n = 16, $R^2 = 0.412$, $P = 0.0073$. The apparent outlier VYR (Veyo Road) was included in the regression. (B) The positive relationship between P/T-ratio (mean annual precipitation/annual mean temperature ratio) and mean reproductive output for 16 blackbrush populations (r = 0.450, n = 14, $P = 0.0086$). The apparent outliers PPS (Potosi Pass) and Veyo Road (VYR) (white circles) were not included in the regression (see text for explanation).

years of mass flowering would increase their pollination efficiency and should be selectively favored.

Seed fill was only weakly correlated with current growing season precipitation ($R^2 = 0.029$, n = 155, $P = 0.019$). When flowering intensity—the major factor influencing seed fill—was included in the regression, the contribution of growing season precipitation was no longer significant according to a t-test ($t = 1.05$, n = 155, $P = 0.2964$). However, including the current-year weather variables spring temperature (positive slope), spring precipitation (positive slope), and fall temperature (negative slope), along with flowering intensity, resulted in the model with the best (most negative) AIC (−532.8) and with an R^2 of 0.474, as compared to the R^2 of 0.432 from linear regression on flowering intensity alone (AIC = −526.9). Warmer, wetter springs and cooler falls were therefore weakly but significantly associated with increased seed fill.

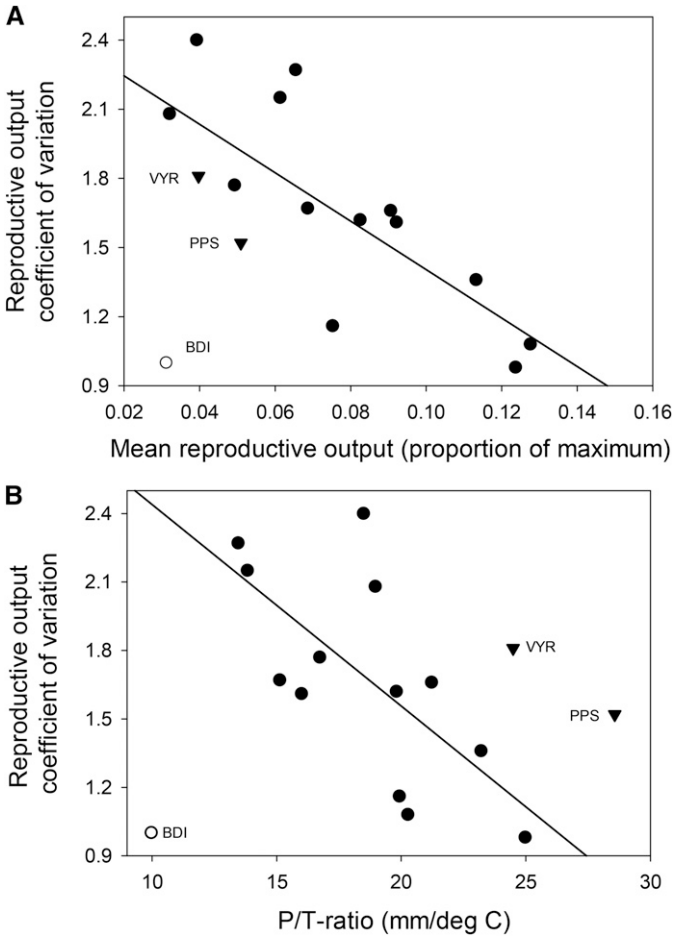

FIGURE 4 The relationship between reproductive output coefficient of variation (CV) and: (A) mean reproductive output and (B) P/T-ratio (mean annual precipitation/annual mean temperature ratio). Both negative relationships are significant (mean reproductive output: $R^2 = 0.575$, n = 15, $P = 0.0011$; PT-ratio: $R^2 = 0.460$, n = 15, $P = 0.011$). Potosi Pass (PPS) and Veyo Road (VYR) sites (outliers in Figure 3B) are indicated as triangles, but are included in the regressions. The Blue Diamond site (BDI, white circle) is not included (see text for explanation).

