esa ECOSPHERE

Environmental and endogenous drivers of tree mast production and synchrony in piñon–juniper–oak woodlands of New Mexico

Robert R. Parmenter,[1,2,†] Roman I. Zlotin,[3] Douglas I. Moore,[2] and Orrin B. Myers[4]

[1]Valles Caldera National Preserve, National Park Service, Jemez Springs, New Mexico 87025 USA
[2]Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131 USA
[3]Department of Geography, Indiana University, Bloomington, Indiana 47405 USA
[4]Department of Family and Community Medicine, University of New Mexico, Albuquerque, New Mexico 87131 USA

Citation: Parmenter, R. R., R. I. Zlotin, D. I. Moore, and O. B. Myers. 2018. Environmental and endogenous drivers of tree mast production and synchrony in piñon–juniper–oak woodlands of New Mexico. Ecosphere 9(8):e02360. 10.1002/ecs2.2360

Abstract. Tree masting (synchronous, episodic reproduction) is common worldwide and is hypothesized to be especially important in ecosystems with low species diversity and productivity as in semi-arid woodlands of the American Southwest. We analyzed mast dynamics of three dominant tree species, one-seed juniper (Cupressaceae: *Juniperus monosperma*), two-needle piñon pine (Pinaceae: *Pinus edulis*), and Sonoran scrub oak (Fagaceae: *Quercus turbinella*), on six sites during 1997–2016 within the Sevilleta National Wildlife Refuge, New Mexico. We tested multiple hypotheses regarding environmental and endogenous variables as controlling mechanisms, analyzing time-series mast production data in relation to weather variables (precipitation, temperature, relative humidity, vapor pressure deficit, wind) over different time frames, and assessed evidence for weather tracking, resource switching, resource depletion, resource cycling, and pollen limitation. We found that (1) in univariate regression analyses, mast production in all three species was inversely related to lagged late-summer/autumn temperatures during fruit primordia formation (1-yr lag for juniper and oak, 2-yr lag for piñon pine). Juniper mast production (n = 412 trees) was positively related to current-year late-winter (February–April) precipitation, combined with a negative relationship with current-year summer temperatures. Piñon pine mast production (n = 210 trees) was positively related to 1-yr lagged total annual precipitation and negatively associated with current-year spring and summer temperatures. Oak mast production (n = 194 trees) also was positively related to current-year late-winter precipitation but was not affected by subsequent summer temperatures. (2) Multivariate environmental logistic regression models produced reasonable fits to observed field mast values. (3) High-mast years in juniper and oak were characterized by greater proportions of trees producing mast and increased mast production per tree. (4) Juniper, oak, and piñon pine mast years were highly synchronized. (5) We found indirect support for resource depletion in all three species at some sites and indirect support for resource cycling in oak populations. (6) We observed only marginal indirect evidence for resource switching in piñon pine and oak. (7) Analyses of atmospheric pollen abundance relative to mast production produced no significant relationships. Predictive models of mast production have direct applications to regional silviculture, wildlife management, and ecosystem services in Southwestern woodlands.

Key words: climate change; ecosystem productivity; El Niño; ENSO; Monsoon; plant reproduction.

Received 9 June 2018; accepted 13 June 2018. Corresponding Editor: Debra P. C. Peters.

† **E-mail:** Robert_Parmenter@nps.gov

INTRODUCTION

Masting in plants, defined as synchronous, episodic reproduction (Janzen 1971, Silvertown 1980), has been the subject of extensive detailed study for over half a century, particularly with respect to environmental factors, physiological constraints on reproductive processes (e.g., nutrient/energy limitation, pollination efficiency), and evolutionary benefits of enhanced seed survival via predator (frugivore/granivore) satiation and dispersal (see Silvertown 1980, Kelly 1994, Kelly and Sork 2002, Koenig and Knops 2002, Jansen et al. 2004, Pearse et al. 2016). While masting occurs commonly in pines (Pinaceae) and oaks (Fagaceae), many other species of plants have been shown to exhibit masting characteristics (Kelly and Sork 2002, Shibata et al. 2002, Schauber et al. 2002, Kelly et al. 2013). In addition, apparent synchronization of mast years among many plant taxa within a given geographic area has been observed, suggesting common cues (e.g., weather) among multiple species (Schauber et al. 2002, Kelly et al. 2013, Koenig et al. 2016, Fernandez-Martinez et al. 2017).

A number of proximate mechanistic drivers of masting behavior have been explored using long-term field data sets and mathematical models (reviewed in Pearse et al. 2016). The fundamental basis for mast production is a plant's available limiting resources (carbohydrates, nutrients, and in more arid ecosystems, water balance), and if sufficient (and environmental conditions allow), the plant will allocate some portion of its resources to vegetative growth and reproduction (Smith et al. 1997). In masting species, the portion of resources committed to a reproductive event may be disproportionately large, potentially requiring a post-reproductive recovery period with little or no additional flowering (see review by Crone and Rapp 2014). In addition, many analyses of field mast data also have found significant relationships between annual mast production and weather variables (e.g., temperature, precipitation), indicating that environmental conditions may cue masting events (Moreira et al. 2015, Koenig et al. 2016).

These phenomena have led to several hypothesized proximate mechanisms (sensu Pearse et al. 2016) involved in masting, including the following:

1. The weather tracking hypothesis, where plants track weather variables (temperature, precipitation, soil moisture, etc.) across landscape scales and respond during favorable conditions with increased reproduction activities (Norton and Kelly 1988, Koenig 2002, Koenig et al. 2016);
2. The resource depletion hypothesis (Sork et al. 1993), when a masting event depletes stored resources (carbon, nitrogen, phosphorus) to a sufficiently low level that future reproduction is delayed during some refractory period while plant resources are replenished;
3. The resource switching hypothesis, which states that plants will redirect (switch) limited resources among years between vegetative growth and reproductive activities (Norton and Kelly 1988);
4. The resource cycling hypothesis (Sork et al. 1993, Calama et al. 2011), a variant of resource depletion that applies to species where significant resource depletion effects interact with economies-of-scale phenomena (pollination efficiency, seed-predator satiation, and seed-dispersing animal population dynamics), resulting in an inherent multiyear masting cycle that may be influenced by prior masting events and weather tracking;
5. The pollen limitation hypothesis (Knapp et al. 2001, Sork et al. 2002, Koenig and Ashley 2003), and specifically the pollination Moran effect (Pearse et al. 2016), which states that mast production is influenced by pollination success, which in turn is linked to pollen production and influenced by external environmental factors, such as weather events.

Kelly (1994) identified three categories of masting behavior: (1) strict masting, with highly synchronized masting across the population, and bimodal mast production of either zero or large quantities of mast, in spite of continuous environmental variation; (2) normal masting, under which either bimodal mast distributions are statistically significant or, if not, there is evidence for diversion of plant resources from vegetative growth to reproduction; and (3) putative masting, indicated by high annual variation in reproduction but without evidence of resource switching. Kelly (1994) noted that strict masting is rare in nature, while normal masting is observed in many oaks (*Quercus*), pines (*Pinus*), and beech (*Fagus*); putative masting occurs across many plant species, but seed production is strictly driven solely by environmental variation.

Masting in Southwestern woodlands

In their review of mast seeding in perennial plants, Kelly and Sork (2002) proposed that "masting should be more common in both unproductive habitats and dominant plant species" (Kelly and Sork 2002:436), especially in situations with low species diversity; semi-arid woodlands in the American Southwest, dominated by only a few tree species consisting of piñon pine, juniper, and oak, clearly fit these criteria. While a considerable number of studies have addressed masting behavior in pines and oaks worldwide, few research projects have examined masting in piñon–juniper–oak woodlands.

Most observations of masting in Southwestern piñon–juniper–oak woodlands have focused on piñon pine (Little 1941, Barger and Ffolliott 1972, Ligon 1978, Forcella 1981*a*, *b*, Marzluff and Balda 1992, Betancourt et al. 1993, Jeffers 1994, Costello et al. 2003, Zlotin and Parmenter 2008, Redmond et al. 2012, Barger and Woodhouse 2015). Correlations of masting with weather variables have led to the hypothesis that cool late-summer/autumn temperatures during cone primordia formation lead to larger cone crops two years later (Forcella 1981*a*, *b*, Redmond et al. 2012). In a given year, once the numbers of cone primordia are set, future weather conditions (Zlotin and Parmenter 2008) and biotic interactions (e.g., herbivory; Forcella 1980, Christensen and Whitham 1993, Mueller et al. 2005) are hypothesized to cumulatively subtract from the original total of developing cones.

Southwestern juniper and arid-land oak species have little quantitative information on their reproductive habits, except for our earlier work in New Mexico (Zlotin and Parmenter 2008). For North American junipers, Noble (2004) noted that Rocky Mountain juniper (*Juniperus scopulorum*) produces "heavy seed crops" every 2–5 yr, while Lawson (1990) reported that eastern redcedar (*Juniperus virginiana*) produces "good" berry crops only once every 2–3 yr; however, neither of these reports provided numerical data. van Ommeren and Whitham (2002) reported 10- to 15-fold differences in the annual number of berry-producing junipers (*Juniperus monosperma*) over a 3-yr study of bird–juniper–mistletoe interactions, and Costello et al. (2003) observed only a single "excellent" juniper (combined *J. monosperma*, *J. scopulorum*, *Juniperus deppeana*, and *Juniperus osteosperma*) mast event (1998) during 1993–2000 in northern and southern New Mexico. In arid-land oaks, short-term mast dynamics of Gambel oak (*Quercus gambelii*), wavyleaf oak (*Quercus undulata*), and gray oak (*Quercus grisea*) have been included as ancillary data in a single wildlife study (Costello et al. 2003), again recording only a single "good" mast year (1998) in their 8-yr study.

In this study, our overall goal was to assess reproductive behavior in the three species of trees dominating New Mexico's semi-arid woodlands. We treated tree reproduction as a continuous variable (amount of mast produced each year) and evaluated whether each species fit Kelly's (1994) classification of strict, normal, or putative masting behavior. We addressed a series of questions on masting patterns to evaluate which of the theories described above might apply to our semi-arid woodlands. We have structured many of our research questions directly following the review of Koenig and Knops (2002) on the behavioral ecology of masting in oaks and expanded them to include all three of the tree species in our study area.

The first questions we address are how well our study species meet the definition of mast species:

1. What is the annual variability in mast production by each species within this study area? And how well does this variability meet "mast" criteria: non-normal distributions of mast production by year, non-normal log-transformed distributions, coefficient of variation (CV) >1.0, and negative autocorrelation between mast years and previous years (one- and two-year lags)?
2. Does annual mast production display a bimodal pattern, with distinct high-mast and low-/non-mast years?
3. What is the average interval for each species between mast and non-mast years?
4. Does each species display synchronous mast production patterns among its populations

in terms of kg/ha mast (ecosystem-level), proportion of mast-producing trees in populations (population-level), and kg/tree mast (individual-level) within the study area? On this mast synchrony topic, we also addressed two secondary questions:

(a) At the population-level, how does mast production and synchronization differ across age (size) classes of individuals within each species?
(b) Is mast production for all three of our study species in this semi-arid ecosystem synchronous with each other?

The second set of questions addresses the role of environmental drivers (weather tracking) on mast production:

5. Is mast production associated with current- or prior-year meteorological variables, such as antecedent precipitation, air temperature, soil temperature, vapor pressure deficit, wind speed, and frost (i.e., testing the resource weather tracking hypothesis of Kelly and Sork (2002) and Calama et al. (2011), and specifically including the late-summer/autumn temperature hypothesis of Forcella (1981*a*))?
6. If univariate or multivariate factors are found to be significantly related, can predictive models of mast production be produced to forecast mast events, allowing resource managers lead time to develop management strategies for wildlife, mast harvests, and climate impacts on tree reproduction success?
7. If weather variables with time lags are associated with mast production (current year vs. 1-yr lags, 2-yr lags), are the inter-annual changes in these variables more significant than the absolute values of the variables themselves (i.e., testing the differential cues hypothesis of Kelly et al. 2013)? This is an alternative model to the common weather tracking hypothesis that considers the differential temperature (ΔT) between years to be the actual cue for masting events (Kelly et al. 2013) rather than the absolute temperature values; in this scenario, mast production is better correlated with changes between the 2-yr and 1-yr lagged growing season temperatures than with the absolute values of the recorded temperature patterns.

The next question addresses alternative or concomitant hypotheses of plant resource switching, resource depletion, and cycling:

8. Are high-mast years consistently followed by low-mast or non-mast years, indicating a possible depletion of reproductive resources during mast production, and thereby imposing a mandatory post-masting recovery period on the timing and effectiveness of environmental drivers? The resource switching hypothesis (Norton and Kelly 1988) states that in a given year, plants dedicate resources differentially either to vegetative growth or to reproduction. This concept (equivalent to the stored resource hypothesis of Funk et al. 2016) incorporates presumed limited plant resources (nutrients, carbohydrate production and storage, water availability) which are superimposed on environmental cues. These physiological constraints could possibly modify (amplify or constrain) mast production based on plant condition. Kelly and Sork (2002) suggest that indirect evidence for switching is found in negative autocorrelations of mast production (current-year mast is negatively correlated with the previous year's mast), as well as bimodal distributions of mast production among years. Additional indirect tests for mast cycling and resource depletion have been proposed by Calama et al. (2011), and we incorporate these into our analyses on this topic.

The final question addresses pollen limitation during masting:

9. If pollen is a limiting component of successful mast production, is the annual abundance of atmospheric pollen positively correlated with mast production values?

METHODS

Study sites

In the American Southwest, semi-arid piñon–juniper–oak woodlands dominate mesas and valley slopes at middle elevations (800–2500 m), covering in excess of 17 million ha (West 1988, West and Young 2000). The dominant tree species in this ecosystem vary geographically, but generally, any given woodland stand's tree component will consist of one representative species of piñon pine (*Pinus* spp.), one or two species of juniper (*Juniperus* spp.), and usually one or two species of oak (*Quercus* spp.).

We conducted the study in semi-arid woodlands of the Sevilleta National Wildlife Refuge (NWR), Socorro County, New Mexico, USA (Appendix S1: Table S1 and Fig. S1). The 100,000-ha Sevilleta NWR stretches across the Rio Grande Valley in central New Mexico, bounded on the east by the Los Pinos Mountains and on the west by the Sierra Ladrones. Lower-elevation habitats are characterized by Chihuahuan Desert grassland and desert scrub, grading into juniper savannas and piñon–juniper–oak woodlands at higher elevations. Precipitation is dominated by the summer monsoon, with 57% of annual precipitation falling during June through September. Rain and intermittent snow comprise the winter moisture. Temperatures range from a mean daily maximum of 33.2°C in July to a mean daily minimum of −7.3°C in January. Spring months (March–May) are characterized by extended periods of high-velocity winds from the southwest.

We selected six study locations that represented a topographic elevational gradient (1458–1955 m) and a temperature and precipitation gradient (dryer and warmer at lower elevation, and cooler and wetter at higher elevation; Appendix S1: Table S1 and Fig. S2). All three tree species examined in this study coexisted at the two highest locations (Cerro Montoso and Goat Draw), while the West Mesa site contained only piñon pine and juniper. The sites at the lowest elevations (Sierra Ladrones, McKenzie Flats, and the Field Station) supported only juniper populations.

Study species

Three species of trees comprise the arid and semi-arid piñon–juniper–oak woodlands of central New Mexico: one-seed juniper (Cupressaceae: *Juniperus monosperma* (Engelm.) Sarg.); two-needle piñon pine (Pinaceae: *Pinus edulis* Englem.); and Sonoran scrub oak (Fagaceae: *Quercus turbinella* Greene). These species belong to three different families and have different reproductive cycles of seed development spanning 1 or 2 yr (over 2–3 calendar years; Fig. 1).

The first, one-seed juniper, occurs from Texas to Arizona, and north to Colorado (Appendix S1: Fig. S3). Generally dioecious (but occasionally monoecious), one-seed juniper's reproductive cycle begins with strobili formation in the summer of year 1, followed by wind-borne pollination during the following spring (March–May); fertilization occurs several weeks after pollination, and seed/fruit development continues through the summer of calendar year 2, with mature berries on the trees by August (Chambers et al. 1999; Fig. 1).

Two-needle piñon pine is widely distributed in the Southwest and grows from Texas to California, and from northern Chihuahua, Mexico, northward into southern Wyoming (Appendix S1: Fig. S3), occupying an overlapping, but slightly higher, elevation of 1500–2500 m compared to one-seed juniper (Lanner 1981). Generally monoecious, but occasionally dioecious (Floyd 1983), two-needle piñon pine begins producing cones at ~25 yr of age. Seed and cone production occurs over three growing seasons (Fig. 1; see review by Chambers et al. (1999) and references therein). Primordia strobili form between August and October of calendar year 1, with male and female strobili developing the following spring (calendar year 2). Wind-driven pollination occurs in May–June of year 2, with female strobili growing throughout the summer and into the autumn (September) before overwintering at a size of 17–25% of mature cones. In the spring of calendar year 3, the small green cones grow and swell in size, with fertilization occurring in early July. Seed maturation is complete in August, and the cones dry and open by mid-September. However, many of the seeds (~50%) are unfilled (due to self-pollination and subsequent collapse of the female gametophyte), which, combined with insect seed-predator losses, reduces the number of filled seeds to approximately 4 per cone (Chambers et al. 1999).

