The Effects of Climate on Mast Seeding Behavior in Single-Leaf Pinyon Pine (*Pinus monophylla*)

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ABSTRACT

Climate change poses a threat to the forested ecosystems of California and pinyon-juniper woodlands are particularly vulnerable. Pinyon pine trees conduct "mast seeding," which is a reproductive pattern characterized by high interannual variability and high synchronicity in seed production. This project outlines how masting behaviors of single-leaf pinyon pine trees (*Pinus monophylla*) coincide with variations of important climatic variables. Over a decade of reproduction was examined using the cone scar method and mast seeding patterns were quantified by calculating the coefficient of variation on both individual and population levels. The pinyon seed production timeline is a 26 month process with cone initiation occurring at the beginning and pollination occurring towards the middle. No significant correlation exists between cone production and branch growth during the year of cone maturation for this sample population. There is a negative relationship between cone production and late summer vapor pressure deficit (VPD) during the year of cone initiation, yet no significant relationships were found between VPD during pollination or precipitation during either initiation or pollination. The negative relationship between cone production and VPD has alarming implications when climate change projections are considered. The reproductive success of this population of single-leaf pinyon pines may be compromised soon as temperatures rise.

KEYWORDS

masting, predator satiation, pollination efficiency, vapor pressure deficit, cone scar

INTRODUCTION

Forests provide a wide variety of ecosystem services and are at risk of being permanently altered or lost entirely as climate change persists. Among those ecosystem services are recreation, carbon sequestration, and sources of timber and renewable energy. Mismanagement of forests in California have left them prone to high severity wildfires that are coupled with detrimental effects of drought and disease (Rodriguez-Zaccaro et al. 2019). Many forest ecosystems are on the verge of losing their carbon stocks as well as their ability to perform a multitude of ecosystem services (Bernal et al. 2022). However, land managers can use scientific approaches to design successful management strategies that help return forests to their natural disturbance regime (Slauson et al. 2022). Because there is tremendous diversity amongst forests, each unique ecosystem requires specific considerations when predicting the effects of climate change. Therefore, when studying the effects of climate change on forests, it is imperative to consider that different ecosystems vary in their vulnerability and that these variations affect the time sensitivity of management actions.

Pinyon-juniper woodland forests that dominate the U.S. Southwest are semiarid ecosystems that have been especially affected by the increasingly hotter and drier climate trends that lead to drought conditions and high severity wildfires (Redmond et al. 2023). Due to extreme climatic conditions that are characteristic of semiarid zones, these types of forests may be on the forefront of ecological shifts caused by climate change (Clifford et al. 2011). Pinyon pines (*Pinus edulis, Pinus monophylla*) are key species within these types of ecosystems and face many challenges. Heightened drought conditions combine with ecological and anthropogenic changes to cause surges in pinyon mortality. For example, bark beetle outbreaks following uncharacteristically hot, dry years can lead to massive die-offs (Meddens et al. 2015). In addition, land management objectives such as sensitive species protection and cattle grazing fail to prioritize the protection of pinyon pines (Reinhardt et al. 2023). These trends are especially troubling to indigenous tribes who share the land with their habitat and rely on pinyon seeds, commonly referred to as pine nuts, for cultural purposes. It is crucial that research highlights the sensitivity of semi-arid woodlands to climate change so that they can be sufficiently considered as forestry continues to search for innovative land management practices.

Pinyon pine trees are a masting species in which reproduction occurs in the form of mast seeding that is carried out in unison by a given population. Masting years occur on an irregular basis when an entire population will produce a large seed crop one year with minimal seed production in intervening years. Empirical evidence shows that mast seeding behavior allows for predator satiation and increased pollination efficiency (Pearse et al. 2016). However, populations of trees that perform mast seeding may be particularly vulnerable to changes in climate because of the all-or-nothing nature of mast seeding and climate effects on seed production are poorly understood in masting species (Redmond et al. 2016). Although masting studies have been conducted for two-needle pinyon (*Pinus edulis*), there is a lack of research on single-leaf pinyon (*Pinus monophylla*). Climate during seed cone initiation and pollination is strongly associated with mast seeding events among other semi-arid pine species and we can use it to predict these unique reproductive events (Mooney et al. 2011). Because masting behaviors are key for reproductive success amongst pinyon pines, it is important to understand the processes behind them and how they may be changing with the climate.

