ECOSPHERE

Declines in pinyon pine cone production associated with regional warming

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Abstract. Global climate change is expected to produce large shifts in vegetation distribution and has already increased tree mortality, altering forest structure. However, long-term shifts will be partly dependent on the ability of species to reproduce under a novel climate. Few studies have examined the impact of climate change on the reproductive output of long-lived 'masting' species, or species characterized by episodic reproductive events. Here, we show that seed cone production among pinyon pine (*Pinus edulis*), a masting species, declined by 40% from the 1974 decade (1969–1978) to the 2008 decade (2003–2012) in revisited stands throughout New Mexico and northwestern Oklahoma. Seed cone production was highly correlated with late summer temperatures at the time of cone initiation. Further, declines in seed cone production were greatest among populations that experienced the greatest increases in growing season temperatures, which were the populations located at the cooler, upper elevations. As growing season temperatures are predicted to increase across this region over the next century, these findings suggest seed cone production may be an increasingly important bottleneck for future pinyon pine regeneration, especially in areas with greater increases in temperature. Declines in seed cone production may not only affect pinyon pine population dynamics but also the various wildlife species that rely on pinyon pine seeds. Because pinyon pine has similar reproductive strategies as other semi-arid pine species, increasing temperature may negatively influence reproductive output of other conifers. Further investigation into the full geographic and taxonomic extent of these seed declines is warranted.

Key words: climate change; mast seeding; *Pinus edulis*; pinyon-juniper woodlands; regeneration; reproduction.

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INTRODUCTION

Altered precipitation regimes and increasing land surface temperatures associated with global climate change have resulted in significant shifts in vegetation distribution over the past several decades (Parmesan and Yohe 2003, Kelly and Goulden 2008, Chen et al. 2011), and these patterns are predicted to continue over the next century (Pearson et al. 2002). Regional warming has resulted in recent increases in tree mortality by increasing water deficits (van Mantgem and Stephenson 2007, van Mantgem et al. 2009, Allen et al. 2010), insect outbreaks (Raffa et al. 2008, Mitton and Ferrenberg 2012), and wildfires (Westerling et al. 2006), which have dramatically changed forest and woodland structure. Many trees that died in these regional mortality events established under climatic conditions that may be rare or may no longer exist. Thus, a clear need exists to better understand the key bottlenecks to forest and woodland regeneration given recent
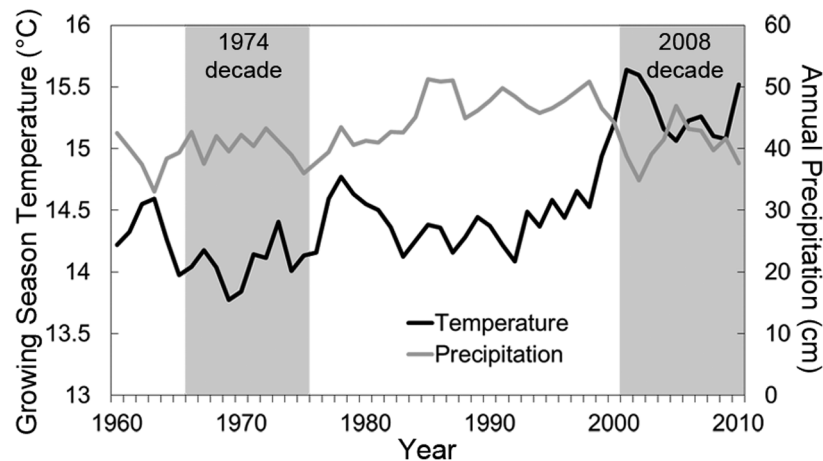
Fig. 1. Three-year moving averages of mean growing season (March–October) temperature (°C) (black line) and annual precipitation (cm) (grey line) from 1960 to 2010. Climate data are from the PRISM Climate Group and were averaged across all 9 sites. The two shaded bars indicate the climate at the year of seed cone initiation during the two sampling periods (1974 decade and 2008 decade).

large-scale mortality events and predicted changes in climate.

Research examining forest and woodland regeneration in response to recent changes in climate has focused mainly on germination, growth and survival (Kitzberger et al. 2000, Castro et al. 2004). Few studies, however, have examined the impacts of climate change on reproductive outputs, especially in mast seeding species (species with highly synchronous intermittent production of large seed crops) (but see Mutke et al. 2005 and Pérez-Ramos et al. 2010). This is likely due to the fact that annual reproductive outputs are highly variable across time and space, requiring sources of long-term data.

Numerous studies have shown that climatic fluctuations influence mast seeding (Norton and Kelly 1988, Sork 1993, Houle 1999, Piovesan and Adams 2001, Kelly and Sork 2002, Pérez-Ramos et al. 2010). Thus, it logically follows that reproductive outputs of mast seeding tree species may be affected strongly by changing climate. Indeed, in a long-term rainfall exclusion experiment, Pérez-Ramos and colleagues (2010) observed negative impacts of increased drought on acorn production in *Quercus ilex*. Although the mechanisms by which climate regulated masting events are not well understood, the leading hypotheses are that masting occurs during favorable climatic conditions due to higher available resources (e.g., resource-matching hypothesis) or that climate serves as an adaptive synchronizing cue (Sork 1993, Kelly 1994, Kelly and Sork 2002). Certain mast-seeding low elevation conifers, including pinyon pine (*Pinus edulis*), ponderosa pine (*Pinus ponderosa*), and stone pine (*Pinus pinea*), grow in water-limited environments and have higher reproductive output during cool and/or wet summers (Forcella 1981b, Mutke et al. 2005, Mooney et al. 2011). Thus, recent changes in precipitation and temperature patterns associated with global climate change may be adversely affecting reproductive output of these species.