Sonoran scrub oak occurs from New Mexico to California and Baja, Mexico, and north to Colorado, Utah, and Nevada, growing at elevations of 800–2000 m (Appendix S1: Fig. S3). Sonoran scrub oak is an evergreen drought-deciduous species, is monoecious, and is in the white oak

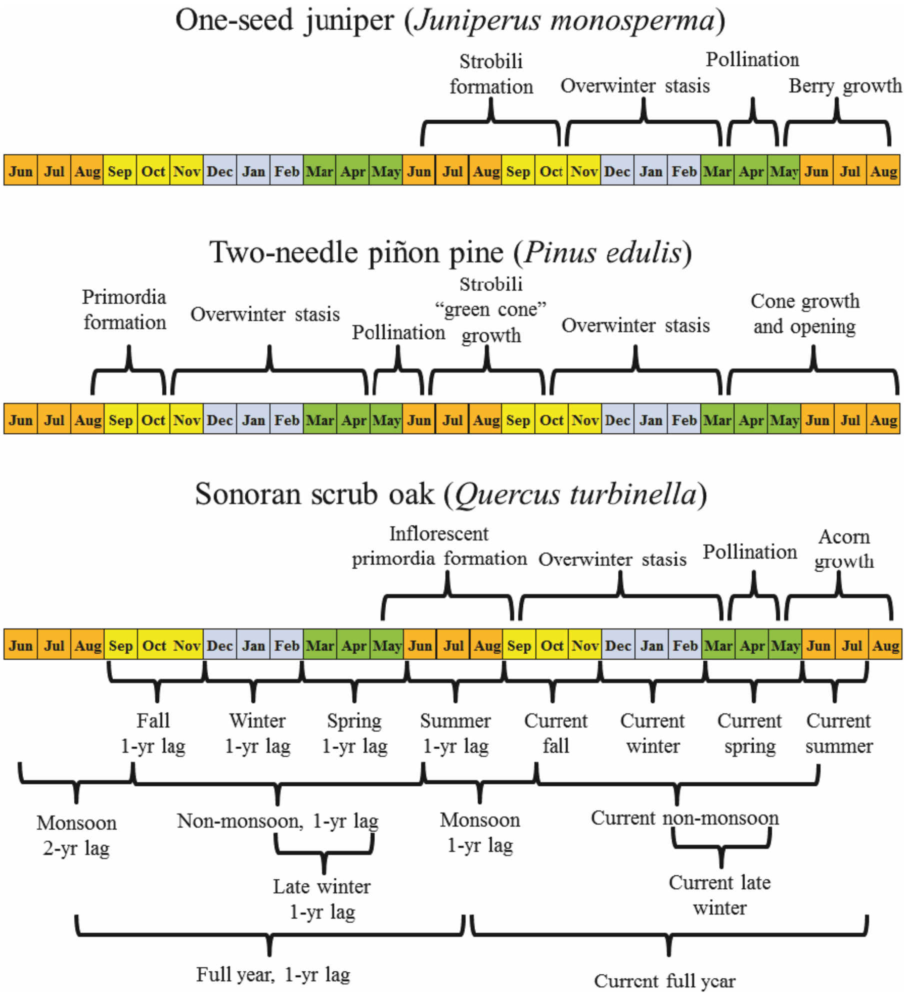

Fig. 1. Timelines for mast development in one-seed juniper, two-needle piñon pine, and Sonoran scrub oak in relation to time periods for meteorological correlation analyses.

group characterized by having a pollination-to-acorn production period within a single year (Fig. 1) in contrast to the red oak group having a 2-yr period. The reproduction cycle in white oaks begins the calendar year prior to acorn formation (see Rauscher and Hubbard 2012 and references therein), with staminate inflorescence primordia developing in May to August of year 1, and forming immature anthers and filaments by autumn. Simultaneously, pistillate inflorescent stalks differentiate from axillary primordia, completing initial development by late summer. The following spring (calendar year 2), anthers, pollen and catkins, and pistillate inflorescences complete development, with wind-driven pollination occurring during March–May. Acorns develop during the summer, maturing in August–September. As with piñon pine nuts, acorns may suffer from unfilled seeds and insect attack, thereby reducing the effective number of viable seeds by autumn.

Field sampling methods

Mast measurements were taken from 1997 through 2016. The first field site (Sierra Ladrones) was established in 1997, with additional sites added to the study in 1998 (Cerro Montoso, Goat Draw, and West Mesa), 2000 (Field Station), and 2001 (McKenzie Flats). Field measurements of annual mast production on each tree within a 1-ha square plot were made in August of each year, coinciding with maturation of juniper berries, piñon pine cones, and oak acorns. All trees within the plots were permanently marked with individually numbered aluminum tree tags (except the West Mesa site). Detailed field sampling methods are described in Zlotin and Parmenter (2008) and in Appendix S2.

Meteorological variables

Measures of potential meteorological drivers (antecedent precipitation, air temperature, soil temperature, vapor pressure deficit, and wind speed) of mast production were compiled for different time periods relating to each species' reproduction cycle (see Fig. 1, illustrating the relationships among time periods of mast production and time intervals used in the analyses). Meteorological data were collected from the nearest Campbell meteorological station (Campbell Scientific, Logan, Utah, USA) to each site (see Appendix S1: Fig. S1; data source: http://sev.lternet.edu/content/meteorology-data-sevilleta-national-wildlife-refuge-new-mexico-1988-present). Missing values in the meteorological data set were imputed with predicted values based on among-site co-variance patterns for each variable. We used the following definitions to develop variables for analyses.

1. Precipitation: current-year total (mm) in prior 12 months (July back to the previous August); current-year summer total (June–July); current-year spring total (March–May); current-year winter total (December–February); current-year fall total (September–November); total current-year non-monsoon period (October–May; this is the period during which central New Mexico receives markedly increased (+~50%) precipitation during El Niño years, and decreased precipitation (~−50%) during La Niña years); current year's late-winter period (February–April); previous-year (August$_{t-2}$–July$_{t-1}$) total precipitation; totals of previous-year summer (June$_{t-1}$–August$_{t-1}$), spring (March$_{t-1}$–May$_{t-1}$), winter (December$_{t-1}$–February$_{t-1}$), fall (September$_{t-1}$–November$_{t-1}$), non-monsoon (October$_{t-1}$–May$_{t-1}$), monsoon (June$_{t-1}$–September$_{t-1}$), and late-winter (February$_{t-1}$–April$_{t-1}$); and 2-yr lagged monsoon total (June$_{t-2}$–September $_{t-1}$).
2. Relative humidity: mean daily relative humidity (%) for the same time periods listed above.
3. Vapor pressure deficit: Mean daily vapor pressure deficit (VPD) is the difference (deficit) between how much moisture the air can hold when it is saturated and the actual amount of moisture in the air. The meteorological stations on the study sites calculated saturation vapor pressure (SVP), and SVP was multiplied by the relative humidity to derive the vapor pressure (VP). Vapor pressure deficit was computed as:

$$\mathrm{VPD} = \mathrm{SVP} - \mathrm{VP}$$

4. Air temperature: mean daily maximum temperature (°C), mean daily minimum temperature, and mean daily temperature for the same time periods listed above.
5. Soil temperature: mean daily soil temperature at 10 cm depth for time periods listed above.
6. Wind speed: mean daily and mean daily maximum wind speed (m/s) for time periods listed above.

Given that many of the weather variables co-varied with each other, we analyzed the degree of correlation among these variables with Spearman's correlation analyses. For example, it was likely that growing season periods with more precipitation would have cooler mean temperatures, whereas periods with low precipitation would be warmer on average (due to differences in cloud cover and evaporative heat losses). The levels of co-variance would inform interpretation of any significant results, particularly in cases where two or more variables proved simultaneously significant.

We also tested the effects of two additional meteorological variables on subsequent mast production (kg/ha) with univariate Spearman rank correlation analyses. The first was the date of the last frost in the spring of the current year (Julian date), as well as the dates of last frost in the previous year's spring. A late frost could potentially kill flowers or young fruits, reducing mast production.

Based on the hypothesis of Forcella (1981*a*) for piñon pine that late-summer/autumn temperatures (specifically, cold periods) during primordia formation influence the eventual number of cones of piñon pine, we correlated piñon pine, juniper, and oak mast production with 1-yr (juniper and oak) and 2-yr (piñon pine) lagged mean daily minimum, average, and maximum temperatures during five late-summer/autumn periods: 15–31 August; 1–15 September; 16–30 September; 1–15 October; and 16–31 October.

Pollen measurements

We obtained daily atmospheric pollen count data from the Air Quality Division, City of Albuquerque, New Mexico. These data included the city's entire pollen record of 2003–2016, with the exception of 2013 during which large gaps in collection existed. Data were collected in the northeast quadrant of the city (35°08′03.5″ N, 106°35′06.8″ W, elevation 1593 m), which was ~80 km north of the Sevilleta NWR. City staff identified and counted daily pollen samples for different plant taxa, including juniper, pine, and oak (for detailed methods, see https://www.cabq.gov/airquality/todays-status/pollen/pollen-collection-counting). As these data were collected in an urban environment with nearby natural areas, the pollen data would have included multiple species of juniper, pine, and oak which were not identified to species. The juniper data would likely have been dominated by one-seed juniper, as this species is common throughout the city and suburban areas. The pine pollen would likely have been a mix of piñon pine and Ponderosa pine (*P. ponderosa*), both species being present throughout the area. The oak pollen data would have been dominated by Gambel oak (*Quercus gambelii*) and Sonoran scrub oak, also common species in the city and adjacent natural areas.

Statistical analyses

Mast production.—As a general summary of the data at the ecosystem-level, we first analyzed the patterns of annual mast production in kg/ha by species and site throughout the study period, calculating means and ranges of each species' annual production by site by year. Numbers of years with zero mast production were identified. To quantify population-level patterns of mast production for each site in each year, we calculated the proportion of mast-producing trees, as well as the population-wide site-specific mean mast quantity per tree (mean number of juniper berries, acorns, or pine nuts per tree). In evaluating mast behavior for individual trees within populations (sites), we calculated the dry mass (g) of mast production for each tree in each year by multiplying the number of berries, nuts, or acorns per tree by the average dry mass measured (0.10 g/juniper berry, 0.22 g/pine nut, and 0.45 g/acorn; see Appendix S2). We tracked years since previous mast production (regardless of total mast amount) for each tree and year and used these measures to assess lag effects on productivity.

For demographic analyses, we classified all individual trees into age/size categories. Juniper and piñon pine were classified into young, medium, old, and very old age classes as described in Zlotin and Parmenter (2008; see Appendix S2). Oaks were classified into size quartiles based on canopy area (m^2). Uniformity of categorical age/size distributions among sites was assessed using Fisher's exact tests. Oak canopy size differences across sites were also assessed using a nonparametric Kruskal-Wallis test.

Individual tree-level mast production was assessed for 412 junipers, 194 oaks, and 210 piñon pines (trees from the West Mesa site were not included in tree-level analyses, as individual trees were not marked at this site). Differences in overall proportions of trees producing mast in each age/size class and site for annual mast production were assessed using generalized mixed model regression with a logit link, and the binomial distribution to estimate the probability of mast occurrence while accounting for repeated measures on trees (Laird and Ware 1982, Fitzmaurice et al. 2004). Analyses included random effects for years and trees, in addition to fixed effects for site and age/size classes. Continuous measures of tree-level mast values (grams or seed counts per tree) were analyzed using a similar mixed model regression approach. Residual random variation within trees was assumed to be normally distributed but correlated, with the strength of the correlation decreasing exponentially over time. Continuous mast values were log-transformed before analysis, after adding 0.5 to all original values to account for years with zero mast produced. Marginal least-squares-adjusted means and confidence intervals were back-transformed for reporting.

*Mast species characterizations.—*To assess the degree to which each tree species fit the definition of a strict, normal, or putative masting species (Kelly 1994), we evaluated each species in our study area using the following criteria (see Koenig and Knops 2002 and Crone et al. 2011 and references therein):

1. The distribution of annual mast production values (kg mast/ha) should be non-normal, both for raw values and for log-transformed values. Normality tests were performed on all data sets by site and species using the Shapiro-Wilk test (Shapiro and Wilk 1965).
2. The coefficient of variation (CV) of annual mast production values should be >1.0; CVs were calculated for each species at all sites as: CV = standard deviation/mean.
3. Autocorrelation between the annual mast production in year t and the prior year, $t-1$, should be negative; in addition, we tested autocorrelations with a 2-yr lag ($t-2$) given the multi-year seed development biology of piñon pine. Linear regression analyses were performed to calculate regression slopes for all species by site, with mast production (kg/ha) in year t as the dependent variable, and mast production in year $t-1$ or $t-2$ as the independent variable.
4. Distributions of annual mast production should be bimodal, having greater numbers of years with either zero or very low production values and other years with high mast production, with fewer years of intermediate values. For each species, we grouped site-specific annual mast production values into three clusters (lowest third, intermediate third, and highest third) based on the range of absolute values (kg/ha) and tallied whether or not the number of intermediate years were fewer than the number of low and high years.
5. Mast species will not produce mast every year, and therefore will have species-specific mast production intervals greater than a year. We determined average mast production intervals (years between events) for each species at each site using two measures: (a) any year with mast production vs. zero mast production years; and (b) years defined as mast years in which the annual standardized deviate ($\text{ASD}_{i,t}$) of mast production (kg/ha) exceeded the absolute value of the lowest standardized deviate (see LaMontagne and Boutin 2009). The annual standardized deviate (ASD) was calculated for each species at each site (i) in each year (t) using the equation formulated by LaMontagne and Boutin (2009):

$$\text{ASD}_{i,t} = \frac{(\text{Mean mast production in year } t) - (\text{Long-term mean mast production})}{\text{Standard deviation calculated over all years at site } i}$$

The number of years with $\text{ASD}_{i,t}$ values exceeding the absolute value of the minimum $\text{ASD}_{i,t}$ values was divided into the number of years of data record at each site to compute the average mast-year occurrence interval; site-specific mast intervals were then averaged to estimate a species-specific mast-year interval during the study period (1997–2016).

6. Mast species should synchronize mast production among populations across the landscape. We analyzed synchronization of mast production across our study area (a) within species at the ecosystem-level (kg/ha), (b) for the proportion of masting-tree populations among sites, (c) for individuals within tree populations, and (d) across tree species. We used pairwise correlation analyses to assess synchrony among species, within species across sites, and within species. Our analyses were similar to those described by Schauber et al. (2002), but we used nonparametric Spearman correlation analyses for continuous measures of mast production (kg/ha, proportion with any mast at a site,

seeds/tree, kg/tree) as our mast distributions were not approximately normally distributed. Synchrony of species was assessed by estimating the correlation between species using the two sites where all tree species occurred: Cerro Montoso and Goat Draw. In addition, for one-seed juniper (which occurred at all six study sites), we tested the hypothesis that synchronicity of site mast production and of the prevalence of trees producing mast (correlation coefficients, r_s) would decrease with increasing distance between sites (see Koenig 1999). To evaluate synchrony among individual trees within species, we calculated Spearman correlations for all pairs of trees both within and between study sites after restricting analyses to trees that had at least two years of positive mast production. Distributions for between-tree correlation coefficients were summarized graphically, and Wilcoxon signed-rank tests were used to test for nonzero correlation (i.e., if median correlation = 0, then no synchrony would exist).

*Meteorological variables.—*We conducted univariate analyses on all meteorological variables at various time scales, so as to identify and link particular weather conditions with each species' reproductive cycle (Fig. 1; see similar approaches by Sork et al. 1993, Cain and Shelton 2000, and Abrahamson and Layne 2003). Our initial analyses to assess the association between meteorological variables and mast production measures at the ecosystem- (kg/ha), population- (site proportion of mast-producing trees), and individual-levels (dry mass or seed counts) used nonparametric Spearman's correlation. Statistical significance was defined as $P \leq 0.05$, and all P-values were adjusted for multiple tests, controlling the false discovery rate for correlated variables (Benjamini and Yekutieli 2001).

Following these ecosystem-level (kg/ha) analyses, we used the most significant variables (with highest r values) identified in the Spearman correlations to evaluate meteorological variables as predictors of population-level and individual tree-level mast production. For population-level analyses, univariate linear and nonlinear least-squares regression analyses were performed between the meteorological variables (independent variable) and the proportion of trees in the population producing mast in site-specific populations (dependent variable); we conducted the same analyses using numbers of berries, acorns, or pine nuts per tree (dependent variables). We then further analyzed the population proportional mast production-meteorological regressions by size/age classes of trees within the overall study population.

Finally, we analyzed the influence of meteorological variables on individual tree mast production using log–log-transformed data and logistic regression analysis. For each species and site, we regressed annual mast production of each individual tree (dry mass [g] of berries, pine nuts, or acorns per tree) with the most significant meteorological variable identified during the ecosystem-level analyses. Regression coefficients (r) were averaged across all individuals per site for significance testing, and coefficients of determination (r^2) were used to partition the proportional role of individual tree responses to meteorological variables vs. population responses (proportion of population producing mast in a given year).

*Multivariate logistic models.—*We used the general approach described above to examine multivariable associations between mast and meteorological variables. In these models, meteorological variables were added as continuous covariates. We selected the meteorological variables from the results of the univariable analyses, including those variables that had the highest correlation coefficients and were not confounded by co-variance issues (i.e., we did not include two variables from the same time period, such as precipitation and temperature, as these were highly correlated with each other). We tested whether slopes varied by sites by adding interaction terms to models. Relative support for models was assessed by comparing Akaike's information criterion, corrected for sample sizes (AIC_c) values obtained using maximum likelihood (SAS v9.4, Laplace's approximation method, GLIMMIX). Statistical significance was inferred at $P < 0.05$. P-value adjustment for post hoc multiple comparisons was made using the Holm step-down method (Holm 1979).

Fit of models was assessed using graphical approaches for continuous mast measures, and we computed empirical r^2 values by squaring the

Pearson correlation estimate for marginal predicted values and observed values. We also used area under the summary receiver operator characteristic curve (AUC) to summarize discrimination accuracy for logistic regression models. AUC values equal to 0.5 are no better than random, values >0.70 may be considered to be good discriminators, and values = 1.0 equal perfect discrimination. This may be interpreted as the probability of correctly ordering the rank of two randomly selected masting prevalence values.

We used a leave-one-out cross-validation approach (LOOCV) to assess predictive capability of models (Hastie et al. 2001). One year at a time was held out from the estimation step, and the out-of-sample predicted value was computed for each site and year ($\hat{y}_{i,-i}$). When the last mast survey year is held out, the LOOCV is the special case of evaluating predictive capability for 1 yr in the future. Average difference between predicted and hold-out values (Bias), mean absolute error (MAE), and predicted residual sum of squares (PRESS) were used to summarize errors between hold-out values and predictions when these values were not used to fit the model.

$$\text{Bias} = \frac{\sum_{i=1}^{n}\left(y_i - \hat{y}_{i,-i}\right)}{n}$$

$$\text{MAE} = \frac{\sum_{i=1}^{n}\left|y_i - \hat{y}_{i,-i}\right|}{n}$$

$$\text{PRESS} = \sum_{i=1}^{n}\left(y_i - \hat{y}_{i,-i}\right)^2$$

We used graphical summaries to show predicted and hold-out values by site and year to assist in identifying influential sites and years.

*Testing the Δ*T *hypothesis.*—We conducted analyses to test for relationships between mast production and inter-annual changes in temperature (Kelly et al. 2013) and precipitation (Koenig et al. 2016). For these analyses, we used raw and log-transformed values of site-level mast (kg/ha) as the dependent variable and employed model-selection procedures (Burnham and Anderson 2002) and regression analyses to associate site mast production and weather variables. Weather values used matched those of Kelly et al. (2013) and Koenig et al. (2016) and included average air temperatures and total precipitation from the most recent spring (T_0_AVG-SPR, PPT_0_SPR), summer (T_0_AVG-SUM, PPT_0_SUM), late winter, February–April (T_0_AVG-FMA, PPT_0_FMA), and growth year (previous July–current August; T_0_AVG-G-Yr, PPT_0_G-Yr), and from the previous time periods with 1-yr lags (T_1) ad 2-yr lags (T_2). Between-year changes in average temperature (ΔT) were computed for the designated time periods as $\Delta T_0 = (T_0 - T_1)$ and $\Delta T_1 = (T_1 - T_2)$. Period-specific T and ΔT variables were added to regression-based models using approaches described above; identical procedures were used for total precipitation (PPT and ΔPPT). Performance of these variables was assessed by comparing AIC_c values among models ($\Delta\text{AIC}_\text{c}$) and by testing whether slopes were different from zero.

Testing the resource switching, resource cycling, and resource depletion hypotheses.—We analyzed the potential for resource switching, cycling, and depletion during mast years by assessing whether years with mast production were consistently followed by years of lower mast production or years with zero mast production. As we did not have direct measures of plant resources (nutrients, carbohydrates, annual growth increments), we followed the procedures of Norton and Kelly (1988), Greene and Johnson (2004), and Calama et al. (2011) in testing for indirect evidence of switching, cycling, and resource depletion. Norton and Kelly (1988) stated that negative autocorrelations of annual mast production, and bimodal distributions of annual mast quantities, would constitute indirect evidence for resource switching. Calama et al. (2011) restricted their analyses to time series of individual trees that were at least six years long and with at least five years of greater than zero mast production. As in the Calama et al. (2011) study on cyclical patterns (mast cycling hypothesis), we analyzed our data by calculating the Spearman rank correlation coefficients for the 1- to 4-yr lagged responses of each series, which were for mast production in kg/ha. Calama et al. (2011) hypothesized that significant positive or negative correlations were indirect evidence in support of cycling and that the resource depletion analysis was based on whether mast amounts in the two years following peak years (defined as in Calama et al. 2011:609) were less than the median of each time series. We also added indicator variables to analysis models to assess effects of mast being produced in the previous year and two years previous.