***Environmental cues for masting*—**Flowering intensity across 16 populations and 11 years was only weakly correlated with current growing season weather variables. The positive relationship with precipitation was significant ($P = 0.0078$, n = 165) but accounted for only 4.5% of the variance in flowering intensity. Reproductive output was not significantly correlated with current growing season precipitation at the population level ($R^2 = 0.0047$, n = 155, $P = 0.3942$). When regressions using all combinations of absolute and relative (Δ) predictor variables were performed with flowering intensity as the response variable, no model that combined absolute and relative predictors resulted in an AIC that was better than the AICs produced by models using only absolute or only Δ predictors. For this reason, the data presentation focuses on comparisons between the best models that use either absolute predictors or Δ predictors.

Growing season temperature variation between years was a significant predictor of current-year flowering intensity (Table 3). The best models incorporated temperature values from all three years.

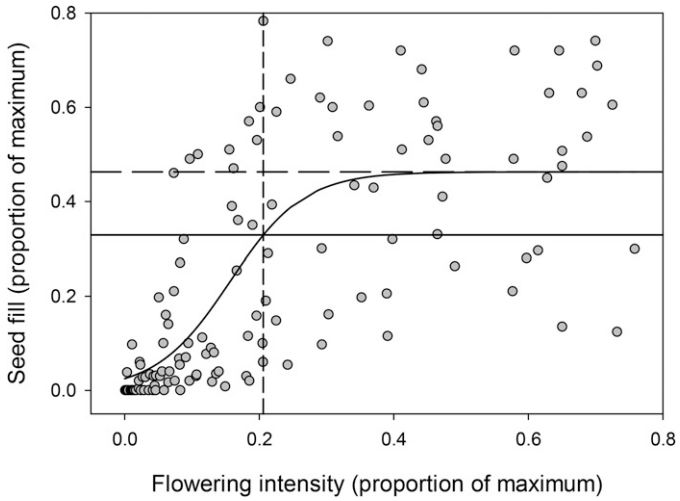

FIGURE 5 The relationship between flowering intensity and seed fill. The fitted curve is from a three-parameter sigmoid equation (f = a/(1+ exp(-(x-x0)/b)) with parameter values of a = 0.4629, b = 0.0548, X0 = 0.1568; $R^2 = 0.5844$, $P < 0.0001$). The vertical short-dashed line indicates mean flowering intensity, the horizontal dashed line indicates fill value at the asymptote, and the horizontal solid line indicates fill value at mean flowering intensity.

The temperature differential model that incorporated both $\Delta T_{0\text{-}1}$ and $\Delta T_{1\text{-}2}$ showed the best fit according to AIC and accounted for 18.6% of the variance in flowering intensity. Precipitation variation between years was a better predictor of flowering than temperature variation (Table 3). As with temperature, the best models incorporated values from all three years. The model based on the precipitation differentials $\Delta P_{0\text{-}1}$ and $\Delta P_{1\text{-}2}$ had the best AIC and accounted for 30.6% of the variation in current-year flowering intensity. When precipitation and temperature predictor variables were combined, model fit generally improved (Table 3), but these improvements were not additive, probably because of collinearity between variables. The best model incorporating both temperature and precipitation included $\Delta P_{0\text{-}1}$ as well as $\Delta P_{1\text{-}2}$ and $\Delta T_{1\text{-}2}$, and accounted for 35.2% of the variation in flowering intensity.

The predictor variables had consistent slopes across all models (Table 3). Previous-year precipitation and $\Delta P_{1\text{-}2}$ always had negative slopes, while previous-year temperature and $\Delta T_{1\text{-}2}$ always had positive slopes. The converse was always true for both current-year and two-year previous precipitation and temperature, as well as for $\Delta P_{0\text{-}1}$ and $\Delta T_{0\text{-}1}$. This means that a year that is warmer and drier than average is more likely to be followed by a mast year, particularly if the year previous to the warm, dry year was cooler and wetter than average. The ability of these predictive models to account for even 35% of the variation in blackbrush flowering intensity is notable in view of the fact that the data set represents a composite of contrasting ecological settings from across a wide geographic range.