In this study, we compare changes in pinyon pine reproductive output from the 1974 decade (1969–1978) to the 2008 decade (2003–2012)—a time period in which mean growing season (March–October) temperatures increased by c. 1.3°C while annual precipitation stayed relatively constant (increased by c. 3 cm) (Fig. 1, Table 1). Pinyon pine is a widely distributed and dominant tree of the southwestern U.S. and provides a range of ecosystem services to humans and critical habitat for a variety of wildlife species (Brown et al. 2001). Additionally, pinyon pine experienced large-scale mortality in vast areas across its range during the most recent multiyear (2002–2003) drought (Breshears et al. 2005,

Table 1. Temperature and precipitation across all sites in the 1974 decade (1974) and the 2008 decade (2008).

Site	Elev (m)	Growing season temp. (°C)		Annual precip. (cm)		Proportion of cool late summers	
		1974	2008	1974	2008	1974	2008
K2	1295	17.2	18.0	39.5	40.0	0.5	0.5
K1	1426	17.2	18.0	39.5	40.0	0.5	0.5
FB	1950	15.4	16.6	43.1	44.8	0.6	0.5
LV	2054	12.8	14.0	40.7	40.1	0.6	0.5
SF	2072	14.3	15.2	28.8	32.1	0.6	0.3
SP	2160	13.1	14.3	47.5	48.0	0.7	0.6
P	2170	11.9	13.8	34.9	41.2	0.6	0.3
MP	2179	12.1	13.8	47.6	60.1	0.5	0.4
R	2213	12.4	13.6	39.4	41.3	0.8	0.4
Overall		14.0	15.3	40.1	43.1	0.6 ± 0.0^{A}	0.4 ± 0.0^{B}

Notes: Growing season temperature (March–October) and annual precipitation were calculated as mean monthly temperature or precipitation during the year of cone initiation (2 years prior to mature cone formation) in both decades. The proportion of years with below average (1950–2010) late summer temperatures was calculated using the mean daily maximum summer temperatures during the two week time period most highly correlated with seed cone production at each site (see Fig. 3). Fort Bayard is missing two years of weekly climate data in the 2008 decade and therefore the proportion was calculated using only 8 years. Values in the lower row are means $\pm$ 1 SE across all sites, with different letters denoting significant differences between the two decades, with $\alpha = 0.05$.

Mueller et al. 2005). Following this widespread mortality event, there is a keen interest in examining potential bottlenecks to pinyon pine regeneration. We compared data of pinyon pine seed cone production, one component of reproductive output, from the 1974 decade to the 2008 decade at 9 sites across New Mexico and northwestern Oklahoma. We addressed the following questions: (1) Has pinyon pine seed cone production changed from the 1974 decade to the 2008 decade across New Mexico and northwestern Oklahoma? (2) Have recent changes in climate, including changes in late summer temperatures and changes in growing season temperatures, influenced pinyon pine seed cone production?

We predicted that increasing temperatures across the region led to declines in seed cone production from the 1974 decade to the 2008 decade. Given the negative exponential relationship between seed cone production and late summer temperatures found by Forcella (1981b), we hypothesized that if late summer temperatures increased in the 2008 decade then seed cone production would decline. Additionally, since increasing growing season temperatures can negatively affect pinyon pine by directly increasing respiratory costs and indirectly by increasing water stress (Adams et al. 2009), we predicted that areas with greater increases in growing season temperatures from the 1974 decade to the 2008 decade would be more vulnerable to

declines in seed cone production.

METHODS

Sampled sites

Nine sites in New Mexico and northwestern Oklahoma previously sampled in 1978 to estimate seed cone production for the previous 10 years were revisited in 2011/2012 for our comparative study. Revisited sites were located within 1 km of the original sites and were similar in elevation (± 100 m), aspect ($\pm 5°$), and slope ($\pm 3°$) as those sampled in 1978. The 9 sites span four different ecoregions (EPA Terrestrial Ecosystems Level III Ecoregion Classification) with 2 sites, Kenton 1 (K1) and Kenton 2 (K2), in the Southwestern Tablelands; 3 sites, Raton (R), Las Vegas (LV) and Pecos (P), in the Southern Rockies; 3 sites, Sandia Park (SP), Mountain Park (MP), and Fort Bayard (FB), in the Arizona/New Mexico Mountains; and 1 site, Santa Fe (SF), in the Arizona/New Mexico Plateau (Fig. 2). During the 2011/2012 sampling, there were no signs of fire, cutting, or any large mortality events in any of the sites, except for the Santa Fe site, which experienced greater than 80% mortality of adult pinyon pines during the 2002–2003 drought.

