



Climate-influenced ponderosa pine (*Pinus ponderosa*) seed masting trends in western Montana, USA

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Abstract

Aim of study: The aim of this study was to analyze 10-year records of ponderosa pine (*Pinus ponderosa*) seed production, in order to confirm synchronic seed production and to evaluate cyclical masting trends, masting depletion effect, and climate-masting relationships.

Area of study: The study area was located in a *P. ponderosa* stand in the northern Rocky Mountains (western Montana, USA).

Material and methods: The study was conducted in one stand that had been subjected to a silvicultural study of uneven-aged management techniques that was carried out in 1984, and which resulted in three separate units consisting of one control, one cut/no-burn treatment, and one cut/burn treatment. Seeds were collected during the 10 years following treatment in 15 traps systematically deployed within each of the stand's three units. The total numbers of seeds collected in each unit were plotted over time to analyze crop synchrony, with Spearman rank correlation coefficient used to test for masting cycles and crop depletion after a mast year. Meteorological records over the period 1983-1994 were related to the occurrence of a mast event (defined as crops exceeding 50,000 viable seeds/ha).

Main results: The seed production pattern was non-cyclical, synchronous, and independent of silvicultural treatment history. A mast-depletion effect was evident but was not statistically significant. Mast events seem to be promoted by the occurrence of optimum mean temperatures at the beginning of spring during both the first (11 °C) and second (9 °C) years of cone maturation. The probability of a mast year was also affected by summer temperature (number of late frost days; negative effect) and precipitation amount (positive effect). All these factors would seemingly explain the observed synchronous pattern in cone production.

Research highlights: The non-cyclical trend of ponderosa pine seed mast years is influenced by specific climate determinants. Fluctuations in mean early spring temperatures, late frost and water availability are likely to affect *P. ponderosa* seed production, with implications for natural regeneration in this region.

Key words: natural regeneration; seed periodicity; reproduction; uneven-aged management; Rocky Mountains.

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Introduction

Recruiting sufficient numbers of ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) seedlings is a persistent challenge for managers seeking to naturally regenerate the species throughout the northern Rocky Mountains. Many factors can constrain ponderosa pine seedling recruitment (Keyes *et al.*, 2007), foremost of which is the availability of seed (Krannitz & Duralia, 2004; Keyes & Maguire, 2007). Pondero-

sa pine is one of the most periodic seed producers among western North American conifer species, with heavy cone production years typically followed by years of few cones or none at all (Sundahl, 1971; McDonald, 1992; Shepperd *et al.*, 2006; Mooney *et al.*, 2011). The number of years between mast crops varies; observations from across the species' range indicate that they occur once per 3 to 8 years (Roeser, 1941; Fowells & Schubert, 1956; Larson & Schubert, 1970; Dahms & Barrett, 1975). However, studies on

the determinants of seed periodicity in ponderosa pine are scarce.

Inter-annual variation in seed production seems to correspond with climate factors (notably, temperature and moisture) affecting critical phenological events during the reproductive cycle (Mooney *et al.*, 2011). Ponderosa pine's reproductive cycle is completed over a period exceeding two years. Flowering initials typically emerge and pollination occurs during June of the first year, and the female strobili develop over summer. Seed cones are developed during spring of the second year and mature over summer, with seed dispersal occurring over the fall months of the second year. This lengthy cycle predisposes the seed production process to a potentially great array of climatic influences. However, the specific factors and the timing of their incur-rences remain unclear. Whether masting occurs on a cyclical basis as a result of crop depletion is also unknown.

The fortunate coincidence of a 10-year ponderosa pine seedfall dataset, combined with very local meteorological data recorded during the same period, allowed for this study's analysis of cyclical masting trends and climate-masting relationships at the University of Montana's Lubrecht Experimental Forest (northern Rocky Mountains, USA). Although the inferential value was limited by the study area's small size and limited data, it afforded a rare opportunity to gain fresh insight into the temporal dynamics of ponderosa pine seedfall. Understanding climate-seedfall relationships will help managers anticipate the occurrence of mast crops and enable them to schedule restoration treatments (such as prescribed burning, or thinning and soil scarification) to coincide with mast crops, and thereby maximize the likelihood of successful ponderosa pine seedling recruitment. The aim of this study was to analyze 10-year records of seed production, in order to confirm synchronic seed production and to evaluate cyclical masting trends, masting depletion effect, and climate-masting relationships in ponderosa pine. We hypothesize that masting pulses in ponderosa pine are governed by climatic factors, which prevail over other ecological processes such as masting cycles or depletion effect.

Methods

Study area

The stand is located in western Montana (N 46.53, W 113.29) at an altitude of 1,231 m asl. Slopes throughout the study area are generally flat. Climate normals

for the period 1981-2010 (calculated from records in nearby Potomac, Montana; N 46.89, W 113.57) indicate a mean annual temperature of 14.4 °C and total average annual precipitation of 384.8 mm. Mean temperature and total precipitation during summer months (June, July, and August) are 15.1 °C and 101.6 mm, respectively. Occurrence of frost events tends to decline in mid-May.