DISCUSSION

***Resource matching vs. selection for economies of scale*—**Our data set showed conclusively that blackbrush exhibits masting according to the broad definition of high interannual variation in seed

TABLE 3. Regression analysis relating flowering intensity (proportion of maximum) to mean annual growing season (October–May) temperature and/or precipitation (proportion of site mean) across 11 years at 16 blackbrush population study sites. $\Delta T_{0\text{-}1}$ and $\Delta P_{0\text{-}1}$ represent the difference between current-year and last-year values; $\Delta T_{1\text{-}2}$ and $\Delta P_{1\text{-}2}$ represent the difference between last-year and year-2-previous values (n = 165).

Weather Variable	R^2	Slope	AIC	P-value
Best Absolute Temperature Model				
Current-year mean T		−0.395	−534.8	0.0451
Last-year mean T	0.1885	1.174		<0.0001
Yr-2-previous mean T		−0.907		0.0002
Best DELTA Temperature Model				
$\Delta T_{0\text{-}1}$	0.1859	−0.362	−536.3	0.0584
$\Delta T_{1\text{-}2}$		0.856		<0.0001
Best Absolute Precipitation Model				
Current year P	0.3005	0.079	−559.3	0.0124
Last year P		−0.216		<0.0001
Yr-2 previous P		0.104		0.0007
Best DELTA Precipitation Model				
$\Delta P_{0\text{-}1}$	0.3062	0.09407	−562.7	0.0002
$\Delta P_{1\text{-}2}$		−0.00056		<0.0001
Best Absolute Combined Model				
Last year P	0.3408	−0.192	−567.1	<0.0001
Yr-2 previous P		0.078		0.0110
Last year mean T		0.605		0.0018
Yr-2 previous mean T		−0.767		<0.0001
Best DELTA Combined Model				
$\Delta P_{0\text{-}1}$	0.3516	0.083	−571.8	0.0009
$\Delta P_{1\text{-}2}$		−0.00045		0.0004
$\Delta T_{1\text{-}2}$		0.5828		0.0010

production, with reproductive output CVs from 1.00–2.41 (Table 1; Kelly, 1994). In contrast to the apparent norm for desert shrubs, however, this interannual variation is not a result of resource matching. While we have no direct test of resource matching (e.g., "switching"; Kelly and Sork, 2002), we present strong evidence that resource matching does not explain masting in blackbrush. The correlation between current-year environmental quality (growing season precipitation) and blackbrush reproductive output was not significant, and even the correlation with flowering intensity was weak, with current growing season precipitation accounting for < 5% of variation. Instead, patterns of variation in flowering, seed fill, and reproductive output provided evidence that blackbrush masts in response to selection for economies of scale associated with both wind pollination efficiency and predator satiation, and that blackbrush uses prior-year weather cues to synchronize flowering, so that mast years occur largely independently of current-year weather conditions.

***Masting variation among populations*—**Masting is predicted to occur more commonly and at wider intervals in less productive habitats, where plants presumably require more time to accumulate sufficient resources to support a mast event (Kelly and Sork, 2002), so that smaller population CVs are associated with more favorable conditions (Kelly and Sork, 2002; Crone et al., 2011). Our results corroborate previous studies in that variation in reproductive output was negatively correlated with site quality as measured by both mean reproductive output and by P/T-ratio (Fig. 4). However, at the extreme low end of the site quality spectrum, the population at the xeric Blue Diamond site had both the lowest mean reproductive output and the lowest CV. This population is on the low-elevation trailing edge of blackbrush distribution that is likely already being impacted by climate warming. Bioclimate envelope models for blackbrush distribution predict widespread extirpation of this species from its lower-elevation habitat by 2060 (Richardson et al., 2014).