*Testing the pollen limitation hypotheses.—*We assessed the relationship between the abundance of atmospheric pollen of juniper, pine, and oak and observed mast production values using Spearman's correlation analyses. For juniper and oak, pollen count data from each annual winter–spring pollination period (range of 150–208 d of recorded pollen) were correlated with that year's mast production, whereas for pine, we correlated the pine pollen count from the previous year's spring (when pollination would have occurred) with the current year's piñon pine mast production. We used Spearman's analysis to test the relationship between pollen counts and late-winter/early-spring precipitation to assess whether pollen counts increased or decreased with precipitation amounts during the pollination season.

RESULTS

Mast production patterns

*Ecosystem-level mast production.—*Inter-annual mast production during the study period varied over three orders of magnitude for juniper (0–1127 kg/ha), but displayed smaller ranges for oak (0–50 kg/ha) and piñon pine (0–22 kg/ha; Fig. 2). Annual mast production was zero at all sites for oak in nine of 19 yr and piñon pine in seven of 19 yr, and depending on the site, juniper produced no mast between 3 and 6 yr of the 20-yr study (Fig. 2).

*Population-level demographics and mast production.—*The age/size class analyses of each species identified significant differences in population structure between sites (see details in Appendix S3) However, during the course of this 16- to 20-yr study, growth of the marked trees was so slow that no tree changed age/size class. Several young piñon pine trees were recruited into the mast-producing populations during the study as they reached maturation age/size, but subsequently died during drought years. In addition, mortality of trees during the study period caused the loss of 4 one-seed junipers and 16 piñon pines, but no oaks. Recruitment and losses were included in all data analyses.

Most trees produced mast in at least one year of the study (93% of one-seed juniper and 95% of piñon pine and Sonoran scrub oak). Measurable amounts of mast were observed in 43.7% of juniper tree-years (95% confidence interval [CI] = 42.5–45.0), in 29.0% of piñon pine tree-years (95% CI = 27.4–30.7), and in 32.2% of oak tree-years (95% CI = 30.4–34.0), although the relative frequency of masting was variable among trees.

Younger and smaller trees were less likely to produce mast than older/larger trees for all three species (Fig. 3; Appendix S3: Table S1). Juniper trees were less likely to produce mast at the Field Station and Sierra Ladrones sites, and for piñon pine and oaks, the relative frequency of mast production was greater at Cerro Montoso (higher, wetter) than at Goat Draw (lower, drier) (Appendix S3: Table S1). There were no site x size interaction effects for juniper ($P = 0.74$) and piñon pine ($P = 0.84$); however, among oak trees, the probability of masting was significantly higher at Cerro Montoso than at Goat Draw among the three upper tree-size quartiles (2nd quartile $P = 0.04$, 3rd quartile $P < 0.001$, 4th quartile $P = 0.04$, site × size interaction $P = 0.004$), but not significant for the smallest quartile.

Mast species characterizations

Analyses of species-specific mast production metrics for assessing the degree to which each species met the criteria of a mast species generally yielded results consistent with mast species definitions, though results were mixed (Table 1). For juniper, neither mast production data nor log-transformed data were normally distributed in any of the six populations. Coefficients of variation exceeded 1.0 at all six sites. Lagged autocorrelation coefficients were negative in three of six populations for both 1-yr lags and 2-yr lags and positive in the other three populations (and only significantly so in one of each). Mast data distributions were bimodal in only two populations (Table 1).

All three piñon pine populations exhibited non-normal mast production data distributions for raw and log-transformed data. All three populations also had coefficients of variation > 1.0 (Table 1). As expected given this species' 2-yr reproduction cycle, autocorrelation coefficients were negative (but not significantly so) for all three populations using 2-yr lags. One of the three populations displayed bimodal mast production distributions (Table 1).

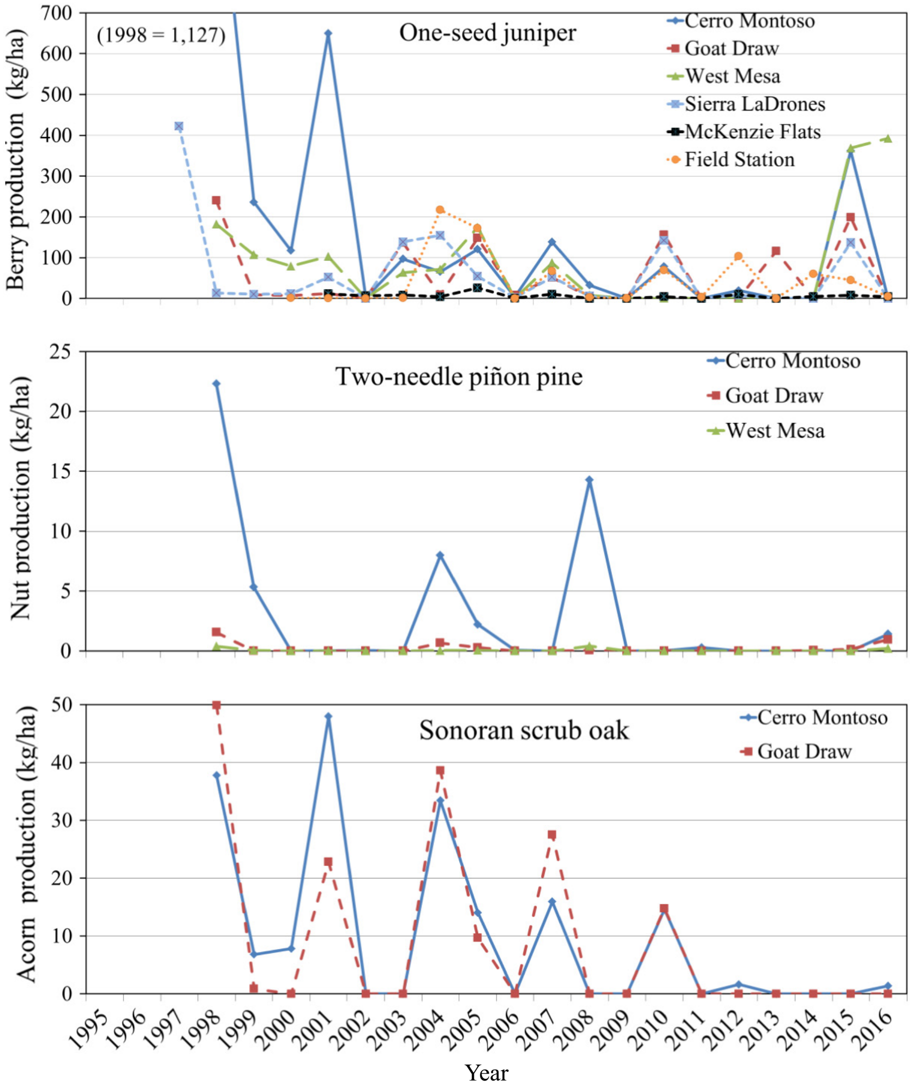

Fig. 2. Temporal dynamics of mast production (1997–2016) in the Sevilleta National Wildlife Refuge, New Mexico. Mast production graphs show annual totals by site for each tree species in kg/ha.

The two oak populations appeared consistent in mast species metrics, with both populations having non-normal raw and log-transformed data distributions. Both populations had coefficients of variation >1.0, and both possessed negative (but not significant) autocorrelation coefficients for 1-yr and 2-yr lags. One population displayed bimodal mast production distributions (Table 1).

At the ecosystem-level, mast production (kg/ha) synchrony among populations was tested with Spearman's correlation analyses. Juniper correlations among sites were significant for most comparisons (Appendix S3: Table S2, top right). Inter-site correlation of juniper mast production (kg/ha) did not decrease with distance (Appendix S3, Fig. S1, left), indicating that all study sites were similarly synchronous within the region. Oak mast production at Cerro Montoso and Goat Draw was significantly correlated ($r_s = 0.910$, $P < 0.0001$), while piñon pine correlations were also high among the three sites supporting pines (Cerro Montoso – Goat Draw: $r_s = 0.684$, $P < 0.005$; Cerro Montoso – West Mesa:

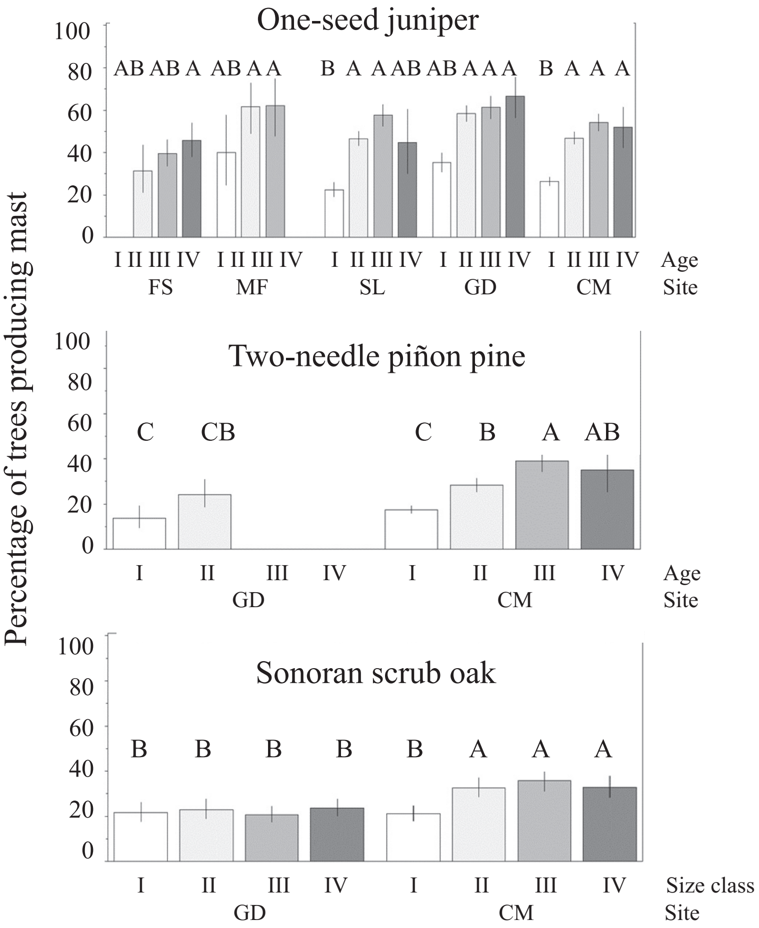

Fig. 3. Proportion of any tree-level mast production by species, site, and age/size class. Error bars are 95% confidence intervals for unadjusted proportions. Letters across the top designate significantly different groups from individual-based generalized mixed model analysis for each species. One-seed juniper and two-needle piñon pine age classes are encoded as I, young; II, medium; III, old; and IV, very old; and oak size classes are canopy area quartiles, small to large. Abbreviations are as follows: FS, Field Station; MF, McKenzie Flats; SL, Sierra Ladrones; GD, Goat Draw; CM, Cerro Montoso.

$r_s = 0.858$, $P < 0.001$; Goat Draw – West Mesa: $r_s = 0.679$, $P < 0.005$).

The synchrony of population-level mast production probability was also assessed with Spearman correlation coefficients calculated between time series of measurements at the different sites. Population proportions of mast-producing oaks at Goat Draw and Cerro Montoso had the strongest correlation ($r_s = 0.862$, $P < 0.001$), and piñon pine proportions of mast-producing trees at these sites were also significantly correlated over time ($r_s = 0.646$, $P = 0.013$). Correlations of the proportions of tree population producing mast for one-seed juniper between sites was also relatively high ($r_s > 0.500$) except for two comparisons of the Field Station site and one comparison of the McKenzie Flats population (Appendix S3: Table S2, lower left portion). As with the ecosystem analysis, correlation of tree-level proportions of mast-producing juniper trees across sites was not significantly associated with inter-site distance (Appendix S3: Fig. S1, right).

Mast production (kg mast per tree) among individual trees within species also exhibited significant synchrony in all tree species. Pairwise Spearman correlation of mast-year amounts showed medians (50th percentiles) were

Table 1. Metric results for evaluating characteristics† of mast-seeding tree species on the Sevilleta National Wildlife Refuge, New Mexico (1997–2016); see Appendix S1: Fig. S1 for site locations.

	Sites					
Species and metric	Cerro Montoso	Goat Draw	Sierra Ladrones	West Mesa	McKenzie Flats	Field Station
One-seed juniper						
Normal Distribution	No ($P < 0.01$)	No ($P < 0.01$)	No ($P < 0.01$)	No ($P < 0.01$)	No ($P < 0.01$)	No ($P < 0.01$)
Lognormal distribution	No ($P < 0.01$)	No ($P < 0.01$)	No ($P < 0.01$)	No ($P < 0.01$)	No ($P < 0.01$)	No ($P < 0.01$)
Coefficient of variation (CV)	1.77	1.39	1.69	1.39	1.05	1.50
Autocorrelation slope (1-yr lag)	0.05	-0.41^{**}	−0.07	0.62^{*}	−0.28	0.10
Autocorrelation slope (2-yr lag)	0.08	0.11	−0.11	−0.18	0.35	−0.13
Bimodal distribution	Yes	No	No	No	No	Yes
Synchronous with individuals of the same species	Yes	Yes	Yes	Yes	Yes	Yes
Synchronous among populations	Yes	Yes	Yes	Yes	Yes	Yes
Piñon pine						
Normal distribution	No ($P < 0.01$)	No ($P < 0.01$)	–	No ($P < 0.01$)	–	–
Lognormal distribution	No ($P < 0.01$)	No ($P < 0.01$)	–	No ($P < 0.01$)	–	–
Coefficient of variation (CV)	2.14	2.14	–	2.11	–	–
Autocorrelation slope (1-yr lag)	0.07	0.00	–	−0.06	–	–
Autocorrelation slope (2-yr lag)	−0.12	−0.11	–	−0.13	–	–
Bimodal distribution	Yes	No	–	No	–	–
Synchronous with individuals of the same species	Yes	Yes	–	Yes	–	–
Synchronous among populations	Yes	Yes	–	Yes	–	–
Sonoran scrub oak						
Normal distribution	No ($P < 0.01$)	No ($P < 0.01$)	–	–	–	–
Lognormal distribution	No ($P < 0.01$)	No ($P < 0.01$)	–	–	–	–
Coefficient of variation (CV)	1.54	1.76	–	–	–	–
Autocorrelation slope (1-yr lag)	−0.15	−0.07	–	–	–	–
Autocorrelation slope (2-yr lag)	−0.20	−0.16	–	–	–	–
Bimodal distribution	Yes	No	–	–	–	–
Synchronous with individuals of the same species	Yes	Yes	–	–	–	–
Synchronous among populations	Yes	Yes	–	–	–	–

† Defining characteristics of mast-seeding species include (1) non-normal distribution of mast production by years, (2) non-normal log-transformed distribution of mast production by years, (3) coefficient of variation (CV) >1.0, (4) negative autocorrelation (negative slope) of mast production through time (Year_t vs. Year_{t-1} or Year_t vs. Year_{t-2}; $^{*}P < 0.05$, $^{**}P < 0.01$), (5) bimodal distribution of mast production years, and (6) synchronous mast productions with conspecific individuals and among populations. Analyses based on site-specific annual mast production measured in kg/ha. (–) = species not present on site.

significantly different from zero for each species ($P < 0.001$, Wilcoxon signed rank test; Appendix S3: Fig. S2).

Mast production (kg/ha) synchrony among tree species was evaluated for Cerro Montoso and Goat Draw, which had measurable mast for all three tree species. Juniper mast production over both sites and all years ($n = 36$) was significantly correlated with oak ($r_s = 0.56$, $P < 0.001$) and piñon pine mast production ($r_s = 0.38$, $P = 0.02$). Oak and piñon pine mast production was also correlated ($r_s = 0.37$, $P = 0.03$). Separate

Table 2. Mean mast production intervals† (years) of mast-seeding tree species on the Sevilleta National Wildlife Refuge, New Mexico (1997–2016).

		Sites					
Metric and species	Mean	Cerro Montoso	Goat Draw	Sierra Ladrones	West Mesa	McKenzie Flats	Field Station
Any mast produced in year							
One-seed juniper	1.32	1.36	1.36	1.43	1.46	1.23	1.06
Piñon pine	2.22	1.58	2.38		2.71		
Sonoran scrub oak	2.31	1.9	2.71				
Annual deviate “mast years”							
One-seed juniper	6.65	6.33	3.17	4.00	4.75	16.00	5.67
Piñon pine	6.33	6.33	6.33		6.33		
Sonoran scrub oak	5.54	6.33	4.75				

† Interval periods based on either any mast produced by a site’s population, or only using mast years defined by annual deviates (see text).

analyses by site produced similarly sized correlation coefficients (r_s = 0.32–0.69).

While there were several years during the study with zero mast production, the average time intervals between years with at least some mast production ranged from ~1 to ~3 yr (Table 2, Fig. 2). In contrast, when examining years designated as mast years using annual deviate measures (sensu LaMontagne and Boutin 2009), the mean species-specific time intervals between mast years increased substantially to ~6 yr (Table 2).

Meteorological variables

A number of the meteorological variables were found to significantly co-vary with one another (Appendix S3: Table S3). Total precipitation and relative humidity were positively correlated with each other, and these in turn were significantly negatively correlated with vapor pressure deficits. Air temperatures (mean, maximum, and minimum) all correlated among themselves and also co-varied negatively with moisture-related variables. The only pairwise analyses that did not show significant correlations were the variable last frost day with precipitation, relative humidity, and wind speed variables (Appendix S3: Table S3). We report below all the variables that significantly correlated with mast production and use the co-variance patterns among meteorological variables in interpreting the observed patterns (see *Discussion*).

*One-seed juniper.—*The results of the univariate Spearman correlation analysis for one-seed juniper revealed several weather variables associated with positive and negative mast production dynamics (Appendix S3: Table S4). First, there were highly significant positive correlations with precipitation during the current year (year of berry production), specifically in the non-monsoon period (prior fall, winter, and spring periods); the current year’s summer precipitation total did not appear to have a significant correlation with mast production. The highest correlation with juniper mast production was precipitation during the current year’s late-winter period, February–April, and the total non-monsoon period precipitation (Appendix S3: Table S4); precipitation-associated variables, such as relative humidity and VPD, predictably exhibited significant correlations. In addition, the current year’s summer average and minimum temperatures showed a negative correlation with mast production (warmer summer temperatures were correlated with reduced mast production). Finally, the current year’s mast production was negatively correlated with the previous winter’s precipitation and positively correlated with the previous year’s winter temperature, indicating potential lag effects related to resource depletion phenomena.