This project outlines how masting behaviors of single-leaf pinyon pine trees (*Pinus monophylla*) are being altered as a result of climate change. The single-leaf pinyon is a shrub-like pine species that features a high crown ratio and grows approximately 20-30 feet tall. It is the only pine species with singular needles that grow from the branch rather than existing in fascicles of two or more. In this study, I first characterized the temporal aspects of mast seeding events within a population of single-leaf pinyons, focusing on frequency and synchronicity. I then examined the relationship between branch growth and cone production to determine patterns between individual tree characteristics and masting success. Finally, I collected precipitation and vapor pressure deficit (VPD) values during two important time frames relevant to mast seeding: the year of cone initiation (two years prior to mature cone development) and the year of pollination (one year prior to mature cone development). I expected that the sampled population would show a high level of synchronization when cone production patterns are analyzed. I anticipated a tradeoff between branch growth and cone production due to the allocation of limited resources. Finally, I predicted that VPD would generally have a negative association with cone production while precipitation will show a positive association. Data on masting events was collected using a robust cone abscission method to quantify the frequency of events (Redmond 2016). Climate data was obtained through the Oregon State PRISM climate group database. The objective of this study is to detect associations between climatic variables and mast seeding behaviors that can provide valuable management implications for the future of these ecosystems.

METHODS

Study Site

The study site lies among the Benton Range of the Eastern Sierras. Trees were picked within an acre plot at 37°44'01.3"N, 118°34'28.1"W (Figure 1). The local ecosystem is dominated by sagebrush (*Artemisia tridentata*) and single-leaf pinyon pine trees (*Pinus monophylla*). Single-leaf pinyon pine is the species of interest for this project. It is native to these semi-arid woodlands within the Eastern portion of California's Sierra Nevada mountain range. This section of the Eastern Sierras is a relatively water-limited ecosystem, making it particularly sensitive to drought and therefore a worthy candidate for a study on the effects of climatic factors on tree growth and development.

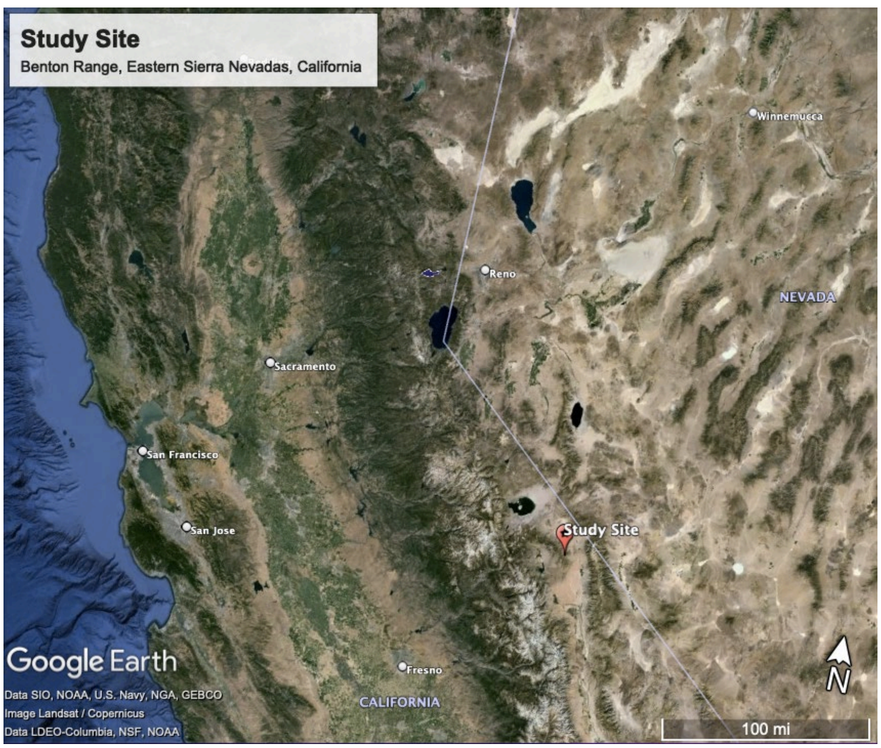


Figure 1. Map of Study Site. Benton, CA is in the Southeastern Sierra Nevadas, near the Nevada border.

Data Collection Procedure

Branch growth and cone production data was recorded in the field. Branch growth was collected by measuring length between annual bud scale scars in millimeters using a digital caliper and recording the value as the growth for each year going back in time from the tip of the branch. We collected data on pinyon pine cone production using the cone scar method. The cone scar method is robust for collecting seed cone data on two-needle pinyon pines (*Pinus edulis*) while also being minimally invasive and non-destructive to the live tree (Redmond et al. 2016). The cone scar method involves counting annual growth segments on randomly selected branches and counting cone scars found at any segments (Figures 2a, 2b, &2c). Using this method, we determined when and how often pinyon pine trees within the study area produce cones.