We also produced limited evidence that some blackbrush populations at the upper elevational limit had reduced reproductive output in spite of their mesic climates. Site mean annual temperature and precipitation are coarse measures of local climate, which did not clearly explain the site differences that resulted in high reproductive output at Browse but in low reproductive output at Veyo Road and Potosi Pass. Presumably, there are specific climate features at these upper elevation sites that produced the large reduction in reproductive output that we observed (Fig. 3, Appendix 2 Table 2). Aridity limits reproductive output at the lower end of the blackbrush elevational range, but other factors, possibly associated with frost or rain during flowering, may limit reproductive output at the upper end.

***Flowering intensity and wind pollination efficiency*—**Our empirical test of the Kelly et al. (2001) model demonstrated that masting yields a moderate advantage for blackbrush in terms of wind pollination efficiency (Fig. 5). Pollination efficiency at mean flowering intensity was relatively high. Blackbrush is an obligate outcrosser, which should increase the masting advantage, but it occurs in dense, monospecific stands and usually flowers under low-humidity conditions that facilitate pollen dispersal, making mass-flowering less important to seed set.

Wide variation in seed fill at high flowering intensity was most likely due to post-pollination environmental factors. Resource limitation associated with dry weather during filling probably plays a role, as indicated by the positive effect of spring precipitation. The positive effect of spring temperature on seed fill could be related to the probability of frost events during flowering. Removing 11 low-fill data points associated with known frost events raised the value of the asymptote from 0.404 to 0.463 (data not shown). If low fill

associated with other post-fertilization factors could also be removed from the fitted model, the asymptotic value would be even higher and would signify a more important role for wind pollination efficiency than can presently be demonstrated.

***Mast seeding and predator satiation*—**The predator satiation hypothesis was not tested directly in this study, but evidence from other studies indicates that it is likely a major selective force in the evolution of mast seeding in blackbrush. Auger (2005) demonstrated that Ord's kangaroo rats at the Salt Valley study site (in Arches National Park) used blackbrush seeds as a principal food source, and cached or consumed virtually all of the available seeds during a mast year. Auger (2005) also documented a significant decline in the kangaroo rat population in blackbrush habitat in the nonmast years that followed, whereas a population in a desert shrub-grassland habitat with more varied seed resources did not show this decline. This reduction in the predator population in the years following mast-seeding demonstrates the importance of predator satiation (Norton and Kelly, 1988). Meyer and Pendleton (2005) found that blackbrush emergence was reduced 52–97% in unprotected artificial caches relative to caches protected from rodent predation. In a nine-year seedling establishment study at four sites, substantial blackbrush seedling emergence occurred only after a major mast-seeding event (Meyer and Pendleton, 2015).

The seedling establishment syndrome exhibited by blackbrush is similar to the pattern exhibited by mast-seeding trees of low-disturbance forest communities. Postseedling juvenile survival is relatively high, but growth rates in competition with existing adults are extremely low (Meyer and Pendleton, 2015; Kitchen et al., in press). Just as forest trees form sapling banks, cohorts of blackbrush juveniles form suppressed "seedling banks" that can persist for long periods, but can then respond to gap formation, i.e., the death of a nearby adult, with increased growth (Grime, 1979). The formation of such seedling or sapling banks is an integral part of the evolutionary syndrome associated with masting in response to the need for predator satiation in closed forest systems (Tachiki and Iwasa, 2010). It reduces the fitness penalty associated with failure to produce seed every year by making seedlings that are produced after mast events available for recruitment into the adult size class when gap formation occurs, sometimes many years later.

***Environmental cues for masting*—**Our data support the idea that increased weather differentials between the current and previous year and between the two previous years are associated with mass flowering in blackbrush. Both temperature and precipitation variables had predictive power. A model that combined both temperature and precipitation for all three years and that used differentials rather than absolute values resulted in the best AIC. This model indicates that a cool, wet year followed by a hot, dry year is most likely to lead to subsequent mass flowering in blackbrush.