Pinyon pine seed cone production and cone abscission scar methodology

Pinyon pine seed cones take 3 growing seasons (26 mo) to mature from the time of cone initiation
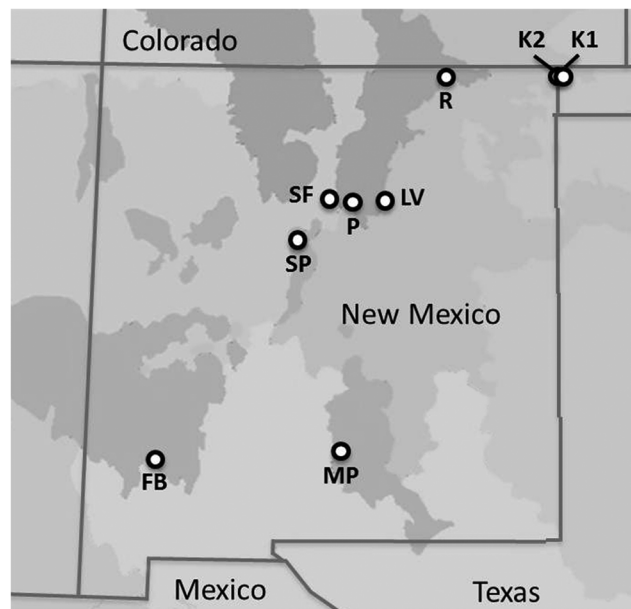
Fig. 2. A map of the 9 sampled sites (white circles). Grey shading indicates different ecoregions (EPA Terrestrial Ecosystems Level III Ecoregion Classification), with; 2 sites, Kenton 1 (K1) and Kenton 2 (K2), in the Southwestern Tablelands; 3 sites, Raton (R), Las Vegas (LV) and Pecos (P), in the Southern Rockies; 3 sites, Sandia Park (SP), Mountain Park (MP), and Fort Bayard (FB), in the Arizona/New Mexico Mountains; and 1 site, Santa Fe (SF), in the Arizona/New Mexico Plateau.

(Little 1938, Mirov 1967). At cone initiation, microscopic buds develop during August or September. From the time of cone initiation to early summer when fertilization occurs, the microscopic buds develop into visible seed cones or conelets, which then overwinter. By the following fall, 26 mo after cone initiation, mature seed cones have formed (Little 1938, Mirov 1967). Similar to other pines (Weaver and Forcella 1986, Kajimoto et al. 1998, Crone et al. 2011), pinyon pine seed cones leave visible abscission scars on tree branches. These abscission scars allow temporal variations in pinyon pine seed cone production to be observed by counting cone scars (as well as any remaining cones or conelets) at each annual whorl on the branches (Forcella 1981a). Here, we used the cone abscission scar methodology to estimate annual seed cone production from 1969–1978 (data from the 1978 sampling) and from 2003–2012 (data from the 2011/2012 sampling). This methodology has been widely used across a range of pine species (Forcella 1981a, b, Weaver and Forcella 1986, Kajimoto et al. 1998, Crone et al. 2011). However, it is important to note that seed cone production

estimates include both mature seed cones and aborted first year seed cones. Additionally, there is no data on whether detection of cone scars declines through time, however, our data showed no trend of a decline in cone scars through time in either the 1978 or 2011/2012 sampling (data not shown).

Field methods

Sites were sampled in January of 1978 and between November 2011 and January 2012 following the methodology outlined by Forcella (1981a, b). At each site we examined 4–10 reproductive pinyon pine trees in order to estimate seed cone production in the 1974 decade (1969–1978) and the 2008 decade (2003–2012). In 2011/2012 sampling, we selected cone-bearing trees that appeared healthy and had a similar basal diameter to those sampled in 1978. At 7 of the 9 sites, the average basal diameter of trees sampled in 2011/2012 was within 2 cm to trees sampled in 1978. At the 2 other sites, Santa Fe and Raton, average basal diameter was 8–10 cm larger in the 2011/2012 sampling.

During both the 1978 and the 2011/2012

sampling, we used the cone abscission scar methodology and counted young seed cones, mature seed cones, and seed cone abscission scars at the 10 most recent annual nodes on 5–10 cone bearing branches on each tree. However, 20 cone-bearing branches were examined on each tree at Kenton 1 in the 1978 sampling. Previous research on pinyon pine from this region found that sampling 4–5 branches on 4–5 trees is a statistically sufficient sample size to estimate annual seed cone production at each site (for details see Forcella 1981a).

Annual seed cone production estimation

We estimated annual seed cone production at each site by calculating the mean seed cones produced per seed cone bearing branch (cones/branch) for each year from 1969–1978 (1974 decade) and from 2003–2012 (2008 decade). Previous research has shown that the number of seed cone bearing branches per tree increases as tree size increases (Forcella 1981a). However, there was no relationship between seed cones per branch and the number of seed cone bearing branches on a tree (Adjusted $R^2 = -0.02$, $P = 0.99$; Appendix). There was also no relationship between the number of cones per branch and canopy area in a site (Adjusted $R^2 = -0.10$, $P = 0.76$; Appendix). As a result, our estimation of annual seed cone production (mean cones per branch) was an appropriate estimation of changes in seed cone production from the 1974 decade to the 2008 decade at the tree-level, regardless of changes in tree density at the site-level.

Mast years

To define mast years, for each site and each time period (1974 decade and 2008 decade), we first expressed yearly seed cone production as a standardized deviate of the annual mean seed cone production to the long-term mean calculated over all 10 years (i.e., (mean cones$_{yearX}$ − mean cones$_{allyears}$)/SD$_{allyears}$). We defined mast years as years in which the standardized deviate was greater than the absolute magnitude of the lowest standardized deviate (LaMontagne and Boutin 2007, 2009). Therefore, average seed cone years will have standardized deviates close to 0, low seed cone years will have negative standardized deviates, and high seed cone years will have positive standardized deviates that are beyond the range of the negative standardized deviates (LaMontagne and Boutin 2007). At all sites and in both decades, at least 80% of the trees produced cones during our defined mast years, highlighting the synchronicity in seed cone production of these populations.