Air temperatures were significantly negatively correlated with juniper mast production during the same time periods. In contrast, the date of last frost (Julian day) in the current mast year was not correlated with juniper mast production (r_s = −0.16, P = 0.10); however, log-transformed mast was significantly correlated (r_p = −0.24,

$P = 0.01$), indicating lower mast production in years with late spring frosts. Date of last frost was correlated with precipitation during February–April ($r_p = -0.22$, $P = 0.028$), but when a multivariable model was used to adjust for late-winter precipitation, the effect of last frost was not significant. Average soil temperature also displayed a significant negative correlation with mast production during the spring of the current year, and some lagged effects were observed in the previous years (Appendix S3: Table S4). With respect to wind as a possible pollination success factor, there appeared to be a negative correlation between juniper mast production and average wind speed during non-monsoon and related sub-periods of the current year (Appendix S3: Table S4).

At the tree population-level, the probability of a juniper producing mast within a site's population was significantly positively associated with current-year late-winter precipitation (Fig. 4). All of the site populations exhibited very similar patterns in terms of recruiting masting individuals with increasing February–April precipitation. In addition, late-winter precipitation was positively associated with increasing mean numbers of berries per tree at most sites (Appendix S3: Fig. S3).

For individual trees, analyses also produced positive relationships between late-winter precipitation and both the probability (logistic model, Fig. 5 top) and quantity (linear model, Fig. 5 bottom) of tree-level mast production at all juniper sites. Partitioning the tree populations by age classes supported previous results in Fig. 3 and

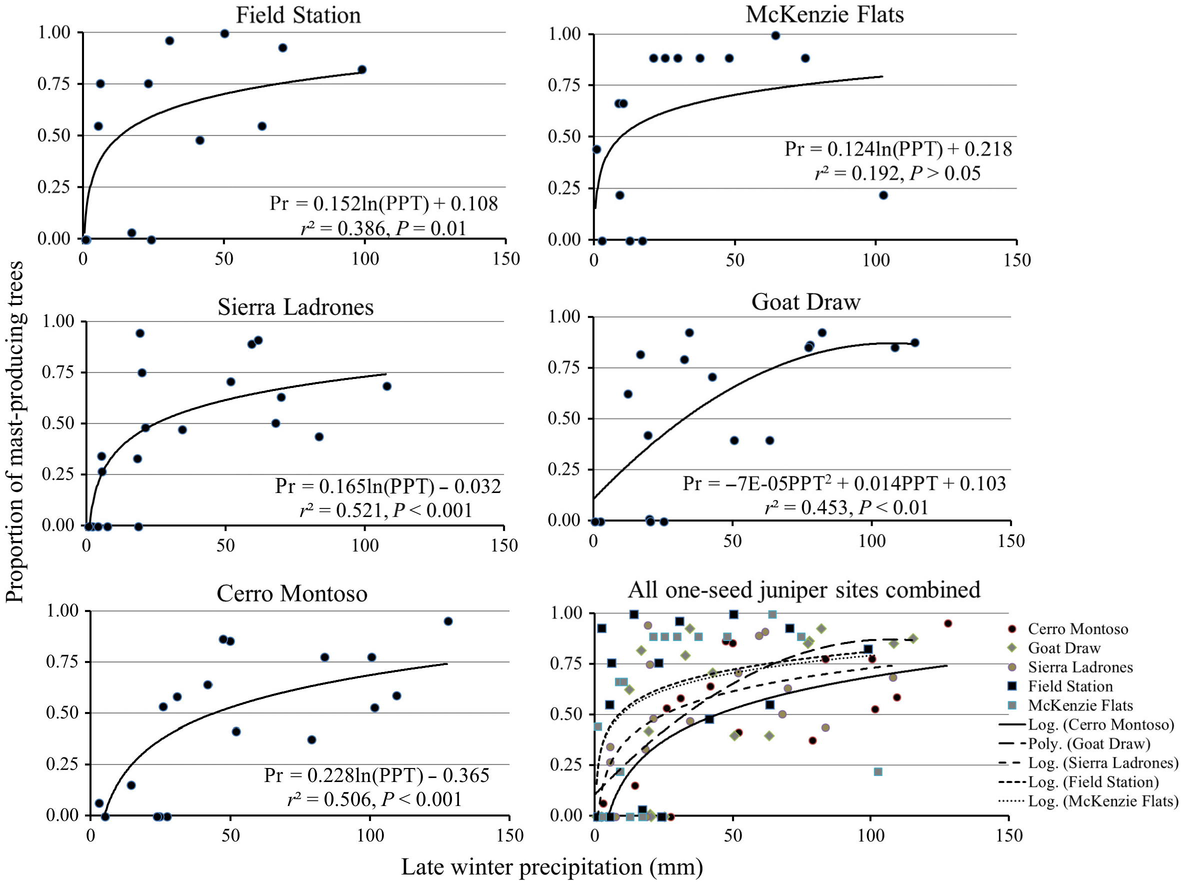

Fig. 4. Population-level association between late-winter precipitation (February–April, mm) and the population proportion of mast-producing one-seed juniper trees (*Juniperus monosperma*) by study site on the Sevilleta National Wildlife Refuge, New Mexico, 1997–2016.

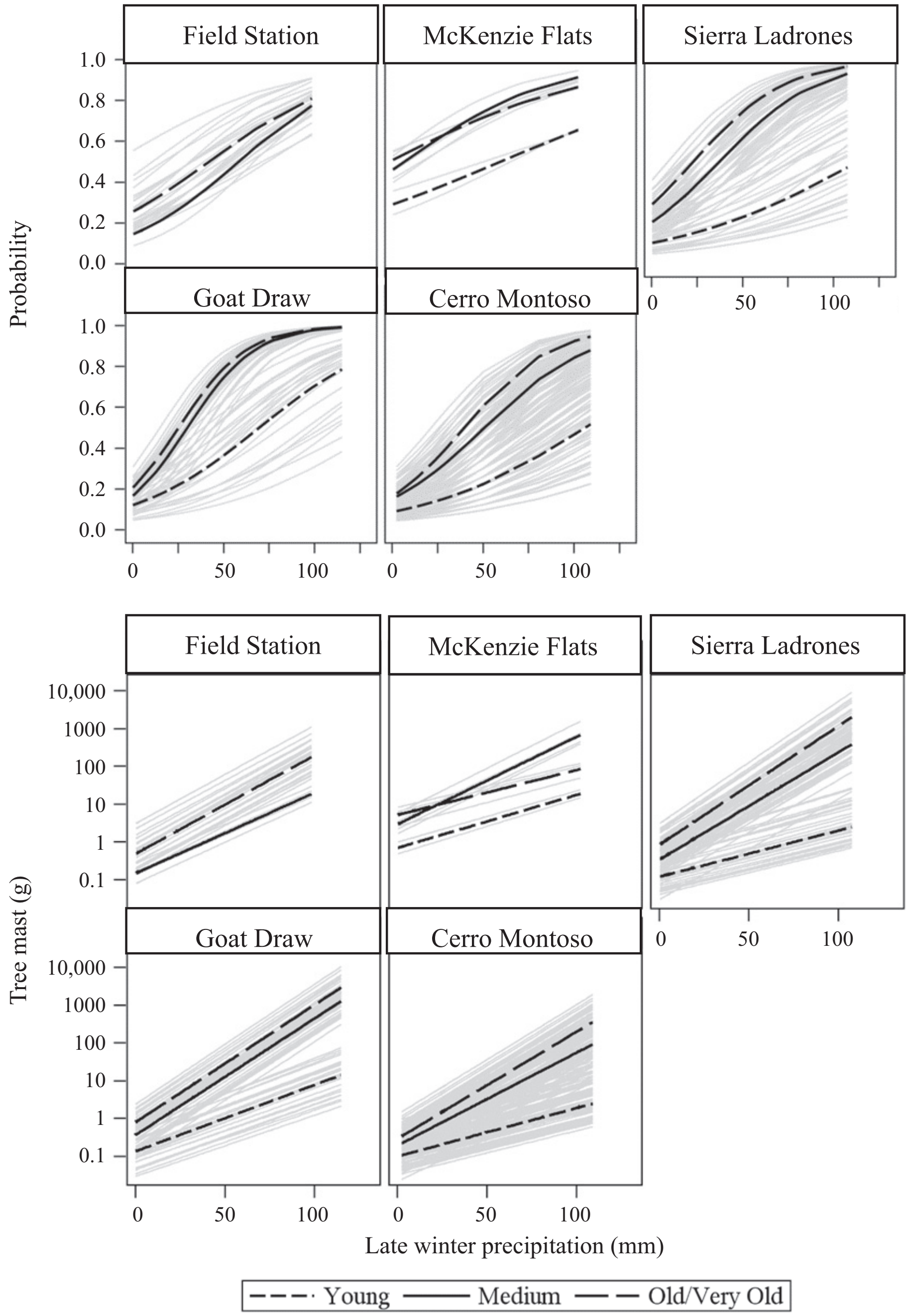

Fig. 5. Individual tree-level association between late-winter precipitation (February–April) and masting probability (top) and mast production (bottom) among one-seed juniper trees (*Juniperus monosperma*) by study site. Black lines are averages by age class; gray lines are individual trees. See text for age class definitions. Note that young juniper trees exhibit decreased probability of mast production compared to the medium and old/very old age/size classes.

Appendix S3: Table S1 that younger trees had a lower probability of producing mast than older trees (Fig 5); however, the magnitude of the difference was less when precipitation was lower compared to more precipitation (precipitation × age class interaction $P = 0.004$). The log-probability of trees producing any mast was 0.34 (95% CI: −0.57, −0.12) lower in young trees compared to old trees when late-winter precipitation equaled 5 mm compared to −1.102 (95% CI −1.25, −0.69) when late-winter precipitation equaled 100 mm. Average dry mast (g/tree) was significantly lower in young trees than in older trees ($P < 0.001$), and the magnitude of the age difference increased as late-winter precipitation increased (precipitation x age class interaction $P < 0.001$). The masting prevalence model (logistic) and the mast amount model (linear) each had a random intercept effect, but not a random slope effect, so that variation in individual tree model curvature was driven by their individual probability of producing mast and the average amount produced, respectively. Additional tree-level heterogeneity slopes for masting probability and mast amount were explored by adding random effects for slopes to the analyses. We found that after adjusting for site and tree age/size, the remaining variation in slopes was virtually zero. Therefore, we retained the more parsimonious models.

Synthesis of the Spearman analyses across the population-level proportions of mast-producing trees and the individual-level mast production per tree showed that the overall site mast production correlation with late-winter precipitation was a product of both an increasing proportion of the trees producing mast and an increase in the absolute amount of mast per tree (Table 3).

*Piñon pine.—*Piñon pine displayed significant Spearman correlations with precipitation (positive) and temperature (negative), except that these relationships were exhibited in the 1-yr lagged spring, late-winter (February–April), fall, non-monsoon, and full-year periods, rather than the current year (Appendix S3: Table S5). These periods corresponded with the period of formation, pollination, and growth of the female strobili (i.e., first full year of cone development). In addition, there was a positive correlation with 2-yr lagged summer monsoon precipitation (Appendix S3: Table S5), a period of piñon pine primordia formation during the late summer and fall (see Fig. 1). Summer precipitation in current and 1-yr lagged periods appeared to have no correlation with piñon pine mast production.

Table 3. Results of Spearman’s (r_s) analysis between individual-level tree mast production (number of berries, nuts, or acorns per tree) or proportion of trees producing mast (population-level) and the most significant meteorological variable identified in the ecosystem-level analyses (current year’s late-winter precipitation [February–April] for one-seed juniper and Sonoran scrub oak, and total annual prior-year precipitation for piñon pine).

Species and site	Variable	No. trees	No. yr	r_s	P-value
One-seed juniper					
Cerro Montoso	Individual-level	201	19	0.637	<0.05
	Population-level	201	19	0.632	<0.05
Goat Draw	Individual-level	81	19	0.772	<0.01
	Population-level	81	19	0.805	<0.01
Sierra Ladrones	Individual-level	92	20	0.745	<0.01
	Population-level	92	20	0.670	<0.01
Field Station	Individual-level	29	17	0.593	<0.05
	Population-level	29	17	0.748	<0.01
McKenzie Flats	Individual-level	9	16	0.555	0.06
	Population-level	9	16	−0.014	NS
Two-needle piñon pine					
Cerro Montoso	Individual-level	184	19	0.540	<0.05
	Population-level	184	19	−0.136	NS
Goat Draw	Individual-level	26	19	0.083	NS
	Population-level	26	19	0.333	NS
Sonoran scrub oak					
Cerro Montoso	Individual-level	96	19	0.735	<0.01
	Population-level	96	19	0.676	<0.01
Goat Draw	Individual-level	98	19	0.752	<0.01
	Population-level	98	19	0.752	<0.01

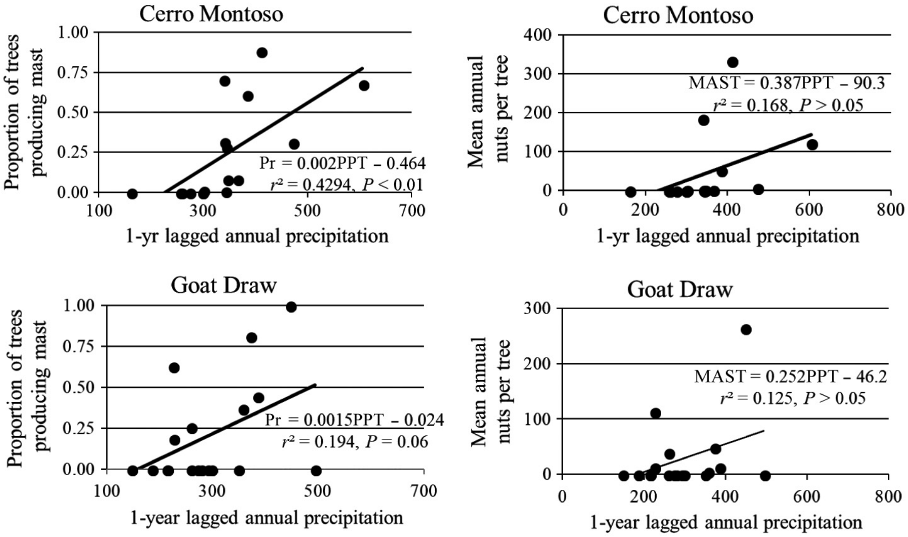

Fig. 6. Population-level association between 1-yr lagged total annual precipitation (mm) and the population proportion (left) and population average numbers of pine nuts/tree (right) of mast-producing two-needle piñon pine trees (*Pinus edulis*) by study site; Sevilleta National Wildlife Refuge, New Mexico, 1997–2016.

Relative humidity (positive correlations) and vapor pressure deficits (negative correlations) followed similar patterns to total precipitation. Air temperatures during the current year's spring (maximum, average, and minimum) and summer (maximum and average) months were negatively correlated with mast production, as well as during the 1-yr lag periods for the full previous year, and specifically the spring, fall, non-monsoon, and February–April periods (Appendix S3: Table S5). Wind speed (maximum and average) showed negative correlations on mast production during the current year's and 1-yr lagged time periods. The only other significant temperature-related variable was a positive correlation of piñon pine mast production and Julian date of last spring frost in the current year ($r_s = 0.28$, $P = 0.039$), indicating greater cone production in years with late frosts.

As 1-yr lagged full-year precipitation produced the strongest univariate correlation with piñon pine mast production, we examined this variable at the population and individual tree-levels. Results were weaker than in juniper and oak for both the population's proportion of trees producing mast and the mean number of nuts per tree (Fig. 6). While regression slopes were positive, considerable variation existed that reduced significance levels.

At the individual tree-level, the logistic model performed well on the Cerro Montoso population, showing significant increases in probability of masting with greater previous-year precipitation levels (Fig. 7); however, while still positive in slope, the Goat Draw population displayed a considerably weaker relationship. In the linear model analysis for absolute nut mass (g) per individual tree, the Cerro Montoso population again exhibited a stronger relationship than Goat Draw. In both populations, young trees had lower values than older trees (Fig. 7). Variation in curves for mast probability and mast amount was driven by individual probability of masting and average mast amounts, as with the juniper and oak results. Finally, in comparing the contribution to masting events of population proportions of masting trees with individual tree production increases, only individual tree productivity in the Cerro Montoso population emerged as a significant factor (Table 3).

Sonoran scrub oak.—Mast production in Sonoran scrub oak was most significantly positively correlated with current-year late-winter precipitation (February–April), and also exhibited positive correlations with spring, non-monsoon (fall–spring seasons), and full-year precipitation (Appendix S3: Table S6). Relative humidity (positive correlation) and vapor pressure deficit and

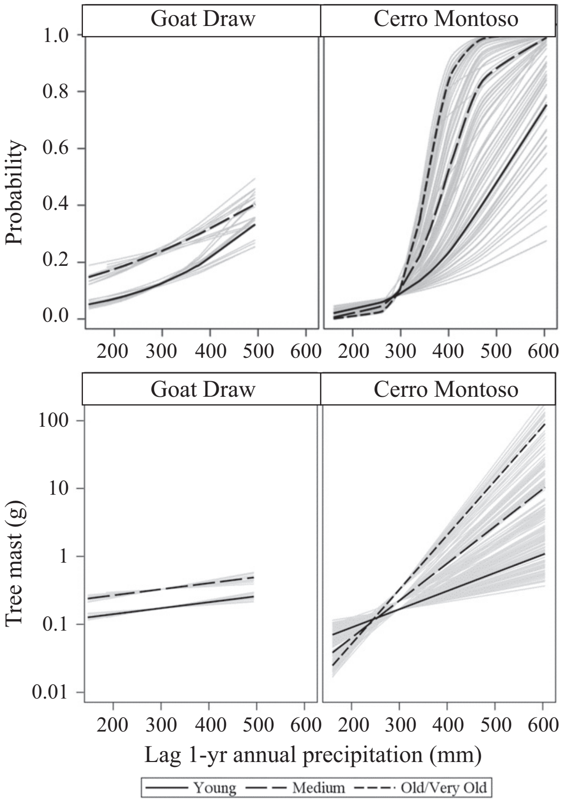

Fig. 7. Individual tree-level association between 1-yr lagged total annual precipitation (mm) and the probability (top) and mast production (bottom) among two-needle piñon pine trees (*Pinus edulis*) by study site. Black lines are averages by age class; gray lines are individual trees. See text for age class definitions. Sevilleta National Wildlife Refuge, New Mexico, 1997–2016.

air temperatures (negative correlations) in the current year also proved significantly associated with oak mast production. Oak mast production was not correlated with any current-year summer meteorological variables and was not significantly correlated with Julian date of last frost ($r_s = -0.08$, $P = 0.65$). Mean and maximum wind speeds showed no significant correlations with oak mast production during any time periods. All correlations with 1-yr and 2-yr lagged meteorological variables were non-significant (Appendix S3: Tables S6).

Population-level analyses of oak mast production relationships with late-winter precipitation produced significant positive associations both for the proportion of the population producing mast and for the average quantity of acorns produced per tree in the population (Fig. 8).

At the individual tree-level, oak trees exhibited highly significant patterns of increasing probability of mast production (logistic model) and total mast production (g/tree, linear model) in regressions with late-winter (February–April) precipitation (Fig. 9). As with one-seed juniper, the logistic regression fit both oak populations ($P < 0.001$), and both populations displayed similar relationships with increasing precipitation. Smaller age/size classes of oaks exhibited lower masting probabilities and lower mast production quantities when compared with larger individuals (Fig 9). Variation in curves for mast probability and mast amount were driven by individual probability of masting and average mast amounts as observed in the one-seed juniper results.