The sampled trees contained immature conelets on the tips of many of their branches at the time of data collection in October of 2023 that will mature in Fall 2024. We recorded those conelets as cone scars for 2024 so that the data shows the years that mature cones were produced. Cone scars are visible as small but distinct circular divots near the annual growth segments where mature cones were once present and eventually fell off. The years of each annual growth segment can be determined by using annual bud scale scars to count backwards from the present conelets at the end of the branches, which were recorded as 2024 cones.

a)

b)

c)

Figure 2. Cone scar method. Cone scars (a & b) are visible for each year that cones were produced. The year of the cone can be determined by observing which annual growth segment (c) lines up with any present cone scar.

We sampled 4-6 branches from each of 6 trees. Trees were chosen randomly, under the qualifications that they were healthy and adult size. Climate data was obtained from PRISM. Information on precipitation and VPD was recorded for the years 2010-2024 at our study site. Precipitation and VPD were recorded from April 15th - May 15th and August 15th - September 15th of each year to reflect the seasonality of pollination and initiation respectively. Cone and branch data prior to 2010 could not be obtained due to diminishing cone scar and bud scale scar visibility.

Data Analysis

To outline the degree of synchrony among individual trees within the population at the study site, the data was organized to show the number of cones produced by each tree during each recorded year. For each tree, I calculated the average cone production per branch for each year and multiplied that by the total number of branches to obtain an estimate of mean annual cone production for each tree. These data were then used to calculate the coefficient of variation at the individual tree level (i.e. a CVi value for each individual tree). In addition, mean annual cone production for each tree was averaged across all the trees for each year (i.e. a value for each year) to calculate the coefficient of variation at the population level (CVp). All CVi and CVp values were averaged to obtain the final metrics. A high CV is indicative of data that has a large spread around the mean. I expected to obtain relatively high values of both CVi and CVp to reflect the sporadic nature of masting.

To compare branch growth to cone production, I measured branch growth in millimeters and averaged it for each year. Similarly, I averaged cone production count for each year. Average branch growth and average cone production were calculated for each tree during each year. The average branch growth reflects the branch growth during the year of cone maturation. These two variables were compared to each other using a linear regression with a negative binomial distribution, which accounts for the inability to assume normality throughout this dataset.

To examine how climate affects cone production in single-leaf pinyon pines, I assessed two variables: precipitation and VPD. Each was examined during cone initiation (two years before mature cone production) and pollination (one year before mature cone production). During the year of cone initiation, only data during the late summer will be assessed because this is when pollen and ovule meiosis takes place. During the year of pollination, data from the late spring will be assessed to reflect when pollination occurs (Redmond et al. 2014). Climate data from these key seasons will be compared to their corresponding year of cone production to assess correlation across the cone development timeline. A linear regression with a negative binomial distribution was used to examine each relationship using the glm.nb function in the R package "MASS" (version 2023.06.0+421, R Core Team, 2024).

RESULTS

Data Collection

Data on pinyon pine cone production was obtained for years 2010-2024 in our sample population. Of the 15 years sampled, cone scars occurred for 10 of them (Table 1). Cone production was especially apparent in 2024, 2019, and 2011, implying that those were mast seeding years. Cone initiation occurred in 2022, 2017, and 2009 while pollination occurred in 2023, 2018, and 2010. The mean and median yearly branch growth for the population are 23.1 millimeters and 21 millimeters respectively.

Table 1. Average cones per tree per year. Average cones produced by sampled trees in each year. Masting years are highlighted in orange.

Year:	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	2024
Cones:	2	32	4	2	0	1	3	4	0	66	1	0	0	0	56

Interannual Variability of Cone Production

The degree of masting within the population was determined by calculating the interannual variability on the individual tree level (CVi) and on the population level (CVp). CVi is 2.23 while CVp is 2.17. Trees within the sample population were observed to mass produce cones during the same years (Figure 3).