Statistical analysis

To examine changes in seed cone production across our study sites, we performed two separate two-tailed paired Student's t-tests to understand how total seed cone production (calculated as mean seed cone production across all 10 years in each decade) as well as how the strength of masting events (calculated as mean seed cone production during mast years in each decade) changed from the 1974 decade to the 2008 decade.

We examined the relationship between annual seed cone production and climate (precipitation and temperature) during the time frame when seed cone initiation occurs in pinyon pine (Aug 7–Sep 24, 2 y prior to mature cone formation) (Little 1938, Mirov 1967). Climate data for 1967–1976 and 2001–2010 were obtained from the closest weather stations to each site (all <40 km) that had available climate data between Aug 7 and Sep 24. One site (Fort Bayard) had missing climate data in 2004 and 2010. Thus, these two years were not included in the analysis. Since the timing of cone initiation may vary between populations at different elevations and latitudes, we used 2-week running averages of daily maximum temperature and precipitation from Aug 7–Sep 24 (Little 1938, Mirov 1967). We chose this time frame a priori, since previous studies on pine species have found climate during seed cone initiation to be highly correlated with seed cone production (Lester 1967, Forcella 1981a, Mutke et al. 2005). We performed Spearman's rank correlation analyses at each site to evaluate the relationship between late summer temperature and precipitation during the year of seed cone initiation and annual seed cone production (i.e., 12 correlations per site since we used 2-week running averages). As temperatures have increased across this region over the past several decades, we hypothesized that there would be a decline in the frequency of years with cool late summer temperatures, which could lead to a decline in the frequency of masting events.

Table 2. Seed cone production across all sites in the 1974 decade (1974) and the 2008 decade (2008).

| | Mean no. cones/branch | | | | Frequency of masting events | |
| | Mast years only | | All years | | | |
Site	1974	2008	1974	2008	1974	2008
K2	2.5	2.8	0.8	1.0	2	2
K1	2.7	2.2	1.2	0.9	2	3
FB	2.5	1.3	0.8	0.4	2	2
LV	2.3	1.3	1.0	0.4	2	2
SF	3.5	1.8	0.9	0.3	2	1
SP	3.5	2.1	1.1	0.7	2	3
P	3.5	1.0	1.0	0.4	2	2
MP	3.7	1.1	0.9	0.3	2	2
R	4.9	1.9	0.8	0.5	1	2
Overall	3.2 ± 0.3^A	1.8 ± 0.2^B	0.9 ± 0.1^A	0.5 ± 0.1^B	1.9 ± 0.1	2.1 ± 0.2

Notes: Values in the lower row are means ± 1 SE across all sites, with different letters denoting significant differences between the two decades, with α = 0.05. In both decades, we calculated mean seed cone production (mean cones/branch) using data from mast years only as well as all years.

Therefore, we performed a two-tailed paired Student's t-test to examine differences in the number of years with below average (1950–2010) late summer temperatures between the 1974 decade and the 2008 decade.

We examined the relationship between changes in seed cone production and changes in growing season temperatures from the 1974 decade to the 2008 decade. We used seed cone production data from mast years only, because the number of masting events may have differed in each decade due to the relatively short timespan sampled. Thus, at each site, we calculated the percent change in seed cone production from the 1974 decade to the 2008 decade, using data only from mast years. At each site, we also calculated the percent change in mean growing season temperatures (March–October) from the 1974 decade to the 2008 decade using climate data from the 3 years prior to seed conelet formation during mast years. We used climate data during the 3 years prior to seed conelet formation (i.e., the year of seed cone initiation and the 2 years prior), because climate of the previous 2–3 years influences growth of pinyon pine (N. N. Barger, *unpublished data*), suggesting that cumulative warm temperatures may reduce non-structural carbohydrate reserves, which can influence seed cone production. We performed a simple linear regression of percent change in seed cone production as a function of percent change in growing season temperatures across our 9 sites.

To better understand regional patterns of seed cone production and how they may vary with growing season temperatures, we performed a simple linear regression of mean seed cone production during mast years as a function of mean growing season temperatures during the 3 years prior to seed conelet formation during mast years. We performed this separately for the 1974 decade and the 2008 decade. Lastly, to better understand how patterns of regional variation in growing season temperatures may have changed from the 1974 decade to the 2008 decade, we performed a simple linear regression of percent change in mean growing season temperatures from the 1974 decade to the 2008 decade as a function of mean growing season temperature in the 1974 decade. For this analysis, we used growing season temperature data during the year of cone initiation in each decade (i.e., 1967–1976 and 2001–2010). For all analyses using growing season temperatures, mean monthly temperature data were from the PRISM Climate Group (PRISM Climate Group 2012) rather than local weather stations, since the PRISM Climate Group had a complete climate record (months of climate data were missing at certain weather stations). All analyses were performed using the statistical software R (R Development Core Team 2011), with α = 0.05.