Comparisons of the Spearman correlation analyses across the population-level proportions of mast-producing trees and the individual-level acorn production per tree revealed that the site mast production correlation with late-winter precipitation was a combination of increasing proportions of the trees producing mast and an increase in acorn mass per tree (Table 3).

Effects of low temperatures during primordia formation.—Low temperatures during the previous fall period for one-seed juniper and Sonoran scrub oak, and 1-yr lagged fall period for piñon pine (Appendix S3: Table S7), during which time primordia were being formed, had a significant effect (negative relationship) on all tree species' mast production; these results indicated that colder fall temperatures resulted in greater numbers of berries and acorns 1 yr later, and pine nuts 2 yr later. To determine whether low temperatures were specific to particular subset time periods, further analyses by 2-week time intervals in August, September, and October found significant negative correlations for most of the periods tested; these findings were consistent with the Forcella (1981*a*) hypothesis that low fall temperatures lead to greater mast production in piñon pine, and expand the application of these results to include both one-seed juniper and Sonoran scrub oak.

Increased mast prevalence with cool fall temperatures may also be due to increased fall

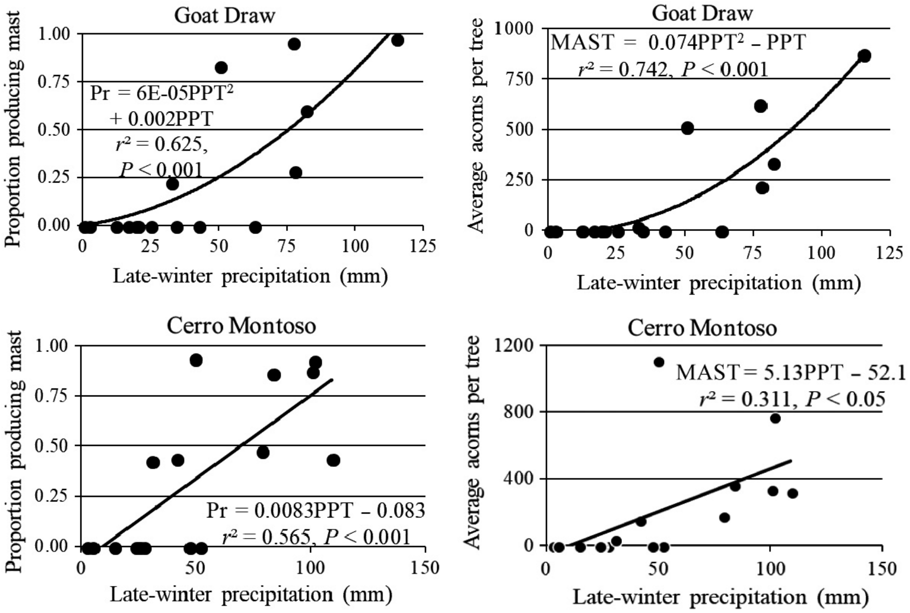

Fig. 8. Population-level association between late-winter precipitation (February–April, mm) and the population proportion (left) and population average numbers of acorns/tree (right) of mast-producing Sonoran scrub oak trees (*Quercus turbinella*) by study site; Sevilleta National Wildlife Refuge, New Mexico, 1997–2016.

precipitation as cooler air temperatures are associated with increased precipitation (e.g., October precipitation and air temperature $r_s = -0.49$, $P < 0.001$). We added lagged October precipitation to prevalence models for juniper, oak, and piñon pine to assess sensitivity to this factor and found that the significant association between prevalence with late-October maximum air temperature persisted ($P < 0.001$ for each species).

Evaluation of the ΔT *hypothesis.*—Kelly et al. (2013) proposed that masting species may detect and use inter-annual differences in temperatures (ΔT), rather than the absolute values of temperatures, as cues for mast production; this approach was expanded by Koenig et al. (2016) to include precipitation (ΔPPT). Our analyses produced 184 possible models incorporating both temperature and precipitation, and the various time periods examined by Kelly et al. (2013) and Koenig et al. (2016). ΔAIC_c values ≤2.0 identified equivalent models, and ΔAIC_c of <10.0 indicated models with some support (see Burnham and Anderson 2002).

For one-seed juniper, three selected models produced $\Delta AIC_c \leq 2.0$, and all included precipitation variables (current year and 1-yr lag) rather than temperature; no selected model included a ΔT or ΔPPT variable (Appendix S3: Table S8). We found six additional models with $\Delta AIC_c \leq 10.0$, and these models all contained current-year and 1-yr lagged precipitation variables, with none having ΔT or ΔPPT variables. A total of 10 non-selected models produced significant slopes using ΔT (six models, two with positive slopes and four with negative slopes) and ΔPPT (four models, all with positive slopes; Appendix S4: Table S1).

For two-needle piñon pine, of the 184 models analyzed, only two models had ΔAIC_c values <2.0, and both of these were based on full-year precipitation for 1-yr and 2-yr lags, not temperature (Appendix S3: Table S8). A total of 19 additional models exhibited ΔAIC_c values between 2.0 and 10.0 (none of these included ΔT variables, while six models included ΔPPT variables; Appendix S4: Table S2). Seven non-selected ΔT models produced significant slopes relating ΔT values with mast production, and all had significantly negative slopes; two non-selected models included ΔPPT variables, and both slopes were significantly negative (Appendix S4: Table S2).

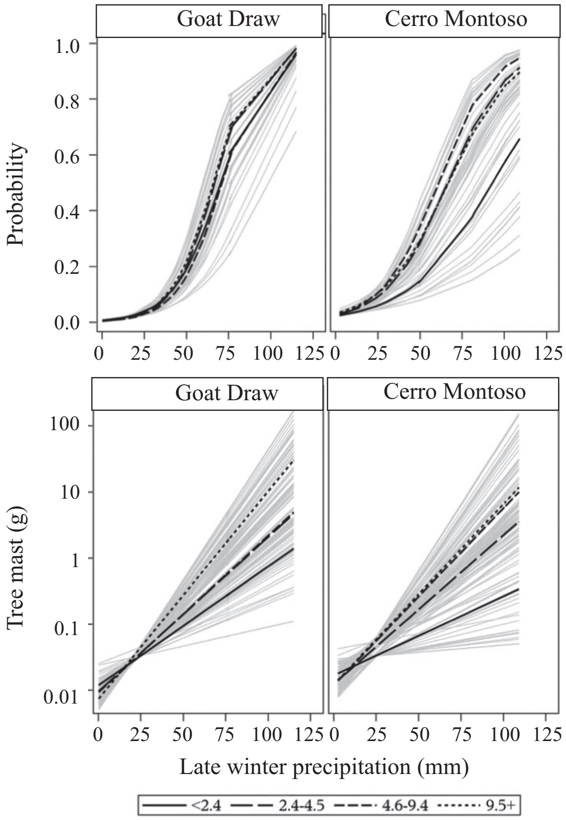

Fig. 9. Individual tree-level association between late-winter precipitation (February–April, mm) and the probability (top) and mast production (bottom) among Sonoran scrub oak trees (*Quercus turbinella*) by study site. Black lines are averages by size class; gray lines are individual trees. See text for size class definitions. Sevilleta National Wildlife Refuge, New Mexico, 1997–2016.

For Sonoran scrub oak, two models were selected with $\Delta AIC_c < 2.0$, and both of these included current-year February–April precipitation as the major variable (Appendix S3: Table S8). Two additional models with $\Delta AIC_c \leq 10.0$ also contained February–April precipitation as the primary variable; no ΔT or ΔPPT variables appeared in the top four models. A total of 48 non-selected models produced significant slopes relating mast production with weather variables, and of these, six included ΔT variables and all had negative slopes. Four non-selected ΔPPT models exhibited positive slopes. The other 38 non-selected models with significant slopes included 20 models with precipitation variables (all of which had positive slopes) and 18 models with temperature variables (of which 14 with current-year temperatures had negative slopes, and four of which used 1-yr lagged temperatures and had positive slopes; Appendix S4: Table S3).

Multivariate models of mast production

The meteorological variables that had the highest correlation coefficients and were not confounded by co-variance issues included (1) fall temperatures during the period of primordia formation, (2) precipitation (current year's late-winter [February–April] precipitation for juniper and oak, and the previous year's total precipitation for piñon pine), and (3) current year's mean summer temperatures.

The models for masting probability were developed using the logistic model having individual slopes and intercepts for each site (Appendix S3: Table S9). For all three tree species, the selected variables were significant model components for most sites, with overall discrimination >0.75 for all species. Time-series comparisons of model results with observed field data produced good correspondence for some of the juniper sites (Appendix S3: Fig. S4) and for oak (Appendix S3: Fig. S5) but proved less accurate for piñon pine (Appendix S3: Fig. S5).

For ecosystem-level mast production (kg/ha), we developed multivariable regression models at two levels: a complex model, using unique slopes and intercepts for individuals sites, and a reduced model, using common slopes for meteorological variables and separate intercepts for each site; the reduced model proved the most parsimonious using ΔAIC_c. For junipers using the full complex model, there was an overall negative association with previous fall temperatures during primordia formation, but slopes for individual sites were variable and no individual site slopes were significantly different from zero (details in Appendix S3: Table S10). Summer temperature also had an overall negative association with mast production, but only one site had a significant slope for this weather variable. Late-winter precipitation association with mast production was more consistent than temperature variables, with individual site slopes between 0.049 and 0.064, and five out of six slopes being statistically significant (Appendix S3: Table S10). We obtained reasonable fits of predicted model results with observed field data using these full complex models for each species (Appendix S3: Fig. S6).

Reducing the one-seed juniper model to a common slope for each meteorological variable and separate intercepts for sites was the most parsimonious (Table 4). The common slopes model had an $r^2 = 0.41$ compared to $r^2 = 0.49$ for the more complex model. Time-series comparisons of model outputs with observed field data produced reasonable correspondence at most one-seed juniper sites (Fig. 10). Leave-one-out cross-validation approach analyses (Hastie et al. 2001) showed that average model bias was less than ±0.1, MAE was less than 3.0 for all sites, and PRESS values ranged from 107 to 201 (Appendix S3: Fig. S7). Qualitatively, the model predicted less accurately during the latter part of the study after persistent drought, when years of zero mast production co-occurred more frequently than in earlier years of the study. Residuals from the common slope model were relatively symmetrical but were only marginally normally distributed (Kolmogorov-Smirnov $P = 0.065$), and inspection of residuals indicated there may have been a nonlinear trend in residuals in relation to late-winter precipitation. We fitted a model with quadratic effects for late-winter precipitation, and that model had a smaller AIC_c (528.16) and $r^2 = 0.45$ which had non-significant terms for fall temperature and for summer temperature. Removing non-significant terms for fall and summer temperature further reduced AIC_c to 526.49 with $r^2 = 0.43$. Residual errors for this model were satisfactory (Kolmogorov-Smirnov goodness-of-fit test, $P > 0.15$).

For piñon pine, late-summer/fall temperatures 2 yr earlier and the previous year's total precipitation displayed significant negative and positive slopes, respectively (Table 4); current summer temperature in the year when mast was measured had a negative slope but was not significantly associated with mast production. Dropping summer temperature from the full model improved AICc substantially. A reduced model with a common slope for lagged fall temperatures and for lagged annual precipitation had an AIC_c (265.9, $r^2 = 0.52$) similar to when fall

Table 4. Mast production (kg/ha) model by species estimated using multivariable regression with common slopes for meteorological variables and unique intercepts for sites; precipitation variable is one-year lagged 12-month total precipitation for piñon pine, and current-year late-winter precipitation for one-seed juniper and Sonoran scrub oak (mast production was log-transformed before analyses).

Species and sites	Intercept			Fall temperature (°C)			Precipitation (mm)			Summer temperature (°C)		
	Estimate	SE	*P*-value	Estimate	SE	*P*-value	Estimate	SE	*P*-value	Estimate	SE	*P*-value
One-seed juniper												
Site				−0.81	0.35	**0.021**	0.053	0.010	**<0.001**	−1.37	0.516	**0.008**
Field Station	47.2	16.0	**0.003**									
McKenzie Flats	44.9	15.7	**0.004**									
West Mesa	44.5	15.4	**0.004**									
Sierra Ladrones	44.8	15.3	**0.003**									
Goat Draw	43.2	15.0	**0.004**									
Cerro Montoso	41.3	14.3	**0.004**									
Two-needle piñon pine												
Site				−1.10	0.39	**0.005**	0.020	0.004	**<0.001**	−0.52	0.578	0.239
West Mesa	17.3	15.1	0.25									
Goat Draw	15.9	14.8	0.28									
Cerro Montoso	15.3	14.2	0.28									
Sonoran scrub oak												
Site				−0.15	0.21	0.48	0.044	0.006	**<0.001**	−0.04	0.325	0.120
Goat Draw	1.7	9.6	0.86									
Cerro Montoso	1.5	9.1	0.87									

Notes: SE, standard error. Significant *P*-values in boldface.

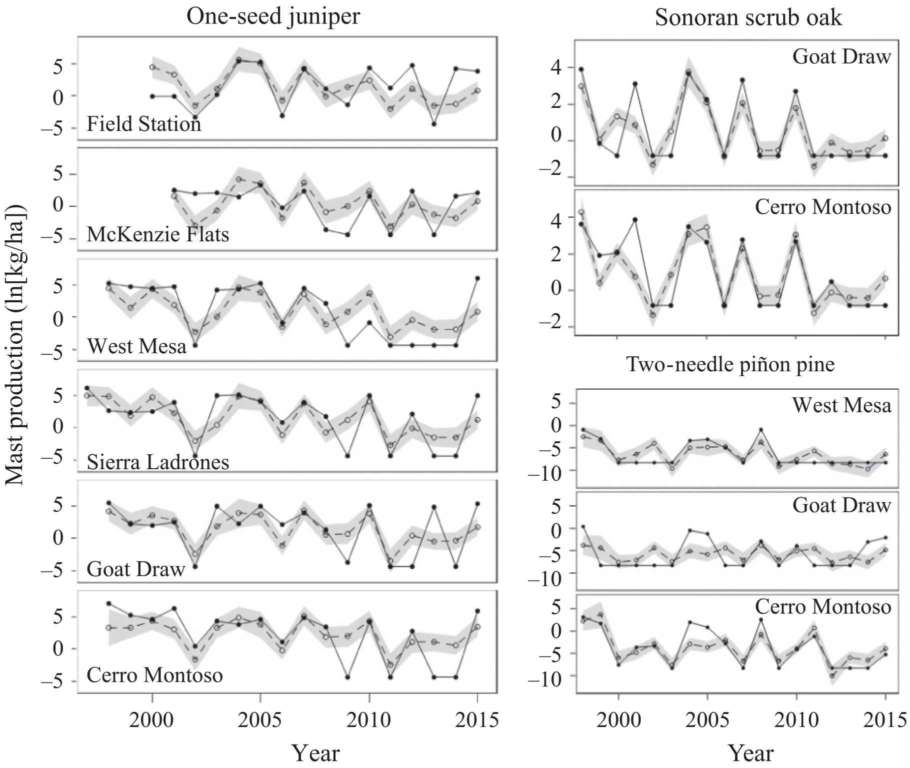

Fig. 10. Comparison of mast production by site estimated using the reduced multivariable regression model (with common slopes for meteorological variables and unique intercepts for sites) compared to observed data. Open circles (○) = predicted values; gray shading (■) = 95% modeled confidence interval; and black-filled circles (●) = observed field values.

slopes could vary by site (265.0, $r^2 = 0.57$) so these two models were nearly equivalent. Time-series comparisons of model results and field data indicated reasonable correspondence, although the model appeared to more accurately predict poor mast production years than the actual quantities of piñon nuts during mast years (Fig. 10). The common slopes model for lagged fall temperature and lagged annual precipitation produced $\Delta AIC_c = 0.9$, and the Kolmogorov-Smirnov test for normality of residuals did not reject for $\alpha = 0.05$ ($P = 0.056$). Examination of residuals showed more observations in the tails of the distribution. The LOOCV analyses for the piñon pine reduced model showed that average model bias was less than ±0.06, MAE was 3.03 or less for all sites, and PRESS values ranged from 76 to 231 (Appendix S3: Fig. S7); these model prediction statistics were similar to those of one-seed juniper.

In the multivariate regression model, Sonoran scrub oak mast production was not associated with previous fall temperature ($P = 0.48$) or with current year's summer temperature ($P = 0.12$; Table 4), and dropping both from the multivariable model produced the two lowest AICc values. The model with a common slope for the two sites had the smallest AIC_c ($\Delta AIC_c = 1.86$), and an $r^2 = 0.70$ compared to $r^2 = 0.72$ for the full model with separate slopes for previous fall temperature, late-winter precipitation, and summer temperature. Time-series comparisons of model results and field data produced very good correspondence (Fig. 10). Residuals from the reduced model were symmetrical and approximately normally distributed (Kolmogorov-Smirnov, $P > 0.15$). The LOOCV analyses for the Sonoran scrub oak reduced model showed that average model bias was very small (<±0.03), MAE was <1.0 for both sites, and PRESS values ranged from 19 to 21 (Appendix S3: Fig. S7); these oak model prediction statistics indicated that this model performed the best of the three study species' models in forecasting mast dynamics.

Resource switching, cycling, and depletion

Evidence of resource switching.—As shown in Table 1, linear regression autocorrelation values of annual mast production varied considerably for juniper, but only one site produced a significant negative autocorrelation, while a second site exhibited a positive significant autocorrelation; the other four sites produced non-significant slopes. Piñon pine exhibited a consistent negative autocorrelation for 2-yr lags, but these also were non-significant. Similarly, oak demonstrated non-significant negative autocorrelations for both 1-yr and 2-yr lags. Thus, autocorrelation results for all three tree species provide little indirect support for resource switching. Bimodal distributions of annual mast totals were observed in only a third of the sites for piñon pine and one-seed juniper, and in only one of two sites for oak (Table 1). Finally, CV values averaged 1.01 ± 0.45 (SE) for one-seed juniper, 2.15 ± 0.01 for piñon pine, and 1.65 ± 0.15 for oak. Kelly (1994) suggested that species with CV values >1.6 empirically had a high probability of exhibiting switching. Piñon pine and oak achieved these CV values, but one-seed juniper did not (Table 1); hence, these CV results indicate some indirect support for resource switching in piñon pine and oak.

Evidence of mast cycling.—The number of years that mast production was assessed was 15–19 for juniper and 18 for oak and piñon pine, leaving 14–18 yr for juniper and 16 yr of data for oak and piñon pine to assess the correlation between current- and previous-year mast production. While no significant correlations for any lag and site were detected for one-seed juniper or piñon pine, the site-level current-year mast production of Sonoran scrub oak trees at both Cerro Montoso (r_s = 0.57) and Goat Draw (r_s = 0.70) was both positively correlated with three-year lagged mast production (Table 5), providing indirect evidence consistent with periodic cycling of mast production for Sonoran scrub oak.

Table 5. Results of testing the cycling hypothesis (Calama et al. 2011) using Spearman correlation (r_s) for 1–4 yr lagged annual mast production (kg/ha) by species and site on the Sevilleta National Wildlife Refuge, New Mexico.