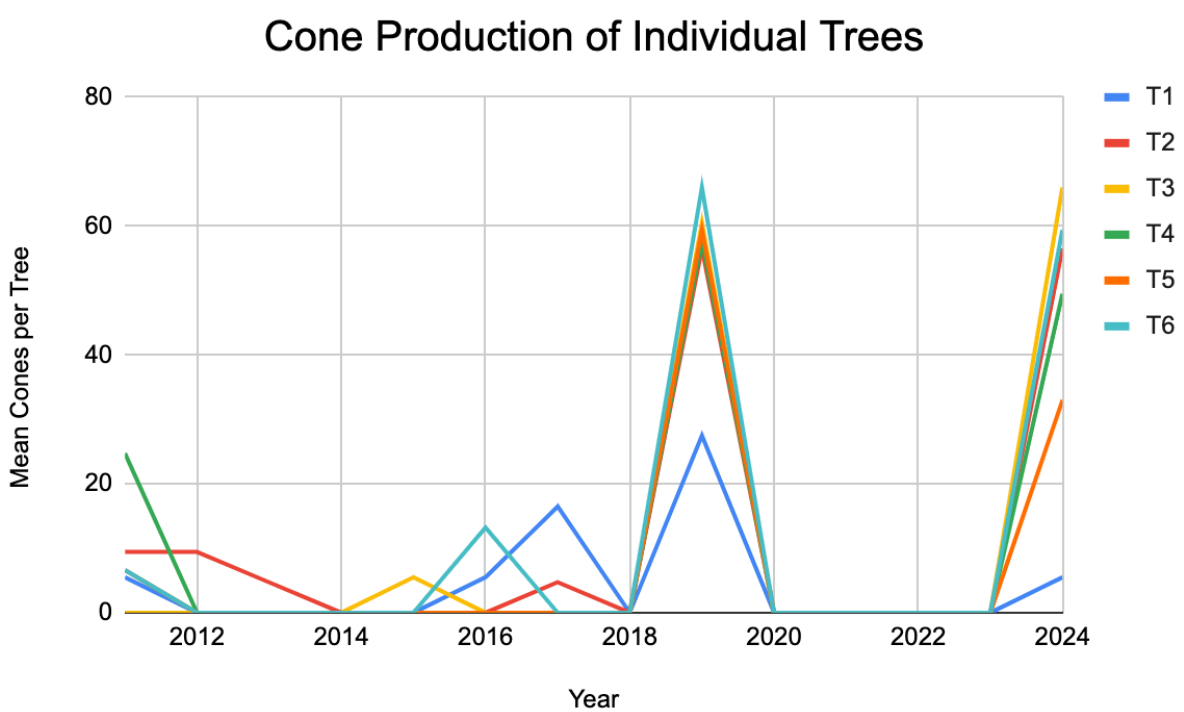


Figure 3. Yearly cone production of each sampled tree. Each colored line represents one of six sampled trees. The masting years are clearly represented as 2011, 2019, and 2024.

Cone Production vs. Branch Growth

There is no significant relationship between cone production and branch growth within the sample population. A slight positive trend may be inferred ($z = 1.69$, $p = 0.09$) but the results of this study question are ultimately inconclusive (Figure 4).

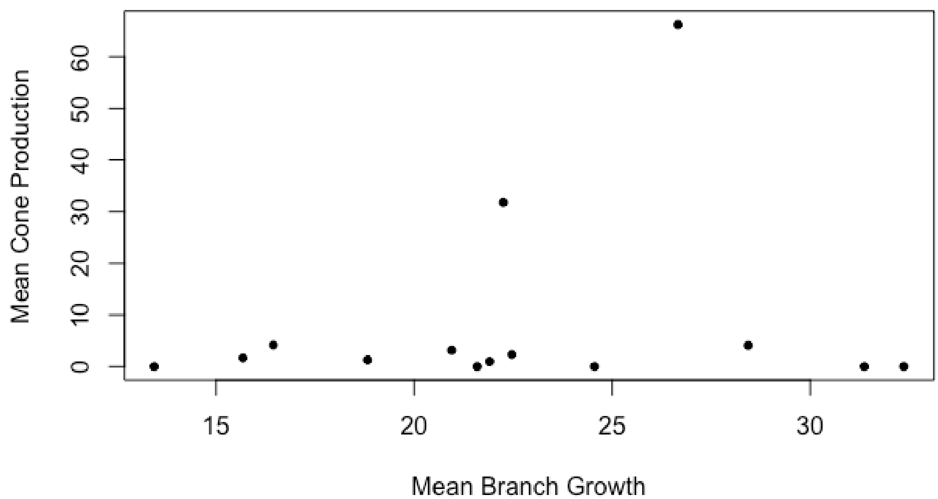


Figure 4. Cone production vs. growth. Scatter plot displays lack of significant relationship between mean branch growth and mean cone production. The 2024 masting year is not reflected because cones were at the pollination stage during data collection. Therefore, it was not possible to collect branch growth during maturation for that year.