RESULTS

Average seed cone production within mast years and total seed cone production declined by 43% and 40%, respectively, from the 1974 decade to the 2008 decade ($P < 0.001$; Table 2). These declines were driven primarily by 7 of the 9 sites,
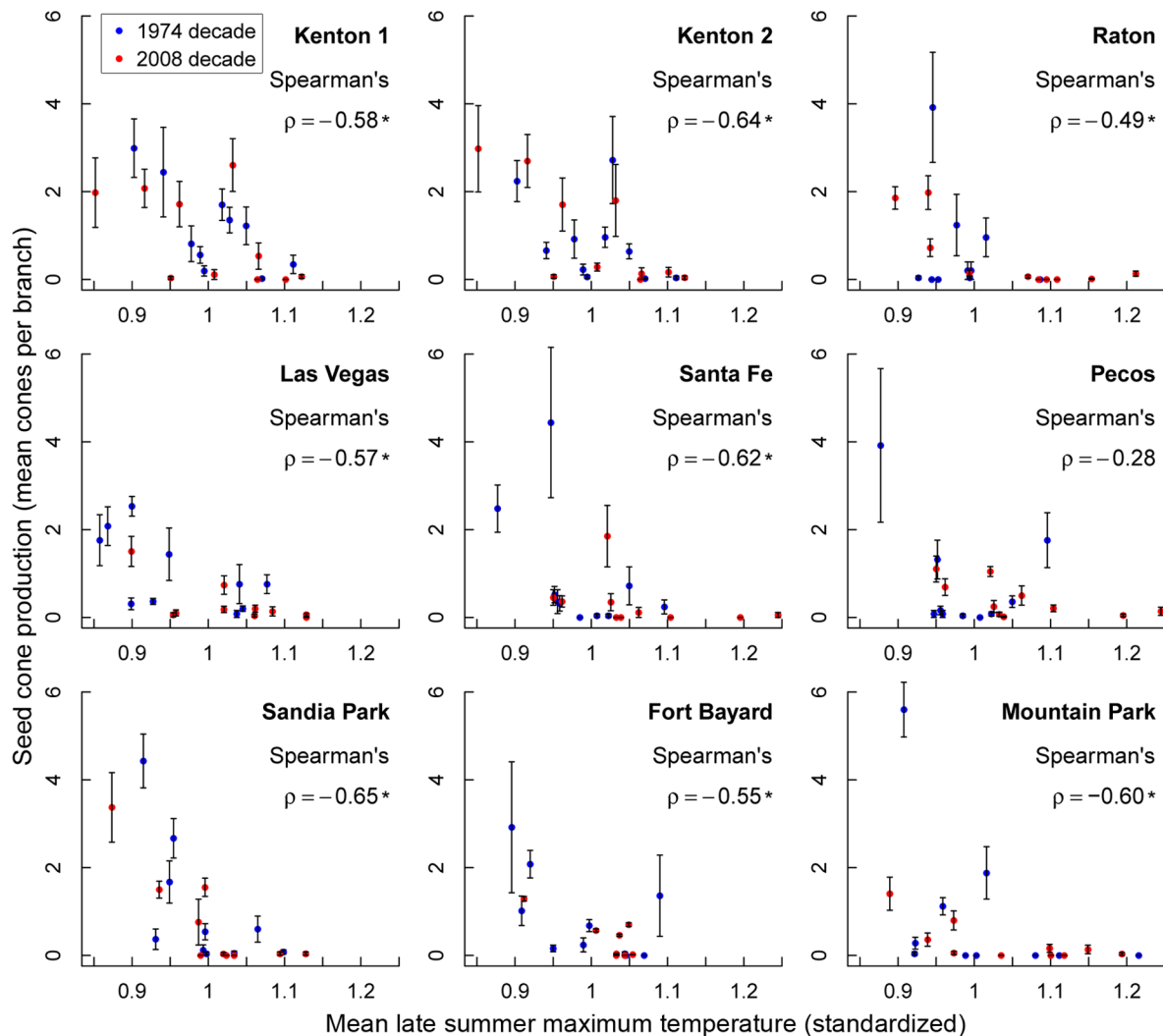
Fig. 3. Seed cone production (mean cones per cone bearing branch) and standardized late summer temperature (temperature in year of cone initiation)/(average 1950–2010 temperature) during cone initiation (2 y prior to mature cone formation) in the 1974 decade (blue circles) and the 2008 decade (red circles). The 2 week time period of late summer temperature that was most strongly correlated with seed cone production is Aug 14–Aug 27 for all sites except Las Vegas (Aug 21–Sep 3) and Fort Bayard (Aug 28–Sep 10). Fort Bayard is missing two years of data in the 2008 decade due to missing climate data. Seed cone production for those years was 1.3 and 0.2. Significance levels at $P < 0.05$ are denoted with an asterisk and error bars are ±1 SE.

which had >40% declines in seed cone production within mast years, whereas the other two sites, Kenton 1 and Kenton 2, showed little change (Table 2).

In 8 of the 9 study sites, seed cone production was negatively correlated with late summer temperature during the year of seed cone initiation (all Spearman's $\rho < -0.55$, all $P < 0.03$; Fig. 3). During the same 2 week period that