	Lag (yr)			
	1	2	3	4
Tree species site	r_s	r_s	r_s	r_s
One-seed juniper				
Field Station	−0.12	−0.12	−0.22	−0.12
McKenzie Flats	−0.28	0.47	−0.07	−0.03
West Mesa	0.28	0.30	0.15	−0.18
Sierra Ladrones	−0.10	−0.01	0.15	−0.18
Goat Draw	−0.45	0.14	0.06	−0.47†
Cerro Montoso	0.13	0.34	0.30	−0.01
Piñon pine				
West Mesa	0.27	−0.01	−0.13	−0.22
Goat Draw	0.03	−0.32	−0.28	−0.14
Cerro Montoso	−0.03	0.03	0.19	−0.00
Sonoran scrub oak				
Goat Draw	−0.11	−0.18	**0.70****	−0.34
Cerro Montoso	−0.10	−0.09	**0.57***	−0.19

Note: Significant *P*-values in boldface. †0.10 < $P \leq 0.05$; $^{*}0.05 < P \leq 0.01$; $^{**}P < 0.01$.

Evidence of resource depletion.—For one-seed juniper, relative mast ranks in the years after peak production were close to the expected value of 0.50 when averaged over the sites, 0.53 for year after peak, and 0.41 for the second year after a peak abundance. Three out of five sites were less than the median in the first year, and in the second year, two sites were less than the median (as was the value for all sites combined). The smallest values were observed at the two lowest, driest sites (Field Station, McKenzie Flats; Appendix S1: Table S1). Spearman correlations for all one-seed juniper sites and lags were between 0.06 and 0.81 (Table 6).

Piñon pine abundance ranks one year after the peak were at or above the median, but Cerro Montoso 2 yr after peak was less than the median, as was the value for both sites combined. Sonoran scrub oak mast rank at Cerro Montoso one year after peak mast was slightly below the median (as was the value for both sites combined), but rank values for two years after the peak were at the median (Table 6).

Pollen limitation

Seasonal pollen count totals ranged over nearly an order of magnitude in juniper (1896–13,377), from 550 to 2208 in pine, and 0 to 329 in

Table 6. Site mast productivity rank† for 1 and 2 yr after peak mast year (after Calama et al. 2011) by species and site on the Sevilleta National Wildlife Refuge, New Mexico.

Species and sites	No. years with mast	Total years	Mast-year rank 1 yr after peak	Mast-year rank 2 yr after peak
One-seed juniper				
Field Station	15	16	0.81	**0.06**
McKenzie Flats	12	15	**0.20**	0.73
Sierra Ladrones	14	19	**0.47**	0.37
Goat Draw	14	18	**0.44**	**0.28**
Cerro Montoso	14	18	0.72	0.61
All sites combined	69	86	0.53	**0.41**
Piñon pine				
Goat Draw	7	18	0.50	0.61
Cerro Montoso	12	18	0.72	**0.28**
All sites combined	19	36	0.61	**0.44**
Sonoran scrub oak				
Goat Draw	7	18	0.56	0.50
Cerro Montoso	9	18	**0.44**	0.50
All sites combined	16	36	**0.47**	0.50

† Mast rank is the ordinal ranking for the year divided by the number of years in the series. Values <0.50 (**boldface**) are less than the median, and evidence in support of the resource depletion hypothesis.

oak (Appendix S3: Fig. S8). Spearman's correlation analyses of pollen counts to mast production produced no significant correlations for any species at any site (Appendix S3: Table S11). In addition, we observed no significant relationships between annual pollen count totals and late-winter/early-spring precipitation (juniper r^2 = 0.02, pine r^2 = 0.06, oak r^2 = 0.16; df = 10, P > 0.05).

DISCUSSION

Mast species characterizations

The overall results of this study indicated that mast production in Southwestern piñon–juniper–oak woodlands is highly variable and episodic, though did not display strict masting dynamics given that some mast production occurred during most years (i.e., mast production was a generally continuous variable, linked with certain weather variables summarized in Table 7). Years characterized by exceptional drought often resulted in zero mast production of any tree species. Two-needle piñon pine and Sonoran scrub oak could be classified as "normal" masting species (Kelly 1994), based on their high inter-annual variability in mast production, with mast coefficients of variation ≥1.6 (an empirical indicator of likely resource switching), and indirect evidence for resource depletion; Sonoran scrub oak also exhibited indirect evidence for resource cycling. One-seed juniper fell under the putative mast species definition (Kelly 1994), exhibiting high inter-annual variability in mast production but smaller CV values, and varying degrees of indirect support for resource depletion (and no evidence of resource cycling).

In addition, high-mast production years were closely linked to environmental (weather) cues, and that the availability of limited resources (including water) appeared to have a potential effect on mast production via the mechanisms of resource switching, resource depletion, and (in oaks) resource cycling (Table 7). Mast production did not appear to be correlated with pollen abundance, indicating that pollen availability may be sufficient during all years suitable for tree flowering events. High-mast years in one-seed juniper and Sonoran scrub oak populations were characterized by an increase in the proportion of the tree population producing mast, combined with a concomitant increase in mast production by individual trees; piñon pine high-mast years were characterized by increased masting in individual trees. One-seed junipers and Sonoran scrub oaks were highly synchronous with each other, and both were significantly synchronous with piñon pine.

Finally, the demographic analyses indicated that mast years in one-seed junipers and Sonoran scrub oaks resulted from both an increase in the proportion of trees producing mast across the population and increased mast production by individual trees, while piñon pine mast years were driven mainly by increased mast in individual trees. We documented that larger/older individuals produced more mast per tree than smaller/younger (due to their larger size with more fruiting branches) and that very old trees' mast production did not differ from medium-aged trees, a finding consistent with other mast demographic analyses (Koenig et al. 2017, Minor and Kobe 2017 and references therein).

Table 7. Summary of hypotheses and drivers influencing mast production in New Mexico's piñon–juniper–oak woodlands.

Tree species and hypothesis	Factor	Time period	Reproductive process	Mast response
One-seed juniper				
Weather tracking	Air temperature	Fall of year $t-1$	Fruit primordia formation	Cooler temperatures increase mast in following year
	Precipitation	Late-winter–spring of year t	Pollination, fruit formation	Increased snow or rain increases mast
	Air temperature	Summer of year t	Fruit development	High summer temperatures reduce mast
Resource depletion	Some indirect evidence at lower-elevation sites	Growing season of year t	Fruit development	Trees need 1–2 yr to replenish resources for masting
Resource switching	No indirect evidence	Growing season of year t	Fruit development	No significant effect
Resource cycling	No indirect evidence	Growing season of year t	Berry development	No significant effect
Pollen limitation	No evidence	Spring of year t	Pollination	No significant effect
Piñon pine				
Weather tracking	Air temperature	Fall of year $t-2$	Fruit primordia formation	Cooler temperatures increase mast two years later
	Precipitation	Full year $t-1$	Pollination, green cone formation	Increased precipitation increases mast
	Air temperature	Summer of year t	Cone final development	High summer temperatures reduce mast
Resource depletion	Some indirect evidence	Growing season of year t and $t-1$	Cone and nut development	Trees need 1–2 yr to replenish resources for masting
Resource switching	Some indirect evidence (CV > 1.6)	Growing season of years t and $t-1$	Cone and nut development	Trees may switch resources from vegetative growth to cone development
Resource cycling	No indirect evidence	Growing season	Cone and nut development	No significant effect
Pollen limitation	No evidence	Spring of year $t-1$	Pollination	No significant effect
Sonoran scrub oak				
Weather tracking	Air temperature	Fall of year $t-1$	Fruit primordia formation	Cooler temperatures increase mast in following year
	Precipitation	Late-winter–spring of year t	Pollination, acorn formation	Increased snow or rain increases mast
Resource depletion	Some indirect evidence	Growing season of year t	Acorn development	Trees need 1 yr to replenish resources for masting
Resource switching	Some indirect evidence (CV > 1.6)	Growing season of year t	Acorn development	Trees may switch resources from vegetative growth to acorn development
Resource cycling	Resource availability for reproduction	3-yr cycle	Resource allocation to acorns	Cycles of resource limitation increases mast every three years, contingent on weather
Pollen limitation	No evidence	Spring	Pollination	No significant effect

Overall, all three tree species in our study area exhibited varying degrees of masting behavior, lending support to Kelly and Sork's (2002) prediction that masting behavior should be common in ecosystems with low species diversity and productivity. While masting-related studies generally do not report the number of non-masting tree species present on study sites (Kelly and Sork 2002, Shibata et al. 2002, Schauber et al. 2002, Kelly et al. 2013), the percentage of masting species would certainly be <100%, whereas in our woodland sites, all species of trees (100%) displayed some level of mast behavior. Mast production dynamics related to site productivity have also been reported for Mediterranean oaks (Pérez-Ramos et al. 2014) and grasses (Tanentzap et al. 2012).

Meteorological variables

The results of our weather analyses provided further support to the hypothesis by Forcella (1981*a*) and Redmond et al. (2012) that mast production in piñon pine is associated with air temperatures during primordia differentiation in the summer/autumn two years prior to cone maturation (cooler temperatures result in greater mast production). Our study also expands this phenomenon to one-seed juniper and Sonoran scrub oak, as these two species also show the same relationship between total mast production and air temperatures one year prior, during the time of primordia differentiation for these species. Cooler air temperatures during this period possibly promote differentiation into floral primordia, whereas warmer temperatures increase vegetative primordia (sometimes through abscission of floral primordia (see review by Atkinson et al. 2013) or possibly via reversion of floral-to-vegetative primordia (see review by Tooke et al. 2005)). Other species also show increased reproductive primordia differentiation, bud induction, flowering and fruit production with cooler fall/winter temperatures prior to the mast growing season (e.g., orange trees, *Citrus sinensis* [Valiente and Albrigo 2004]; Satsuma mandarine, *Citrus unshiu* [Inoue 1989, Inoue and Kataoka 1992]; some cultivars of blackberry, *Rubus* [Takeda et al. 2002]).

Once the maximum numbers of floral primordia have been set during late summer and autumn, a variety of weather conditions act in sequence to either maintain the mast crop or decrementally reduce it. During our study, all three tree species' mast production showed significant positive correlations with moisture variables (precipitation and humidity) and negative correlations with temperature variables (air and soil temperatures), but the timing of these influences differed among species. One-seed juniper and Sonoran scrub oak responded with increased mast production to higher levels of precipitation during the non-monsoon period, and especially in late-winter (February–March) period, during the current year's mast cycle (Appendix S3: Tables S4 and S6).

Piñon pine mast production, in contrast, appeared relatively insensitive to the current year's precipitation; rather, piñon pine mast production was positively correlated with the previous years' (1-yr and 2-yr lagged) precipitation and negatively correlated with temperatures (Appendix S3: Table S5). The 2-yr lag was the period of piñon pine primordia formation, and the 1-yr lag corresponded to the first-year period of strobili development (green cones; Fig. 1).

Sonoran scrub oak acorn production did not appear to be influenced by summer temperatures, a result consistent with other studies; for example, Koenig et al. (2016) examined weather effects on mast production in 15 species of oaks and found only one species (*Q. ellipsoidalis*) with a significant effect of summer temperature. In contrast, one-seed juniper's mast production was negatively influenced by the current summer's temperatures, indicating that summer heat levels were limiting to the final phases of berry development (Fig. 1). While the mechanism for this is unknown, Gruwez et al. (2013, 2016) found in the common juniper (*J. communis*) in Europe that warm temperatures disrupted pollen tube growth, female gametophyte development, and fertilization, resulting in failed embryo development.

In piñon pine, high spring and summer temperatures during the year of cone maturation acted to decrease cone development (Appendix S3: Table S5); high growing season temperatures are known to reduce vegetative growth in piñon pine (Newberry 2010), and Williams and Ehleringer (2000) found that piñon pine root activity is sensitive to higher soil temperatures, resulting in decreased uptake of summer precipitation in shallow surface soil layers.

Direct lethal effects of summer temperatures on plants can occur if leaf temperatures reach 42°–45°C (Alexandrov 1964), but arid-land species have numerous adaptations to maintain leaf and stem temperatures within 2°–3°C of ambient air temperature (Gates et al. 1968, Smith et al. 1997). However, if temperatures within juniper berries or piñon pine cones in direct sunlight reach critical levels, then such conditions could lead to water imbalances, thermal denaturing of enzymes, and loss of metabolic processes, resulting in eventual desiccation of the mast. Such a scenario would be manifest in reduced numbers of mature fruits and seeds, a phenomenon observed in other annual and perennial plants (Hatfield and Prueger 2015).

The lack of correlation between mast production and current year's summer precipitation in any of the three study species is likely associated with the trees' root structure and from which soil layers they procure their water. Piñon pine, juniper, and oak have extensive roots in both shallow and deep soil regions. Previous research has shown that piñon pine can opportunistically use shallow soil water from summer monsoons for photosynthesis and growth (Lajtha and Getz 1993, Breshears et al. 1997, West et al. 2007*a*, *b*, Shim et al. 2011), but generally uses deeper soil water in summer, thereby buffering the tree against summer drought periods and making its mast production independent of summer precipitation. Like many desert shrubs, piñon pine (as well as junipers and oaks) also may benefit from the soil moisture dynamics of hydraulic lift (Richards and Caldwell 1987) during which the trees' taproots transport deep soil water to recharge the tree's water balance at night, with some of the water leaking out of the shallow roots to recharge the shallow soil water content; this shallow water is then available for reabsorption by the shallow roots the following day.

Junipers and oaks are even less dependent on summer rainfall, tapping deep soil water throughout the summer, but capable of summer rainfall uptake if soil moisture exceeds certain thresholds (Lajtha and Getz 1993, Breshears et al. 1997, Leffler et al. 2002, West et al. 2007*a*, *b*, Eggemeyer et al. 2009, Shim et al. 2011). For example, in southern Utah, Flanagan et al. (1992) distinguished seasonal water use by piñon pine and Utah juniper (*J. osteosperma*) using ratios of deuterium to hydrogen in stem xylem water. They reported that in summer, both tree species used a mix of summer monsoon precipitation and groundwater (recharged from winter precipitation). In addition, Williams and Ehleringer (2000) used hydrogen and oxygen stable isotope ratios to partition the sources of xylem water in piñon pine, Utah juniper, and Gambel oak (*Quercus gambelii*, another member of the white oak group with *Quercus turbinella*) across a precipitation gradient in Utah and Arizona; they found that during summer, piñon pine and Utah juniper used a mix of summer monsoon precipitation and subsurface soil water, whereas Gambel oak consistently used deep soil water, despite abundant shallow monsoonal moisture. Taneda and Sperry (2008) also reported nearly exclusive groundwater use by Gambel oak in summer. Finally, Linton et al. (1998) showed that Utah juniper was highly resistant to summer drought (more so than piñon pine), having greater resistance to stem xylem cavitation under summer drought stress.

Multivariate regression weather models of mast production

When the significant univariate weather factors were combined in multivariate regression models of mast production, some of the weather variables dropped out of the most parsimonious models for oak and piñon pine (Table 4, Fig. 10). Logistic models produced reasonable fits to observed mast dynamics both in proportions of the tree populations producing mast and in total quantities of mast produced. Based on fall temperatures (during primordia differentiation) and precipitation, the models for oak and piñon pine can be used to generally predict in springtime the size of the mast crop later in the year; juniper (and to some extent, piñon pine) mast crops would still be susceptible to summer heat and desiccation, so the predictive capability of the logistic model is more limited in the length of lead time prior to mast maturation.

Weather factors have been repeatedly associated with mast events in a wide array of species, although the magnitude, list of weather variables, and direction (positive or negative) of the correlations are often very different among species and locations. Koenig et al. (2016) reviewed studies on 15 species of oak (*Quercus*) across two continents and concluded that "weather plays an important mechanistic role in driving masting behavior in conjunction with resource dynamics." Our results support and concur with this conclusion, given that all three tree species in our study exhibited highly significant mast production relationships with weather variables while showing some indirect evidence for resource depletion and, in oaks, resource cycling.

Studies on masting in other tree genera and other ecosystems lend support to the important role of weather cues. Layne and Abrahamson (2004) examined scrub hickory (*Carya floridana*) mast production in Florida in regard to weather variables (winter rainfall and minimum spring temperatures) and found 25–50% of the variance in nut production could be attributed to weather (compared to 41–72% of mast variance found in our study). Many conifer species display weather-correlated mast behavior. Krebs et al. (2012) found that 2-yr lagged May precipitation and 1- and 2-yr lagged summer temperatures explained 54% of variability in white spruce (*Picea glauca*) seed crops in the Yukon Territory. Keyes and González (2015) observed that seed production in Ponderosa pine (*P. ponderosa*) in Montana was positively correlated with spring temperatures and growing season precipitation. Cain and Shelton (2000) studied seed production for 24 yr in loblolly pine (*Pinus taeda*) and shortleaf pine (*P. echinata*) in the southern United States and found significant positive correlations with summer precipitation 2 yr prior to seed dispersal, and negative correlations with August temperatures 2 yr before seed dispersal; these findings supported similar results reported by Wenger (1957) and Lamb et al. (1973). The negative August correlations corresponded to the period of strobili primordia differentiation, a result also observed in our study. In another conifer tree study, Buechling et al. (2016) compared weather data and Engelmann spruce (*Picea engelmannii*) seed production over 40 yr and noted increased seed production in years with decreased snowpack and associated longer, warmer growing seasons. Pérez-Ramos et al. (2010, 2015) observed precipitation patterns in spring and summer drove mast production in several species of Mediterranean oaks. Finally, García et al. (2000, 2002) found weather patterns and seed production and predation were related in Mediterranean populations of *J. communis*.

Finally, in testing the differential cue hypothesis of Kelly et al. (2013), we found no support for this approach, in that none of the selected models included ΔT or ΔPPT variables (Appendix S3: Table S8). Koenig et al. (2016) found that the absolute values of weather variables (temperature and precipitation) on oak mast production proved somewhat better than differential cue variables (ΔT with different time lags). However, the striking difference between our results and the correlations by Kelly et al. (2013) is that across their more mesic study areas, the correlations between temperature and mast production were positive; our correlations were all negative. This difference illustrates the shift in the role of limiting resources along a moisture–temperature gradient of ecosystems; in hot arid and semi-arid ecosystems, water is the prime limiting resource, and higher temperatures with lower moisture levels lead to water imbalances, reduced photosynthesis, leaf abscission, and stem cavitation (Smith et al. 1997). As mast production in semi-arid woodlands relies on sufficient water to maintain photosynthetic production, the negative correlation with increasing temperatures would be expected. In ecosystems with more moisture and cooler temperatures, mast production would be positively influenced by warmer temperature levels and better growing conditions. Frequent drought and high-heat conditions in hot semi-arid woodland ecosystems appear to curtail tree reproduction in many years, amplifying the patterns of mast behavior by increasing the number of years with low or zero mast production; this phenomenon has been observed in other masting species (Espelta et al. 2008, Bogdziewicz et al. 2017*c*, 2018).