The pattern of response to prior-year masting cues was obscured by the failure of some populations to exhibit high flowering intensity even in predicted mast years, possibly because of site-specific resource limitation. This could be why the model based on environmental cues could only account for 35% of the variation in flowering response, and why synchrony across populations was not necessarily strong in years predicted to be high-flowering years. The lack of a consistent response to environmental masting cues was more often observed at the less productive lower elevation sites (Appendix S2 Tables S2a–S2c). Recent work on masting in mesic environments suggests that plants use current-year carbon resources to produce a mast event rather than accumulated carbon resources (Hoch et al., 2013). Other studies indicate that a mast event depletes stored mineral nutrients, which may be more limiting than fixed carbon (Sala et al., 2012). Patterns of resource use and depletion have not been examined for blackbrush, but it is possible that resource accumulation across years is more important in desert environments, especially at the most resource-limited xeric sites.

Populations, even at the most productive sites, did not produce major mass flowering events in two consecutive years (Fig. 2). This could be interpreted to mean that resource accumulation is generally needed for masting in this species. Alternatively, environmental cues could produce this pattern, because according to the model, appropriate weather cues in the two years previous to a high flowering year cannot be met for two consecutive high flowering years.

The cueing responses described by Kelly et al. (2013) and studies cited therein focus primarily on temperature and temperature differentials as the masting cue in species of mesic ecosystems. This study demonstrates that precipitation differentials can also act as a cue for mass flowering. As precipitation in deserts is much more variable from year to year than temperature, it makes sense that precipitation cues are more important for a desert species.

CONCLUSIONS

This study has demonstrated that both the proximal regulation of mass flowering in blackbrush and the evolutionary drivers that have shaped masting as an adaptive response in this species closely resemble these same processes in species of more mesic environments. The ultimate explanation for masting in blackbrush is selection for the same economies of scale, namely wind pollination efficiency and predator satiation, that select for exaggerated interannual variation in flowering and seed production in many masting species. In addition, the proximal regulation of flowering synchrony through prior-year weather cues, which has been demonstrated for a wide range of masting species, was also a major determinant of flowering synchrony in blackbrush.

Unlike masting species studied previously, however, blackbrush occurs in a generally unproductive desert environment and experiences extreme variation in both habitat quality across its elevational range and year quality in terms of interannual variation in growing season precipitation. Its pattern of response to this environmental variation is superimposed over the basic pattern that it shares with other masting species. By examining a large number of populations in contrasting habitats from across the geographic range over a long series of years, we were able to detect how this environmental variation modulates expression of the basic masting pattern. In optimal environments, blackbrush populations have higher mean reproductive output with lower CV. This is likely because they are able to respond more fully and consistently to prior-year masting cues, because they are less resource-limited in the masting year. In suboptimal environments, populations also respond to prior-year masting cues, in that they rarely if ever mast in years that are not preceded by the prior-year cues, regardless of current year quality. However, populations on these lower-quality sites may be unable to mast strongly because of resource limitation even when the cues are received, and consequently have lower average reproductive output and higher CVs as well as longer intermast intervals than populations

found in more optimal environments. The extreme case is found where site quality is so poor that it may be outside the range possible for long-term blackbrush persistence. In this case, response to the masting cues is almost completely damped, high seed production years are not observed, and both mean reproductive output and reproductive output CV are low.

This study of masting in a desert shrub provides insight into interactions among the factors that control masting in a species in which exaggerated interannual variation in flowering and seed production is clearly under positive selection, yet the environmental context would tend to produce a temporal reproductive pattern more in accord with the resource matching hypothesis. The resulting pattern, namely mast seeding in years that are often suboptimal from a growing season precipitation perspective, attests to the strength of the evolutionary drivers of mast seeding in this species. The mechanism for achieving mast seeding in suboptimal years is probably related to resource accumulation, but this remains a hypothesis for future investigation.

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