was most highly correlated with temperature (see Fig. 3 caption), we also observed a positive relationship between late summer precipitation and seed cone production at 4 of the 9 study sites (Raton, Las Vegas, Sandia Park, and Mountain Park) (all Spearman's $\rho > 0.45$, all $P < 0.05$). Additionally, late summer precipitation and temperature during Sep 3–Sep 17 and Aug 21–Sep 3 was strongly correlated with seed cone
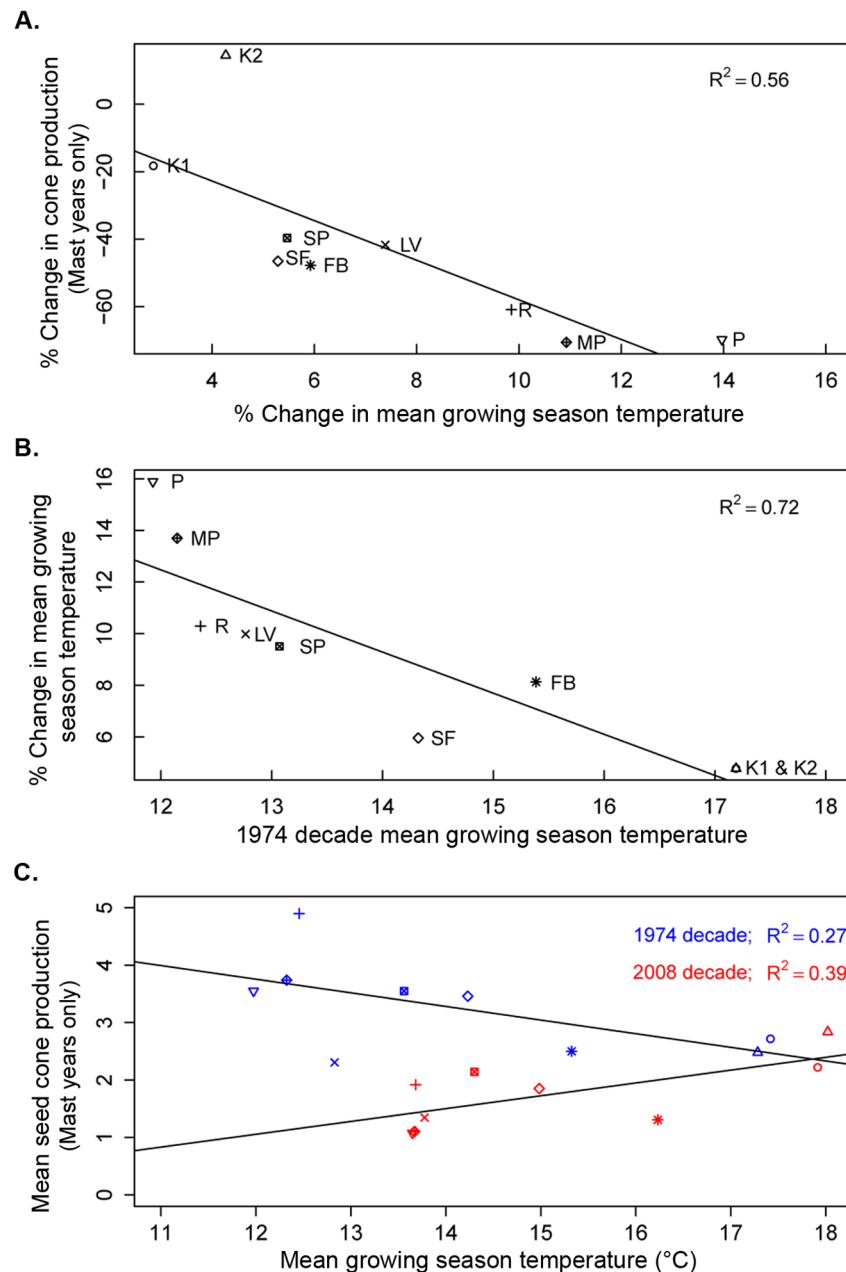
Fig. 4. (A) Percent change in mean seed cone production during mast years from the 1974 decade to the 2008 decade in relation to the percent change in mean monthly growing season (March–October) temperatures during the 3 years prior to seed conelet formation during mast years (slope $= -5.86$, Adjusted $R^2 = 0.56$, $P = 0.01$). Letters at the right of each symbol indicate the corresponding site. (B) Percent change in mean growing season temperatures from the 1974 decade to the 2008 decade during the years of cone initiation (2 years prior to cone maturation) in relation to mean growing season temperatures (℃) in the 1974 decade during the years of cone initiation (slope $= -1.59$, Adjusted $R^2 = 0.72$, $P = 0.002$). (C) Regional variations in seed cone production (mean cones per cone bearing branch during mast years) in relation to mean monthly growing season (March–October) temperatures (℃) during the 3 years prior to seed conelet formation during mast years in the 1974 decade (blue symbols) and the 2008 decade (red symbols). There was a marginally significant negative linear relationship in

production for Fort Bayard and Santa Fe, respectively (precipitation: all Spearman's $\rho > 0.51$, all $P < 0.03$; temperature: all Spearman's $\rho < -0.51$, all $P < 0.03$). Late summer precipitation and temperature were inversely related at 5 of those 6 sites that showed a strong correlation with precipitation and seed cone production (Santa Fe was the exception) (all Spearman's $\rho < -0.45$, all $P < 0.05$), which is consistent with previously observed temperature/precipitation relationships across this region. While seed cone production was correlated with both late summer temperature and precipitation at 6 of the 9 sites, we focus on the temperature relationship, as late summer temperatures increased in the 2008 decade relative to the 1974 decade whereas precipitation remained relatively constant (Fig. 1, Table 1).

As temperatures have increased in the 2008 decade relative to the 1974 decade we expected there to be fewer years in the 2008 decade with cool late summer temperatures, and thus, potentially fewer opportunities for masting. Indeed, we observed a 26% decline in the frequency of years in the 2008 decade with below average late summer temperatures (mean decline $\pm 1\,SE = 26 \pm 7\%$; $P = 0.01$; Table 1). Further, we hypothesized that the decline in seed cone production during mast years may be due to warmer late summer temperatures. However, at 6 of the 9 sites there was no increase in late summer temperatures during mast years from the 1974 decade to the 2008 decade. Las Vegas, Santa Fe, and Pecos, the other 3 sites, had a 0.5°C, 2.4°C, and 0.7°C increase in late summer temperatures during mast years, respectively. These results suggest that late summer temperatures do not solely explain the declines in seed cone production during mast years.