Resource depletion, switching, and cycling

In addition to the strong relationships we observed with weather patterns, all three tree species on our study area also exhibited some indirect evidence for resource depletion, while the oaks displayed indirect evidence of resource cycling; large CV values >1.6 in piñon pine and Sonoran scrub oak also indicate an empirical potential for resource switching (Kelly 1994). Our multivariable models based on weather tracking yielded r^2 values between 0.41 and 0.72, depending on tree species; some of the remaining unexplained variability likely could be attributed to resource limitation phenomena. These results are consistent with many studies indicating some level of resource limitation in masting species. Recent reviews (Crone and Rapp 2014, Han and Kabeya 2017) analyzed resource depletion across many species and found several limiting variables (e.g., nutrients, structural carbohydrates) in some species, but not in others. These studies described the relative roles (important to insignificant) of plant nutrient availability and reserves for masting species, particularly phosphorus (Sala et al. 2012, Ichie and Nakagawa 2013), nitrogen (Montesinos et al. 2012, Sala et al. 2012, Ichie and Nakagawa 2013, Müller-Haubold et al. 2015, Bogdziewicz et al. 2017*a*), and carbon (Alla et al. 2012, Miyazaki 2013, Hoch et al. 2013, Cheng and Palmer 2015, Müller-Haubold et al. 2015). Recently, Keyes and González (2015) found evidence for resource depletion in Ponderosa pine (*P. ponderosa*) in Montana over 10 yr of seedfall data, and Funk et al. (2016) observed in Minnesota that bur oak, *Q. macrocarpa* (a masting species), needed a year to recover from a prescribed burn before producing acorns, whereas pin oak, *Q. ellipsoidalis* (a non-masting species), produced acorns the first year after the fire. Funk et al. (2016) concluded that this supported the stored resource hypothesis for mast species.

In our study, both Sonoran scrub oak and piñon pine displayed negative (though non-significant) sequential-year autocorrelation slopes (Table 1), an indirect indication of potential resource switching. A number of studies have directly addressed associations between vegetative growth and mast production (resource switching) in oaks. For example, Martín et al. (2015) found in *Quercus ilex* "negative correlations between acorn production and annual and late summer–autumn stem growth during masting years." Camarero et al. (2010) reported evidence from remotely sensed landscape NDVI values that holly oak (*Quercus ilex*) mast years in Spain are preceded by maximum tree foliage cover, indicating that vegetative resources are increased prior to mast production. Hirayama et al. (2008, 2012) measured both acorn production and leaf growth in three species of Japanese oaks (*Quercus acuta*, *Q. salicina*, and *Q. sessilifolia*, all members of the subgenus *Cyclobalanopsis* with two-year reproductive cycles) and found that years with increases in vegetative growth alternated with years of acorn production, supporting the resource switching hypothesis. Monks and Kelly (2006) observed decreased tree ring growth in New Zealand beech (*Nothofagus truncata*) during mast years, indicating resource switching; similarly, recent work by Lucas-Borja and Vacchiano (2018) showed that mast production and tree ring width were inversely correlated in Spanish black pine (*Pinus nigra*).

Resource cycling patterns were originally proposed by Sork et al. (1993) in California oak species; they identified 3-yr and 4-yr cycles in species of white oaks and red oaks, respectively. Our oak species, the Sonoran scrub oak, is in the white oak group and exhibited a 3-yr cycle during our study, consistent with Sork et al.'s (1993) findings. We did not, however, detect evidence of resource cycling in our juniper and pine species, a result that also is consistent with previous observations; Calama et al. (2011) found no evidence of cycling in stone pine (*P. pinea*) during their 13-yr study period in northern Spain.

Pollen limitation

Variability of pollen as a driver of masting and synchrony has been proposed in numerous studies, with mixed results in terms of importance in regulating mast production (Norton and Kelly 1988, Kelly et al. 2001, Koenig and Ashley 2003, Satake 2004, García-Mozo et al. 2007, Lyles et al. 2009, 2015, Mooney et al. 2011, Koenig et al. 2012, Moreira et al. 2014, Koenig et al. 2015, Lyles et al. 2015, Pearse et al. 2015, Pesendorfer et al. 2016, Venner et al. 2016, Bogdziewicz et al. 2017*b*, Bykova et al. 2018). Our results show no correlation between general atmospheric pollen deposition and mast production. Comparable negative results were reported by Fernández-Martínez et al. (2012), who observed no relationship between pollen production and inter-annual acorn production in Spanish oaks (*Q. ilex* and *Q. pubescens*), and also as in our study, that moisture variables (spring water deficit) were associated with annual variation in mast production (Fernández-Martínez et al. 2015). Similarly, Moreira et al. (2014) monitored 217 Ponderosa pine (*P. ponderosa*) in Colorado for 20 yr and found that the relative investment to male and female reproduction did not shift between non-mast and mast years, although pollination efficiency was enhanced during mast years.

We caution, however, that daily atmospheric pollen deposition as measured in our study at some distance from our study sites, and in a suburban setting, is not the ideal data set with which to compare wildland mast production. In our case, the pollen monitoring site (the northeast heights of Albuquerque, NM) was ~80 km from the sites with mast measurements, and pollen taxa were identified only to family level. However, such pollen records should reasonably be expected to segregate high pollen production years from low years at the landscape level, and yet we observed no correlation at all between pollen counts and mast production (with r^2 values near zero; Appendix S3: Table S11); this result leads us to minimize the importance of pollen limitation for our study species. Conversely, Koenig and Ashley (2003) emphasized the role of inter-tree distance and size of neighborhood tree populations in pollination (pollination success increases over short distances with more nearby conspecifics), so our coarse-scale correlations may have masked the importance of localized pollen dynamics. Additional work on this topic of pollen limitation in piñon–juniper–oak woodlands is clearly needed.

Implications of masting in Southwestern woodlands

In terms of ecological implications of masting on the structure and functioning of the piñon–juniper–oak woodland ecosystem, the occurrences of mast years are consistent with the definition of a resource pulses, that is, "episodes of increased resource availability in space and time that combine low frequency (rarity), large magnitude (intensity), and short duration (brevity)" (Yang et al. 2008:621). Resource pulses in Southwestern woodlands can produce both short-term and longer-term impacts on resource–consumer interactions, leading to dramatic dynamics in ecosystem structure. In the case of masting behavior, pulses of fruits and seeds can lead to episodic recruitment of tree cohorts into woodlands, ultimately structuring tree stand demographics for decades or centuries (Betancourt et al. 1993). Mast events contribute to pulsed litter and nutrient additions to woodland soils, particularly for nitrogen and phosphorus (e.g., California oak woodlands; Callaway and Nadkarni 1991, Caritat et al. 2006). In addition, mast-consuming wildlife species are common; for example, Hope and Parmenter (2007) documented seven species of rodents feeding on mast on the Sevilleta NWR. Some wildlife species have exhibited large population increases and/or changes in foraging behavior following periods of abundant woodland mast production; examples include rodents (Christensen and Whitham 1993), bears (Costello et al. 2003), birds (Bailey 1928, Ligon 1961, 1978, Christensen et al. 1991, Christensen and Whitham 1993, van Ommeren and Whitham 2002), and insects (Forcella 1978, 1980, Christensen and Whitham 1993, Cobb et al. 1997). Mast dynamics have also been shown to be influenced by biotic feedback loops via insect herbivory (Forcella 1980, Mueller et al. 2005), potentially leading to changes in competitive interactions among other seed predators, such as birds and squirrels (Christensen and Whitham 1993).

Given these documented ecosystem effects, an understanding of driving variables and an ability to forecast mast years in Southwestern woodlands should prove valuable for a wide variety of economic, silvicultural, wildlife management, and ecosystem services applications, as has been demonstrated in this and other ecosystems (Jeffers 1994, Greene and Johnson 2004, Calama et al. 2008, Barger et al. 2009, Jacobs 2011, Greenberg and Parresol 2002, Greenberg et al. 2012, Rose et al. 2012). Our predictive models provide one approach for central New Mexico, although other regions of the Southwest would have to develop area-specific calibrations of parameters. Still, across the Southwestern woodlands, using the identified current weather variables of temperature and moisture compared to long-term averages should yield reasonable forecasting capability, although the models have the caveat that sudden extreme summer heat may cancel most or all mast production.

Additional work on modeling mast dynamics in the Southwest is still needed. We suggest that future work on masting in piñon–juniper–oak woodlands should expand to larger regional scales and incorporate new technologies to address landscape patterns (e.g., remote sensing imagery and unmanned aerial systems, UAS). Also, more detailed measures of biologically important environmental variables (e.g., direct measures of soil moisture and temperature in the root zones beneath canopies of individual trees) are needed, along with data on short-term dynamics in vegetative growth and plant resources to test directly for resource depletion, switching, and cycling. We believe these new approaches will enhance understanding of mast processes and provide additional details for further advances in mast predictive models.

ACKNOWLEDGMENTS

We thank the U.S. Fish and Wildlife Service, Sevilleta National Wildlife Refuge, for the use of their refuge lands for this study. Field logistical support was provided by the University of New Mexico's Sevilleta Research Field Station, and we thank the many staff and students who participated in the project over the 20 yr of the study; comments from two anonymous reviewers contributed to manuscript improvements. Funding for this research was provided by the National Science Foundation to the University of New Mexico's Sevilleta Long Term Ecological Research Program (NSF Grants DEB-9411976, DEB-0080529, DEB-0217774, DEB-0620482, DEB-1232294, DEB-1440478, DEB-1655499), the Ecology of Infectious Diseases Program (NSF/NIH EF-0326757), and the NSF EAGER Program (#1748133). This is publication #797 of the Sevilleta LTER Program. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

Abrahamson, W. G., and J. N. Layne. 2003. Long-term patterns of acorn production for five oak species in xeric Florida uplands. Ecology 84:2476–2492.

Alexandrov, V. 1964. Cytophysiological and cytoecological investigations of heat resistance of plant cells toward the action of high and low temperature. Quarterly Review of Biology 39:35–77.

Alla, A. Q., J. J. Camarero, M. Maestro-Martinez, and G. Monterrat-Marti. 2012. Acorn production is linked to secondary growth but not to declining carbohydrate concentrations in current-year shoots of two oak species. Trees – Structure and Function 26:841–850.

Atkinson, C. J., R. M. Brennan, and H. G. Jones. 2013. Declining chilling and its impact on temperate perennial crops. Environmental and Experimental Botany 91:48–62.

Bailey, F. M. 1928. Birds of New Mexico. Judd & Detweiler Inc., Washington, DC, USA.

Barger, N. N., H. D. Adams, C. Woodhouse, J. C. Neff, and G. P. Asner. 2009. Influence of livestock grazing and climate on pinyon pine (*Pinus edulis*) dynamics. Rangeland Ecology and Management 62:531–539.

Barger, R. L., and P. F. Ffolliott. 1972. Physical characteristics and utilization of major woodland tree species in Arizona. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA. Research Paper RM-83:1–80.

Barger, N. N., and C. Woodhouse. 2015. Piñon pine (*Pinus edulis* Engelm.) growth responses to climate and substrate in southern Utah, USA. Plant Ecology 216:913–923.

Benjamini, Y., and D. Yekutieli. 2001. The control of the false discovery date in multiple testing under dependency. Annals of Statistics 29:1165–1188.

Betancourt, J. L., E. A. Pierson, K. A. Rylander, J. A. Fairchild-Parks, and J. S. Dean. 1993. Influence of history and climate on New Mexico piñon-juniper woodlands. Pages 42–62 in E. F. Aldon and E. W. Shaw, editors. Managing piñon-juniper ecosystems for sustainability and social needs. General Technical Report RM-236. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Bogdziewicz, M., et al. 2017*b*. Masting in wind-pollinated trees: system-specific roles of weather and pollination dynamics in driving seed production. Ecology 98:2615–2625.

Bogdziewicz, M., E. E. Crone, M. A. Steele, and R. Zwolak. 2017*a*. Effects of nitrogen deposition on reproduction in a masting tree: Benefits of higher seed production are trumped by negative biotic interactions. Journal of Ecology 105:310–320.

Bogdziewicz, M., M. Fernández-Martínez, R. Bonal, J. Belmonte, and J. M. Espelta. 2017*c*. The Moran effect and environmental vetoes: Phenological synchrony and drought drive seed production in a Mediterranean oak. Proceedings of the Royal Society B 284: https://doi.org/10.1098/rspb.2017.1784

Bogdziewicz, M., M. A. Steele, S. Marino, and E. E. Crone. 2018. Correlated seed failure as an environmental veto to synchronize reproduction of masting plants. New Phytologist. https://doi.org/10.1111/nph.15108

Breshears, D. D., O. B. Myers, S. R. Johnson, C. W. Meyer, and S. N. Martens. 1997. Differential use of spatially heterogeneous soil moisture by two semiarid woody species: *Pinus edulis* and *Juniperus monosperma*. Journal of Ecology 85:289–299.

Buechling, A., P. H. Martin, C. D. Canham, W. D. Shepperd, and J. A. Battaglia. 2016. Climate drivers of seed production in *Picea engelmannii* and response to warming temperatures in the southern Rocky Mountains. Journal of Ecology 104:1051–1062.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York City, New York, USA.

Bykova, O., J.-M. Limousin, J.-M. Ourcival, and I. Chuine. 2018. Water deficit disrupts male gametophyte development in *Quercus ilex*. Plant Biology 20:450–455.

Cain, M. D., and M. G. Shelton. 2000. Revisiting the relationship between common weather variables and loblolly-shortleaf pine seed crops in natural stands. New Forests 19:187–204.

Calama, R., F. J. Gordo, S. Mutke, and G. Montero. 2008. An empirical ecological-type model for predicting stone pine (*Pinus pinea* L.) cone production in the Northern Plateau (Spain). Forest Ecology and Management 255:660–673.

Calama, R., S. Mutke, J. Tomé, J. Gordo, G. Montero, and M. Tomé. 2011. Modelling spatial and temporal variability in a zero-inflated variable: the case of stone pine (*Pinus pinea* L.) cone production. Ecological Modelling 222:606–618.

Callaway, R. M., and N. M. Nadkarni. 1991. Seasonal patterns of nutrient deposition in a *Quercus douglasii* woodland in central California. Plant and Soil 137:209–222.

Camarero, J. J., J. Albuixech, R. López-Lozano, M. A. Casterad, and G. Montserrat-Martí. 2010. An increase in canopy cover leads to masting in *Quercus ilex*. Trees – Structure and Function 24:909–918.

Caritat, A., E. Garcia-Berthou, R. Lapena, and L. Vilar. 2006. Litter production in a *Quercus suber* forest of Montseny (NE Spain) and its relationship to meteorological conditions. Annals of Forest Science 63:791–800.

Chambers, J. C., S. B. Vander Wall, and E. W. Schupp. 1999. Seed and seedling ecology of pinyon and juniper species in pigmy woodlands of western North America. Botanical Review 65:1–38.

Cheng, K. J., and K. Palmer. 2015. Chaos in a model for masting. Discrete and Continuous Dynamical Systems 20:1917–1923.

Christensen, K. M., and T. G. Whitham. 1993. Impact of insect herbivores on competition between birds and mammals for pinyon pine seeds. Ecology 74:2270–2278.

Christensen, K. M., T. G. Whitham, and R. P. Balda. 1991. Discrimination among pinyon pine trees by Clark nutcrackers: effect of cone crop size and cone characters. Oecologia 86:402–407.

Cobb, N. S., S. Mopper, C. A. Gehring, M. Caouette, K. M. Christensen, and T. G. Whitham. 1997. Increased moth herbivory associated with environmental stress of pinyon pine at local and regional levels. Oecologia 109:389–397.

Costello, C. M., D. E. Jones, R. M. Inman, K. H. Inman, B. C. Thompson, and H. B. Quigley. 2003. Relationship of variable mast production to American black bear reproductive parameters in New Mexico. Ursus 14:1–16.

Crone, E. E., E. J. B. McIntire, and J. Brodie. 2011. What defines mast seeding? Spatio-temporal patterns of cone production by whitebark pine. Journal of Ecology 99:438–444.

Crone, E. E., and J. M. Rapp. 2014. Resource depletion, pollen coupling, and the ecology of mast seeding. Annals of the New York Academy of Sciences 1322:21–34.

Eggemeyer, K. D., T. Awada, F. E. Harvey, D. A. Wedin, X. Zhou, and C. W. Zanner. 2009. Seasonal changes in depth of water uptake for encroaching trees *Juniperus virginiana* and *Pinus ponderosa* and two dominant C_4 grasses in a semiarid grassland. Tree Physiology 29:157–169.

Espelta, J. M., P. Cortes, R. Molowny-Horas, B. Sanchez- Humanes, and J. Retana. 2008. Masting mediated by summer drought reduces acorn predation in Mediterranean oak forests. Ecology 89: 805–817.

Fernández-Martínez, M., J. Belmonte, and J. M. Espelta. 2012. Masting in oaks: disentangling the effect of flowering phenology, airborne pollen load and drought. Acta Oecologia 43:51–59.

Fernández-Martínez, M., M. Garbulsky, J. Peñuelas, G. Peguero, and J. P. Espelta. 2015. Temporal trends in the enhanced vegetation index and spring weather predict seed production in Mediterranean oaks. Plant Ecology 216:1061–1072.

Fernandez-Martinez, M., S. Vicca, I. A. Janssens, J. M. Espelta, and J. Penuelas. 2017. The North Atlantic Oscillation synchronises fruit production in western European forests. Ecography 40:864–874.

Fitzmaurice, G. M., N. L. Laird, and J. H. Ware. 2004. Applied longitudinal analysis. John Wiley & Sons, New York, New York, USA.

Flanagan, L. B., J. R. Ehleringer, and J. D. Marshall. 1992. Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon-juniper woodland. Plant Cell and Environment 15:831–836.

Floyd, M. E. 1983. Dioecy in five *Pinus edulis* populations in the southwestern United States. American Midland Naturalist 110:405–411.

Forcella, F. 1978. Irregularity of pinyon cone production and its relation to pinyon cone moth predation. Madroño 25:170–172.

Forcella, F. 1980. Cone predation by pinyon cone beetle (*Conopthorus edulis,* Scolytidae): dependence on frequency and magnitude of cone production. American Naturalist 116:594–598.

Forcella, F. 1981*a*. Ovulate cone production in pinyon – negative exponential relationship with late summer temperature. Ecology 62:488–491.

Forcella, F. 1981*b*. Estimating pinyon cone production in New Mexico and western Oklahoma. Journal of Wildlife Management 45:553–556.

Funk, K. A., W. D. Koenig, and J. M. H. Knops. 2016. Fire effects on acorn production are consistent with the stored resource hypothesis for masting behavior. Canadian Journal of Forest Research 46:20–24.

García, D., R. Zamora, J. M. Gomez, and J. A. Hodar. 2002. Annual variability in reproduction of *Juniperus communis* L. in a Mediterranean mountain: relationship to seed predation and weather. Ecoscience 9:251–255.

García, D., R. Zamora, J. M. Gomez, P. Jordano, and J. A. Hodar. 2000. Geographical variation in seed production, predation and abortion in *Juniperus communis* throughout its range in Europe. Journal of Ecology 88:436–446.

García-Mozo, H., M. T. Gómez-Casero, E. Domínguez, and C. Galán. 2007. Influence of pollen emission and weather-related factors on variations in holm-oak (*Quercus ilex* subsp. *ballota*) acorn production. Environmental and Experimental Botany 61:35–40.

Gates, D. M., R. Alderfer, and E. Taylor. 1968. Leaf temperatures of desert plants. Science 159:994–995.

Greenberg, C. H., D. J. Levey, C. Kwit, J. P. McCarty, S. F. Pearson, S. Sargent, and J. Kilgo. 2012. Long-term patterns of fruit production in five forest types of the South Carolina Upper Coastal Plain. Journal of Wildlife Management 76:1036–1046.