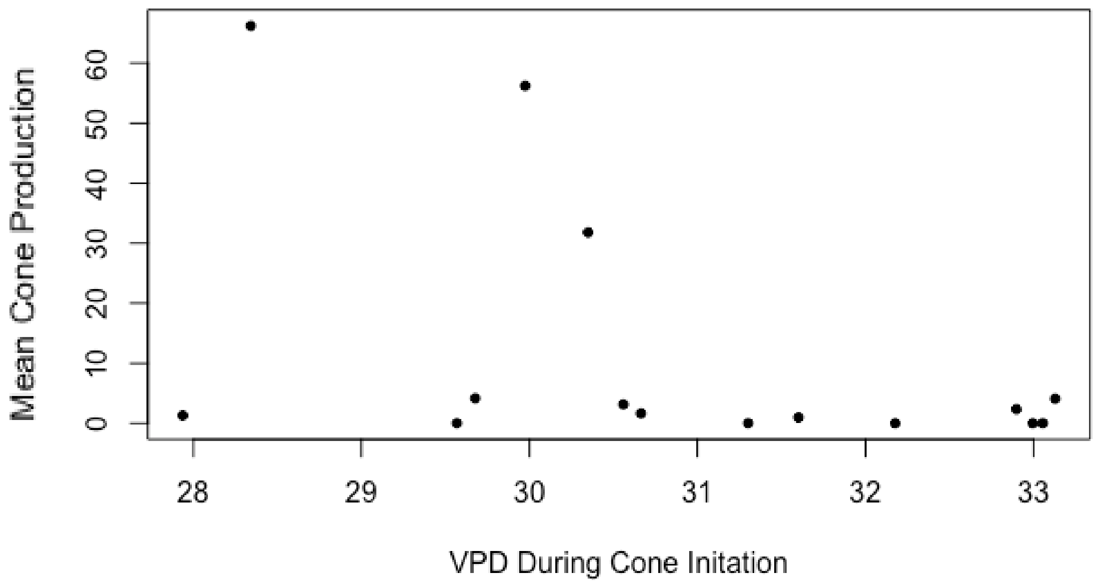
Effect of Climate on Cone Production

There is a significant negative relationship between cone production and VPD during the year of cone initiation. No significant relationships were found between cone production and VPD during pollination, or cone production and precipitation during either initiation or pollination (Table 2 & Figures 5a, 5b, 5c, & 5d).

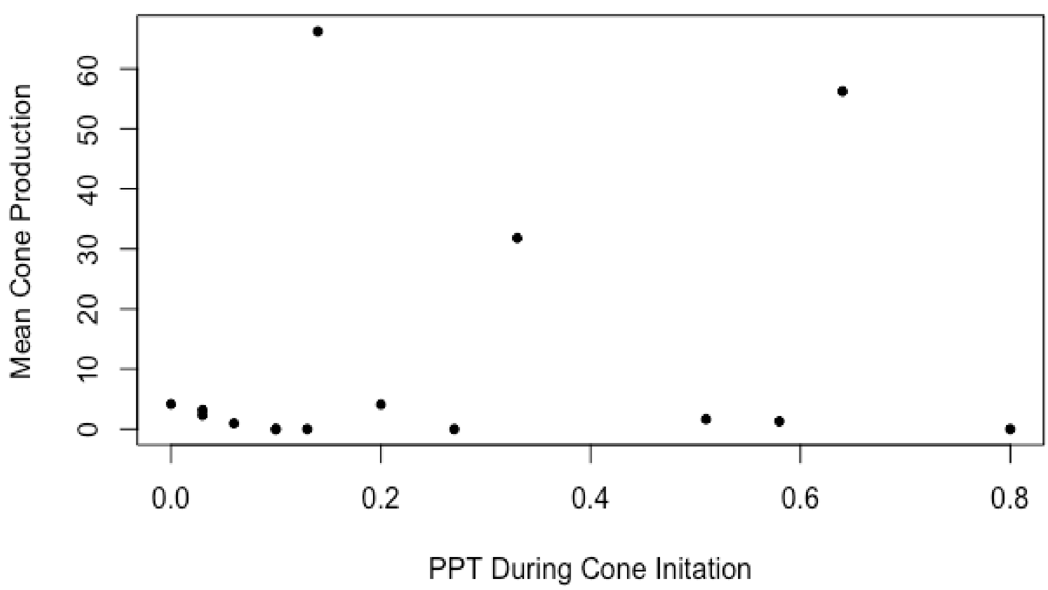
Table 2. VPD and PPT during initiation and pollination. Of the tested variables, the only statistically significant relationship that was found was between cone production and VPD at initiation.