Growing season temperatures increased across all sites from the 1974 decade to the 2008 decade (Table 1), but sites were highly variable in the percent increase in growing season temperatures (5 to 16%) (Table 1). Interestingly, study sites with a greater increase in growing season

temperature during the 3 years prior to seed conelet formation during mast years typically had a greater decline in seed cone production during mast years (Adjusted $R^2 = 0.56$, $P = 0.01$; Fig. 4A).

When we compared how regional patterns of seed cone production during mast years varied with growing season temperatures in the 1974 decade, we found a marginally significant, weak negative association between growing season temperatures during the 3 years prior to seed conelet formation during mast years and seed cone production during mast years (Adjusted $R^2 = 0.27$, $P = 0.09$; Fig. 4C), suggesting populations located in cooler areas had higher seed cone production in the 1974 decade. Contrary to the 1974 decade, in the 2008 decade there was a positive association between mean growing season temperature during the 3 years prior to seed conelet formation during mast years and seed cone production during mast years (Adjusted $R^2 = 0.38$, $P = 0.04$; Fig. 4C). Areas with cooler growing season temperatures in the 1974 decade had much greater increases in growing season temperatures from the 1974 decade to the 2008 decade (Adjusted $R^2 = 0.72$, $P = 0.002$; Fig. 4B). Therefore, this shift from a weak negative relationship to a positive relationship between seed cone production and growing season temperatures from the 1974 decade to the 2008 decade may be due to the greater declines in seed cone production that occurred at the cool, upper elevation sites (Table 1 and Fig. 4A), as those sites had greater increases in growing season temperatures (Table 1 and Fig. 4B).

Discussion

Growing attention has focused on the impacts of climate change, namely increasing temperatures and altered precipitation, on vegetation distribution and function (Walther et al. 2002, Parmesan and Yohe 2003, Kelly and Goulden 2008, Adams et al. 2009, Chen et al. 2011). However, little is known about the impacts of

(continuation of Fig. 4 legend)

the 1974 decade (slope $= -0.24$, Adjusted $R^2 = 0.27$, $P = 0.09$) and a significant positive relationship in the 2008 decade (slope $= 0.23$, Adjusted $R^2 = 0.39$, $P = 0.04$). Each symbol corresponds to the site with the same symbol in (A) and (B).

climate change on reproductive output of conifers. Results of our comparative study revealed clear declines (>40% at the majority of sites) in pinyon pine seed cone production from the 1974 decade (1969–1978) to the 2008 decade (2003–2012). Mutke and colleagues reported similar patterns of declines in seed cone production from 1960 to 2000 in stone pine in Spain at the stand level (Mutke et al. 2005), which highlights that declines in seed cone production may be occurring across a wide range of pine species. Further, our study shows that declines in seed cone production were greatest in areas with greater increases in growing season temperatures, which suggests seed cone production may be an important bottleneck to pinyon pine regeneration with climate change.

Similar to results of Forcella (1981b), we found late summer temperatures during the year of seed cone initiation to be strongly related to seed cone production across 8 of the 9 study sites (Fig. 3). These results are consistent with other studies that have found climate during seed cone initiation to be strongly correlated with seed cone production (Lester 1967, Houle 1999, Mutke et al. 2005) and suggest cool late summer temperatures are an adaptive synchronizing cue to initiate masting and/or strongly influence available resources (see Kelly and Sork 2002 for an overview of hypothesized reasons for mast seeding). In support of the adaptive synchronizing cue hypothesis, Forcella (1981b) observed high annual variability in biweekly temperatures during late summer (as opposed to mid-summer), which would provide the temperature extremes that are important for a synchronizing cue. Alternatively, in these semi-arid ecosystems, cool late summer temperatures may be important for reducing stress during the hottest time of the year and thus may influence available resources.

While we are unclear of the mechanism(s) underlying the negative relationship between seed cone production and late summer temperatures, there was a decrease in the frequency of cool late summers from the 1974 decade to the 2008 decade (Table 1), indicating there were fewer years in the 2008 decade with suitable masting conditions. Fewer years with cool late summer temperatures will likely continue with climate change and may lead to a decline in the frequency of masting events. However, longer-term data are needed to examine changes in the frequency of masting events that occur on time scales of every 3–5 years.

Our results suggest that increases in growing season temperatures are an important predictor of declines in seed cone production. From the 1974 decade to the 2008 decade, mean growing season temperature increased on average by c. 1.3°C across our study sites (Fig. 1, Table 1), while annual precipitation remained relatively constant (increased by c. 3 cm) (Fig. 1, Table 1). Further, while we found an overall decline in seed cone production from the 1974 decade to the 2008 decade, sites were highly variable in the percent change in seed cone production (12 to −70%) and also in the percent increase in growing season temperatures (5 to 16%) (Table 1, Fig. 4B). Notably, sites with greater increases in growing season temperatures had significantly greater declines in seed cone production (Fig. 4A). Additionally, while cool late summer temperatures were highly correlated with seed cone production and may be a cue to initiate masting or are favorable climatic conditions, our results indicate that late summer temperatures did not, or at least not solely, affect changes in seed cone production within mast years from the 1974 decade to the 2008 decade. Although temperatures have increased over the past several decades, mean late summer temperatures during mast years did not increase from the 1974 decade to the 2008 decade at the majority (6 out of 9) of sites. Thus, late summer temperatures alone do not fully explain the decline in the strength of masting events at most of our sites.