Greenberg, C. H., and B. R. Parresol. 2002. Dynamics of acorn production by five species of southern Appalachian oaks. Pages 149–172 in W. J. McShea and W. M. Healy, editors. Oak forest ecosystems. Ecology and management for wildlife. Johns Hopkins University Press, Baltimore, Maryland, USA.

Greene, D. F., and E. A. Johnson. 2004. Modelling the temporal variation in the seed production of North American trees. Canadian Journal of Forest Research 34:65–75.

Gruwez, R., P. De Frenne, K. Vander Mijnsbrugge, P. Vangansbeke, and K. Verheyen. 2016. Increased temperatures negatively affect *Juniperus communis* seeds: evidence from transplant experiments along a latitudinal gradient. Plant Biology 18:417–422.

Gruwez, R., O. Leroux, P. De Frenne, W. Tack, R. Viane, and K. Verheyen. 2013. Critical phases in the seed development of common juniper (*Juniperus communis*). Plant Biology 15:210–219.

Han, Q., and D. Kabeya. 2017. Recent developments in understanding mast seeding in relation to dynamics of carbon and nitrogen resources in temperate trees. Ecological Research 32:771–778.

Hastie, T., R. Tibshirani, and J. Friedman. 2001. The elements of statistical learning. Springer Series in Statistics. Springer, New York, New York, USA.

Hatfield, J. L., and J. H. Prueger. 2015. Temperature extremes: effect on plant growth and development. Weather and Climate Extremes 10:4–10.

Hirayama, D., T. Fujii, S. Nanami, A. Itoh, and T. Yamakura. 2012. Two-year cycles of synchronous acorn and leaf production in biennial-fruiting evergreen oaks of subgenus *Cyclobalanopsis* (*Quercus*, Fagaceae). Ecological Research 27:1059–1068.

Hirayama, D., S. Nanami, A. Itoh, and T. Yamakura. 2008. Individual resource allocation to vegetative growth and reproduction in subgenus *Cyclobalanopsis* (*Quercus*, Fagaceae) trees. Ecological Research 23:451–458.

Hoch, G., R. T. W. Siegwolf, S. G. Keel, C. Körner, and Q. Han. 2013. Fruit production in three masting tree species does not rely on stored carbon reserves. Oecologia 171:653–662.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics 6:65–70.

Hope, A., and R. R. Parmenter. 2007. The diets of rodents inhabiting the arid and semi-arid ecosystems of central New Mexico. Special Publications of the Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico, USA 9:1–75.

Ichie, T., and M. Nakagawa. 2013. Dynamics of mineral nutrient storage for mast reproduction in the tropical emergent tree *Dryobalanops aromatica*. Ecological Research 28:151–158.

Inoue, H. 1989. Effects of temperature on bud dormancy and flower bud differentiation in Satsuma mandarin. Journal of the Japanese Society for Horticultural Science 58:919–926.

Inoue, H., and K. Kataoka. 1992. Effects of nutrition and temperature on flower bud differentiation of Satsuma mandarin. Journal of the Japanese Society for Horticultural Science 60:771–776.

Jacobs, B. F. 2011. Spatial patterns and ecological drivers of historic piñon-juniper woodland expansion in the American Southwest. Ecography 34:1085–1095.

Jansen, P. A., F. Bongers, and L. Hemerik. 2004. Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. Ecological Monographs 74:569–589.

Janzen, D. H. 1971. Seed predation by animals. Annual Review of Ecology and Systematics 2:465–492.

Jeffers, R. M. 1994. Pinyon seed production, collection, and storage. Pages 191–197 in D. W. Shaw, E. F. Aldon and C. LoSapio, technical coordinators. Desired Future Conditions for Pinyon-Juniper Ecosystems (Proc.). USDA General Technical Report RM-258. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Ogden, Utah, USA.

Kelly, D. 1994. The evolutionary ecology of mast seeding. Trends in Ecology and Evolution 9:465–470.

Kelly, D., et al. 2013. Of mast and mean: Differential-temperature cue makes mast seeding insensitive to climate change. Ecology Letters 16:90–98.

Kelly, D., D. E. Hart, and R. B. Allen. 2001. Evaluating the wind pollination benefits of mast seeding. Ecology 82:117–126.

Kelly, D., and V. L. Sork. 2002. Mast seeding in perennial plants: Why, how, where? Annual Review of Ecology and Systematics 33:427–447.

Keyes, C. R., and R. M. González. 2015. Climate-influenced ponderosa pine (*Pinus ponderosa*) seed masting trends in western Montana. USA. Forest Systems 24(1):e021.

Knapp, E. E., M. A. Goedde, and K. J. Rice. 2001. Pollen-limited reproduction in blue oak: implications for wind pollination in fragmented populations. Oecologia 128:48–55.

Koenig, W. D. 1999. Spatial autocorrelation of ecological phenomena. Trends in Ecology and Evolution 14:22–26.

Koenig, W. D. 2002. Global patterns of environmental synchrony and the Moran effect. Ecography 25:283–288.

Koenig, W. D., et al. 2016. Is the relationship between mast-seeding and weather in oaks related to their life-history or phylogeny? Ecology 97:2603–2615.

Koenig, W. D., and M. V. Ashley. 2003. Is pollen limited? The answer is blowin' in the wind. Trends in Ecology and Evolution 18:157–159.

Koenig, W. D., K. A. Funk, T. S. Kraft, W. J. Carmen, B. C. Barringer, and J. M. H. Knops. 2012. Stabilizing selection for within-season flowering phenology confirms pollen limitation in a wind-pollinated tree. Journal of Ecology 100:758–763.

Koenig, W. D., and J. M. H. Knops. 2002. The behavioral ecology of masting in oaks. Pages 129–148 in W. J. McShea and W. M. Healy, editors. Oak forest ecosystems. Ecology and management for wildlife. Johns Hopkins University Press, Baltimore, Maryland, USA.

Koenig, W. D., J. M. H. Knops, W. J. Carmen, and I. S. Pearse. 2015. What drives masting? The phenological synchrony hypothesis. Ecology 96:184–192.

Koenig, W. D., J. M. H. Knops, W. J. Carmen, and M. B. Pesendorfer. 2017. Testing the terminal investment hypothesis in California oaks. American Naturalist 189:564–569.

Krebs, C. J., J. M. LaMontagne, A. J. Kenney, and S. Boutin. 2012. Climatic determinants of white spruce cone crops in the boreal forest of the southwestern Yukon. Botany-Botanique 90:113–119.

Laird, N. M., and J. H. Ware. 1982. Random-effects models for longitudinal data. Biometrics 38:963–974.

Lajtha, K., and J. Getz. 1993. Photosynthesis and water-use efficiency in pinyon-juniper communities along an elevation gradient in northern New Mexico. Oecologia 94:95–101.

Lamb, R. C., M. P. Waters, and E. V. Brender. 1973. Apparent influence of weather upon seed production of loblolly pine. USDA Forest Service, Southeastern Forest Experiment Station, Asheville, North Carolina, USA . Research Note SE-183:1-7.

LaMontagne, J. M., and S. Boutin. 2009. Quantitative methods for defining mast-seeding years across species and studies. Journal of Vegetation Science 20:745–753.

Lanner, R. M. 1981. The piñon pine. A natural and cultural history. University of Nevada Press, Reno, Nevada, USA.

Lawson, E. R. 1990. *Juniperus virginiana* L. Eastern redcedar. Pages 240–259 in R. M. Burns and B. H. Honkala, editors. Silvics of North America: 1. Conifers. Agriculture Handbook 654. USDA Forest Service, Washington, DC, USA.

Layne, J. N., and W. G. Abrahamson. 2004. Long-term trends in annual reproductive output of the scrub hickory: factors influencing variation in size of nut crop. American Journal of Botany 91:1378–1386.

Leffler, A. J., R. J. Ryel, L. Hipps, S. Ivans, and M. M. Caldwell. 2002. Carbon acquisition and water use in a northern Utah *Juniperus osteosperma* (Utah juniper) population. Tree Physiology 22:1221–1230.

Ligon, J. S. 1961. New Mexico birds and where to find them. University of New Mexico Press, Albuquerque, New Mexico, USA.

Ligon, J. D. 1978. Reproductive interdependence of Piñon Jays and piñon pines. Ecological Monographs 48:111–126.

Linton, M. J., J. S. Sperry, and D. G. Williams. 1998. Limits to water transport in *Juniperus osteosperma* and *Pinus edulis*: implications for drought tolerance and regulation of transpiration. Functional Ecology 12:906–911.

Little Jr, E. L.. 1941. Managing woodlands for pinyon nuts. Chronica Botanica 6:348–349.

Lucas-Borja, M. E., and G. Vacchiano. 2018. Interactions between climate, growth and seed production in Spanish black pine (*Pinus nigra* Arn. ssp *salzmannii*) forests in Cuenca Mountains (Spain). New Forests 49:399–414.

Lyles, D., T. S. Rosenstock, and A. Hastings. 2015. Plant reproduction and environmental noise: How do plants do it? Journal of Theoretical Biology 371:137–144.

Lyles, D., T. S. Rosenstock, A. Hastings, and P. H. Brown. 2009. The role of large environmental noise in masting: general model and example from pistachio trees. Journal of Theoretical Biology 259:701–713.

Martín, D., J. Vázquez-Piqué, F. S. Carevic, M. Fernández, and R. Alejano. 2015. Trade-off between stem growth and acorn production in holm oak. Trees 29:825–834.

Marzluff, J. M., and R. P. Balda. 1992. The pinyon jay. Behavioral ecology of a colonial and cooperative corvid. T & A D Poyser Ltd, London, UK.

Minor, D. M., and R. K. Kobe. 2017. Masting synchrony in northern hardwood forests: Super-producers govern population fruit production. Journal of Ecology 105:987–998.

Miyazaki, Y. 2013. Dynamics of internal carbon resources during masting behavior in trees. Ecological Research 28:143–150.

Monks, A., and D. Kelly. 2006. Testing the resource-matching hypothesis in the mast seeding tree *Nothofagus truncata* (Fagaceae). Austral Ecology 31:366–375.

Montesinos, D., P. García-Fayos, and M. Verdú. 2012. Masting uncoupling: Mast seeding does not follow all mast flowering episodes in dioecious juniper tree. Oikos 121:1725–1736.

Mooney, K. A., Y. B. Linhart, and M. A. Snyder. 2011. Masting in ponderosa pine: comparisons of pollen and seed over space and time. Oecologia 165:651–661.

Moreira, X., L. Abdala-Roberts, Y. B. Linhart, and K. A. Mooney. 2014. Masting promotes individual- and population-level reproduction by increasing pollination efficiency. Ecology 95:801–807.

Moreira, X., L. Abdala-Roberts, Y. B. Linhart, and K. A. Mooney. 2015. Effects of climate on reproductive investment in a masting species: assessment of climatic predictors and underlying mechanisms. Journal of Ecology 103:1317–1324.

Mueller, R. C., B. D. Wade, C. A. Gehring, and T. G. Whitham. 2005. Chronic herbivory negatively impacts cone and seed production, seed quality and seedling growth of susceptible pinyon pines. Oecologia 143:558–565.

Müller-Haubold, H., D. Hertel, and C. Leuschner. 2015. Climatic drivers of mast fruiting in European beech and resulting C and N allocation shifts. Ecosystems 18:1083–1100.

Newberry, T. L. 2010. Effect of climatic variability on δ^{13}C and tree-ring growth in piñon pine (*Pinus edulis*). Trees – Structure and Function 24:551–559.

Noble, D. L. 2004. *Juniperus scopulorum* Sarg. Rocky Mountain juniper. Pages 209–231 in R. M. Burns and B. H. Honkala, technical coordinators. Silvics of North America: 1. Conifers. Agriculture Handbook 654. USDA Forest Service, Washington, DC, USA.

Norton, D. A., and D. Kelly. 1988. Mast seeding over 33 years by *Dacrydium cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: the importance of economies of scale. Functional Ecology 2:399–408.

van Ommeren, R. J., and T. G. Whitham. 2002. Changes in interactions between juniper and mistletoe mediated by shared avian frugivores: parasitism to potential mutualism. Oecologia 130:281–288.

Pearse, I. S., W. D. Koenig, K. A. Funk, and M. B. Pesendorfer. 2015. Pollen limitation and flower abortion in a wind-pollinated masting tree. Ecology 96:587–593.

Pearse, I. S., W. K. Koenig, and D. Kelly. 2016. Mechanisms of mast seeding: resources, weather, cues, and selection. New Phytologist 212:546–562.

Pérez-Ramos, I. M., C. Aponte, L. V. García, C. M. Padilla-Díaz, and T. Marañón. 2014. Why is seed production so variable among individuals? A ten-year study with oaks reveals the importance of soil environment. PLoS ONE 9:e115371.

Pérez-Ramos, I. M., J. M. Ourcival, J. M. Limousin, and S. Rambal. 2010. Mast seeding under increasing drought: results from a long-term data set and from a rainfall exclusion experiment. Ecology 91: 3057–3068.

Pérez-Ramos, I. M., C. M. Padilla-Díaz, W. D. Koenig, and T. Marañón. 2015. Environmental drivers of mast-seeding in Mediterranean oak species: Does leaf habit matter? Journal of Ecology 103:691–700.

Pesendorfer, M. B., W. D. Koenig, I. S. Pearse, J. M. H. Knops, and K. A. Funk. 2016. Individual resource limitation combined with population-wide pollen availability drives masting in the valley oak (*Quercus lobata*). Journal of Ecology 104:637–645.

Rauscher, H. M., W. G. Hubbard, (eds) 2012. Forest Encyclopedia Network. Oak Reproduction Biology. http://www.forestencyclopedia.net/p/p2204/view

Redmond, M. D., F. Forcella, and N. N. Barger. 2012. Declines in pinyon pine cone production associated with regional warming. Ecosphere 3(12):120. https://doi.org/10.1890/ES12-00306.1

Richards, J. H., and M. M. Caldwell. 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. Oecologia 73:486–489.

Rose, A. K., C. H. Greenberg, and T. M. Fearer. 2012. Acorn production prediction models for five common oak species of the eastern United States. Journal of Wildlife Management 76:750–758.

Sala, A., K. Hopping, E. J. B. McIntire, S. Delzon, and E. E. Crone. 2012. Masting in whitebark pine (*Pinus albicaulis*) depletes stored nutrients. New Phytologist 196:189–199.

Satake, A. 2004. Modeling spatial dynamics of episodic and synchronous reproduction by plant populations: the effect of small-scale pollen coupling and large-scale climate. Population Ecology 46:119–128.

Schauber, E. M., D. Kelly, P. Turchin, C. Simon, W. G. Lee, R. B. Allen, I. J. Payton, P. R. Wilson, P. E. Cowan, and R. E. Brockie. 2002. Masting by eighteen New Zealand plant species: the role of temperature as a synchronizing cue. Ecology 83:1214–1225.

Shapiro, S. S., and M. B. Wilk. 1965. An analysis of variance test for normality (complete samples). Biometrika 52:591–611.

Shibata, M., H. Tanaka, S. Iida, S. Abe, T. Masaki, K. Niiyama, and T. Nakashizuka. 2002. Synchronized annual seed production by 16 principal tree species in a temperate deciduous forest, Japan. Ecology 83:1727–1742.

Shim, J. H., H. H. Powers, C. W. Meyer, W. T. Pockman, and N. McDowell. 2011. The role of interannual, seasonal, and synoptic climate on the carbon isotope ratio of ecosystem respiration at a semiarid woodland. Global Change Biology 17:2584–2600.

Silvertown, J. W. 1980. The evolutionary ecology of mast seeding in trees. Biological Journal of the Linnean Society 14:235–250.

Smith, S. D., R. K. Monson, and J. E. Anderson. 1997. Physiological ecology of North American desert plants. Springer-Verlag, New York City, New York, USA.

Sork, V. L., J. Bramble, and W. Sexton. 1993. Ecology of mast-fruiting in three species of North American deciduous oaks. Ecology 74:528–541.

Sork, V. L., F. W. Davis, P. E. Smouse, V. J. Apsit, R. J. Dyer, J. F. Fernandez-M, and B. Kuhn. 2002. Pollen movement in declining populations of California valley oak, *Quercus lobata*: Where have all the fathers gone? Molecular Ecology 11:1657–1668.

Takeda, F., B. C. Strik, D. Peacock, and J. R. Clark. 2002. Cultivar differences and the effect of winter temperature on flower bud development in blackberry. Journal of the American Society for Horticultural Science 127:495–501.

Taneda, H., and J. S. Sperry. 2008. A case-study of water transport in co-occurring ring-versus diffuse-porous trees: contrasts in water-status, conducting capacity, cavitation and vessel refilling. Tree Physiology 28:1641–1651.

Tanentzap, A. J., W. G. Lee, and D. A. Coomes. 2012. Soil nutrient supply modulates temperature-induction cues in mast-seeding grasses. Ecology 93:462–469.

Tooke, F., M. Ordidge, T. Chiurugwi, and N. Battey. 2005. Mechanisms and function of flower and inflorescence reversion. Journal of Experimental Botany 56:2587–2599.

Valiente, J. I., and L. G. Albrigo. 2004. Flower bud induction of sweet orange trees [*Citrus sinensis* (L.) Osbeck]: effect of low temperatures, crop load and bud age. Journal of the American Society of Horticultural Science 129:158–164.

Venner, S., et al. 2016. Fruiting strategies of perennial plants: a resource budget model to couple mast seeding to pollination efficiency and resource allocation strategies. American Naturalist 188:66–75.

Wenger, K. F. 1957. Annual variation in the seed crops of loblolly pine. Journal of Forestry 55:567–569.

West, N. E. 1988. Intermountain deserts, shrub steppes, and woodlands. Pages 209–230 in M. G. Barbour and W. D. Billings, editors. North American terrestrial vegetation. Cambridge University Press, Cambridge, Massachusetts, USA.

West, A. G., K. R. Hultine, K. G. Burtch, and J. R. Ehleringer. 2007*a*. Seasonal variations in moisture use in a piñon-juniper woodland. Oecologia 153:787–798.

West, A. G., K. R. Hultine, T. L. Jackson, and J. R. Ehleringer. 2007*b*. Differential summer water use by *Pinus edulis* and *Juniperus osteosperma* reflects contrasting hydraulic characteristics. Tree Physiology 27:1711–1720.

West, N. E., and J. A. Young. 2000. Intermountain valleys and lower mountain slopes. Shrub steppes, and woodlands. Pages 255–284 in M. G. Barbour and W. D. Billings, editors. North American terrestrial vegetation. Cambridge University Press, Cambridge, Massachusetts, USA.

Williams, D. G., and J. R. Ehleringer. 2000. Intra- and interspecific variation for summer precipitation use in pinyon-juniper woodlands. Ecological Monographs 70:517–537.

Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright. 2008. What can we learn from resource pulses? Ecology 89:621–634.

Zlotin, R. I., and R. R. Parmenter. 2008. Patterns of mast production in pinyon and juniper woodlands along a precipitation gradient in central New Mexico (Sevilleta National Wildlife Refuge). Journal of Arid Environments 72:1562–1572.

DATA AVAILABILITY

Data associated with this paper are available through the LTER Network: Data set on mast measurements: http://sev.lternet.edu/data/sev-204. Weather data: http://sev.lternet.edu/content/meteorology-data-sevilleta-national-wildlife-refuge-new-mexico-1988-present

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2360/full