Climate Variable	z-value	p-value
VPD (Initiation)	-2.859	0.00425
PPT (initiation)	0.807	0.4194
VPD (pollination)	-1.082	0.2792
PPT (pollination)	-0.561	0.57456

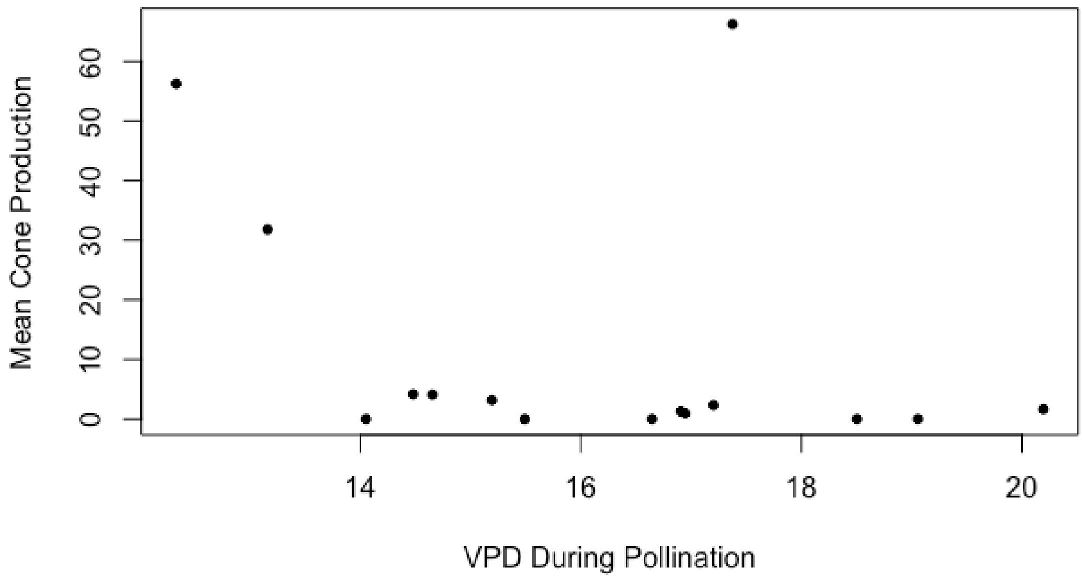
a)


Mean Cone Production
0
10
20
30
40
50
60
28
29
30
31
32
33
VPD During Cone Initation

b)


Mean Cone Production
0
10
20
30
40
50
60
0.0
0.2
0.4
0.6
0.8
PPT During Cone Initation

c)



d)