The relationship between declines in seed cone production with increasing growing season temperatures in years leading up to masting events suggests that longer term temperature related stress may be an important factor in seed cone production. Higher temperatures can have both direct (respiratory costs) and indirect effects (water stress) on internal carbohydrate reserves in pinyon pine (Adams et al. 2009), which are necessary for mast seeding species to reproduce (Isagi et al. 1997, Satake and Iwasa 2000, Miyazaki et al. 2002). Thus, increases in temperature may strongly influence internal carbohydrate reserves, effecting reproductive ability (Isagi et al. 1997, Satake and Iwasa 2000, Miyazaki et al. 2002). These results support the

resource-matching hypothesis of mast seeding by highlighting how climate, which in our case are increases in growing season temperatures, can constrain resources and influence reproductive output in mast seeding species.

The results presented here suggest that areas with greater increases in temperature may be more vulnerable to declines in seed cone production. Climate models predict greater temperature increases at higher elevations (Giorgi et al. 1997), which is consistent with changes in growing season temperature across our research sites (Table 1, Fig. 4B). Thus, while populations at the upper elevation of species limits typically experience cooler climates and are predicted to be a refugia with increased warming (Pearson et al. 2002), these populations may be more vulnerable to declines in reproductive output due to greater increases in temperature. Indeed, in the 1974 decade, sites with cool growing season temperatures tended to have higher seed cone production (Fig. 4C). Contrary, in the 2008 decade, sites with warmer growing season temperatures tended to have higher seed cone production (Fig. 4C). This may be explained by the greater declines in seed cone production that occurred at the cool, upper elevation sites (Fig. 4A, Table 1), which had the greatest increases in growing season temperatures (Fig. 4B). These results highlight how the cool, upper elevation populations may be more vulnerable to climate change than previously predicted.

The shift from a negative relationship between seed cone production and growing season temperatures in the 1974 decade to a positive relationship in the 2008 decade suggests populations are locally adapted to climate. If populations were not locally adapted to climate, we would expect the relationship between seed cone production and growing season temperatures to remain negative in the 2008 decade. However, this was not the case. Rather, populations located in warmer climates had higher seed cone production in the 2008 decade as compared to the populations located in cooler climates, which experienced greater increases in growing season temperatures and greater declines in cone production. Thus, the declines in seed cone production that occurred at the cool, upper elevation sites and led to the positive relationship between cone production and growing season tempera-

ture in the 2008 decade (Fig. 4C) suggest that local adaptation may play an important role in future species distributions. Most empirical climate change studies and species distribution modeling studies use space-for-time substitutions (Pickett 1989, Araújo and Rahbek 2006), which assume that species distributions and assemblages are in a constant steady-state with climate and do not incorporate local adaptation (Araújo and Rahbek 2006, Pearson and Dawson 2003). However, our results suggest local adaptation may be important for understanding how populations may respond to climate change. For example, if we were to use a space-for-time substitution approach in the 1974 decade to understand how pinyon pine seed cone production may be influenced by climate change, we would predict that seed cone production would be negatively affected by increasing temperatures (i.e., Fig. 4C, 1974 decade pattern). However, if we instead did the study in the 2008 decade, we would predict that seed cone production may increase with increasing temperatures (i.e., Fig. 4C, 2008 decade). Thus, the instability in the relationships between climate and seed cone production between the 1974 decade and the 2008 decade (Fig. 4C), likely due to population level adaptation and differential warming, highlights the potential inaccuracies of the space-for-time substitution approach in predicting how ecosystems may respond to climate change.

The declines in seed cone production (>40% at the majority of sites) that have occurred could have significant impacts on pinyon pine population dynamics, especially given recent widespread mortality. Recruitment events among semi-arid pines are known to be highly episodic and dependent upon cool, wet climate periods (Brown and Wu 2005, League and Veblen 2006, Romme et al. 2009, Barger et al. 2009), highlighting how conditions for successful recruitment are limited. With declines in seed cone production, successful recruitment may become even more infrequent and seed production may become an important bottleneck to pinyon pine regeneration.

Not only may declines in seed cone production influence future regeneration of these populations, but declines may negatively affect the variety of wildlife species that consume pinyon pine seeds (Brown et al. 2001), such as pinyon

jays (*Gymnorhinus cyanocephalus*) and Clark's nutcrackers (*Nucifraga columbiana*). While our research was on pinyon pine, similar declines may be occurring in other tree species, especially other semi-arid pines. We recommend further investigation of tree species reproduction to better understand the full geographic and taxonomic extent of these declines.

Acknowledgments

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Supplemental Material

Appendix

Relationship between cones per branch,
tree size, and stand density among pinyon pine

Using pinyon pine seed cone production data from the 1974 decade (1969–1978) from 11 sites scattered throughout New Mexico and northwestern Oklahoma (see Forcella 1981*a* for methods), we performed a linear regression to examine the relationship between the total number of cone bearing branches on each tree (5 trees at each site) and the mean number of cones per branch produced during the highest seed cone production year. We found no significant linear relationship between the number of cone bearing branches per tree and the number of cones per branch (linear regression, Adjusted $R^2 = -0.02$, $P = 0.99$, df $= 56$). Additionally, we performed a linear regression to examine the relationship between pinyon pine canopy cover in each 600 m^2 sampling plot and the average number of cones per branch produced during the highest seed cone production year at each site (11 sites total). We found no significant linear relationship between total pinyon pine canopy cover and the maximum number of seed cones per branch (linear regression, Adjusted $R^2 = -0.10$, $P = 0.76$, df $= 9$).