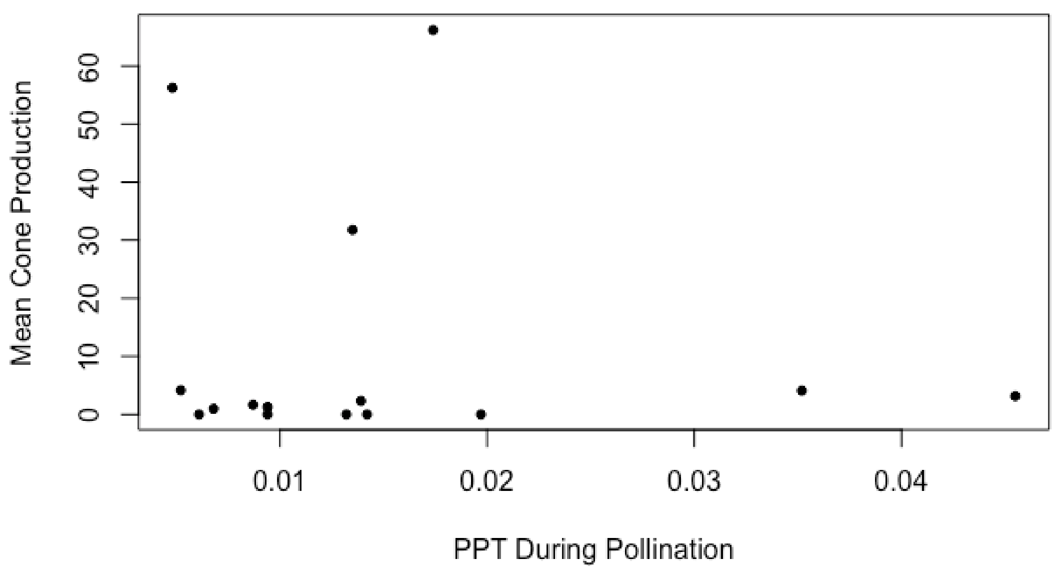


Figure 5. Scatterplots showing climatic relationships with cone production. Precipitation and VPD were analyzed during times of cone initiation and pollination. Only VPD during initiation had a statistically significant relationship with cone production.

DISCUSSION

The pinyon pines in the study area exhibited clear mast seeding behavior. Throughout the 15 year sample period, 2011, 2019, and 2024 stood out as mast seeding years. Other years produced either zero cones or fewer than five cones total throughout the entire population. There was no significant tradeoff found between cone production and branch growth. A slight positive trend between cone production and branch growth is observed, which would contradict the original hypothesis. However, these findings do not provide evidence of any relationship between cone production and branch growth. Of the tested climatic factors, there is a significant negative relationship is between cone production and VPD in the year of cone initiation. VPD during pollination and precipitation during both initiation and pollination did not show significant correlations with cone production.

Degree of Masting Within Sample Population

The sampled population of pinyon pines within the Benton range showed a relatively high level of interannual variability at the tree level (CVi = 2.23) and at the population level (CVp = 2.17). This pattern of high variation in cone production throughout the years is typical of masting species (Wion et al. 2023). It was important to include this analysis in the study to confirm masting years before comparing them to climatic factors. The tendency to mast can vary across populations within a species (Crone et al. 2011). Analyzing the degree of masting within a given population may be necessary to make certain management decisions. Masting populations may be especially vulnerable to climate change if the climate is causing wide temporal gaps between reproductive events. Management techniques such as artificial regeneration may benefit a masting population especially in areas where climate is projected to change in a way that will limit the frequency of cone production.

Cone production vs. Branch growth

There was no tradeoff found between branch growth and cone production. The original hypothesis stated that branch growth and cone production would be negatively correlated due to resource limitations (i.e., if a tree is producing cones, it will have less energy to grow its branches). This was not found to be true. In fact, there is limited empirical evidence that branch growth and cone production might be positively correlated. Branch growth was recorded for the year of cone maturation. For example, if the cone scar was found at an annual growth segment for 2011, the corresponding branch growth is the growth that occurred in-between pollination in 2010 and the development of the mature cone. Comparably, positive relationships between radial trunk growth and cone production have been found in other masting pine species when recording growth two years prior to cone maturation (Bowman et al. 2023). It is possible that similar results could be observed with branch growth when comparing cone production to growth between the initiation and pollination phases (i.e. growth two years prior to cone maturation). Such findings could offer a minimally invasive technique for determining masting years, especially when cone scar visibility diminishes as you move further down the branch.

Effect of Climate on Cone Production

Vapor pressure deficit (VPD) was strongly negatively correlated with cone production in the year of cone initiation (two years prior to mature cone formation). Similar correlations have also been discovered in *Pinus edulis*, two-needle pinyon pine (Wion et al. 2019). Other climatic factors tested which displayed no significant relationships included VPD in the year of pollination and precipitation in both initiation and pollination years. The negative relationship detected between VPD and cone production has alarming implications concerning climate change, as VPD is positively and exponentially correlated with temperature (Schönbeck et al. 2022). Thus, we can expect VPD to be greatly affected by the rising temperatures predicted by climate change projections (Figure 6).

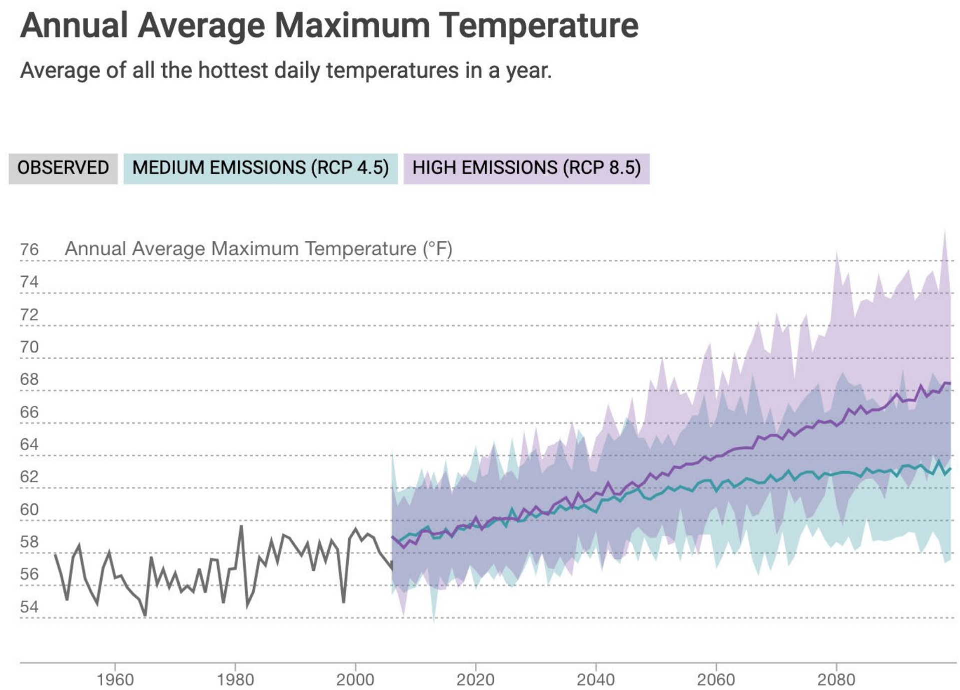


Figure 6. Local climate change snapshot for Mono County. The study site in Benton, CA is in Mono County. The annual average maximum temperature is predicted to rise significantly in upcoming decades (Cal-Adapt 2024).

No significant correlations were discovered between precipitation and cone production. Pinyon pines have extensive roots that allow them to cope with limited water supply (McHugh et al. 2006). This adaptation may contribute to the lack of significant relationship between precipitation and cone production. It should not be assumed that adaptations relevant to climate will be sufficient in keeping up with anthropogenic climate change. Alternatively, it may be that our low sample size (only three mast years) limited our ability to detect a relationship. Indeed, there was very limited seed production during the first five years of our study with the lowest precipitation during cone initiation (Figure 5). High VPD can contribute to drought stress and increase an ecosystem's demand for precipitation (Noguera et al. 2023). A positive relationship between precipitation and cone production may become more apparent with projected increases in temperature.

The results of this study imply that climatic factors affect cone production during cone initiation periods, but not during pollination. A positive relationship between cone production and precipitation and a negative relationship between cone production and VPD during pollination has been observed in *Pinus edulis*, two-needle pinyon (Wion et al. 2019). The tree sample size for the two-needle study was much larger (n = 187) while the number of years sampled was similar (n = 14). While a small sample size may have influenced the results of this study, it is notable that it did not prevent the discovery of a significant relationship between VPD and cone production at initiation. Factors such as wind and canopy closure can have significant effects on pollination success in wind-pollinated conifers (Muñoz-Reinoso 2023). It is possible that while climatic factors drive initiation success in this population of single-leaf pinyons, pollination success is influenced more significantly by wind patterns and stand structure.

Using climate to predict cone production provides a framework for making management decisions especially when reproduction is affected by fluctuations in certain climatic variables. This study found that climate during cone initiation is correlated with cone production, suggesting that it could be possible to forecast cone production two years in advance for *Pinus monophylla*. This climate prediction method for forecasting reproductive events can be used to better plan seed collection and planting efforts for reforestation. As such, artificial regeneration of pinyon pines may be crucial as the magnitude of climatic factors that are negatively associated with cone production increase with the changing climate.

Limitations

The cone scar method has proved to be a robust method for examining mast seeding behaviors in two-needle pinyon pines (Redmond 2016). The results of this study support that the same is true for single leaf pinyon, with a sample size of six trees being sufficient. However, this relatively small sample size may not have been sufficient for analysis regarding climatic factors. Masting years in *Pinus edulis* tended to follow periods of low VPD and high precipitation during initiation and pollination when analyzed across 23 sites (Wion et al. 2020). While creating a larger sample size by surveying more trees would be possible, it is difficult to increase the number of years sampled. As you go further back in time on a branch, the annual growth segments and cone scars become less visible and more difficult to distinguish. This creates a high risk for human error and ultimately produces a dataset with many omitted values. Resampling populations on a regular basis would help build a robust archive of seed data that may be valuable for future research on masting species.

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