This stand was part of a silvicultural experiment in uneven-aged stand management techniques established in August 1984 (Fiedler, 2000; Arno & Fiedler, 2006). Prior to treatments, the stand consisted of an irregular uneven-aged mixture, with *Pinus ponderosa* dominant in the canopy and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) dominant in the midstory and understory. The stand was divided into three adjoining irregular units of 2.10 ha (Unit 1), 3.24 ha (Unit 2) and 2.19 ha (Unit 3), into which a control, a cut/no-burn treatment, and cut/burn treatment were randomly assigned. In the cutting units, trees were cut from all age classes in order to promote the development of a balanced, uneven-aged stand; securing ponderosa pine natural regeneration was an explicit treatment goal. Whole-tree harvesting left identical residual basal areas (13.3 m²/ha), with Douglas-fir prioritized for removal. In Unit 3, the cut/burn treatment was completed with a post-harvest broadcast burn later that same year (October 1984).

Data collection

A seed monitoring system was established immediately after treatment completion. Each treatment unit was overlain with a systematic grid of 20.1 m × 20.1 m, buffered by 20.1 m from the unit edge. Seed traps with a collecting surface of 0.405 m² were relegated to 15 randomly-selected grid intersections per unit. From 1985 to 1994, all trapped seeds were collected and counted once annual seed release was completed. Seed origin species were determined, and seeds were distinguished as viable or non-viable. Only viable seeds from ponderosa pine were used in the present study.

According to Shepperd *et al.* (2006), *P. ponderosa* crops can be considered as exceptional in our range of stand densities when they exceed 250,000 viable seeds/ha; crops are considered low at less than 50,000 viable seeds/ha. In the present study, we adopted the latter value as a threshold value, defining a crop as a mast pulse when at least one unit exhibited viable seed amounts beyond 50,000 viable seeds/ha. Differences among crops in mast years were investigated through a Tukey's test of simultaneous inference. A square root transformation was applied to seed amounts in

order to satisfy the parametric assumptions of normality and homoscedasticity.

Daily meteorological data recorded at the NWCC (National Water and Climate Center, U.S. Department of Agriculture) Snotel Station 604, Lubrecht Flume (N 46.53, W 113.19) from 1983 to 1994 were retrieved, consisting of: (1) first seven correlative days with no frost (NFW), (2) number of freezing days after the occurrence of the NFW until the 31th of August (FD), (3) mean temperature during the 15 days following NFW occurrence, or until the 31th of August if NFW happens to take place within 15 days before that date (T), and (4) total precipitation from May 1st to August 31st (PP). We calculated these metrics for both one and two years prior to seed release, which frames the full period needed for cone maturation. Preliminary graphical analysis seemed to indicate that NFW is a good indicator metric signifying the end of winter conditions. During the period of study (1985-1994), the occurrence of NFW varied from the beginning of May to mid-July.

Synchronic seed production, cyclical masting and crop depletion

In order to confirm the existence of a synchronous pattern of seed production (masting habit) in *P. ponderosa*, Kendall's coefficient of concordance (W) was assessed. This coefficient tests the independence of the by-year rank of collected seeds among the different traps from each unit. A W coefficient equaling 1 indicates perfect synchrony, whereas W equaling 0 denotes rank independence (Legendre, 2005).

Whether cyclical masting (year-to-year fluctuations in seed crops) occurs in ponderosa pine as a result of crop depletion has not previously been demonstrated. Our key hypothesis was that seed production is controlled by climate factors. A cyclical masting effect would obfuscate that relationship, so we first tested whether such endogenous cycles were evident (*sensu* Greene & Johnson, 2004). First, we analyzed synchrony among crops by plotting the series of trapped seeds per unit over time. Subsequently, we calculated separately for each unit the Spearman rank correlation coefficients for 2-year, 3-year and 4-year lagged per-unit totals of annual seed counts. As applied to the present study, this non-parametric statistic assesses the ability of a monotonic function to describe the relationship among series of lagged crops. Such an assessment was suggested by Greene & Johnson (2004) for these types of data, as the observations are not expected to be normally distributed. To test for a crop-depletion effect after a mast year, we assessed the same calcula-

tions considering a lag of 1 year between crops (Greene & Johnson 2004). Should such a crop-depletion effect exist, a significant negative correlation would be expected between consecutive observations.

Climate influence on masting habit

To study likely relations between climate and bumper crops, we carried out a preliminary graphical analysis in order to search for specific patterns. We computed the average value of the total collected seeds from each unit and plotted them against climate variables that might influence the process: FD, T and PP two years prior (flowering phase) and one year prior (cone initiation phase) to seed release (FD2, FD1; T2, T1; PP2, PP1). The total number of seeds collected within each unit was transformed to create a binary variable equaling 1 when a mast year takes place, and zero in all other cases (30 observations). We tested the effect of the selected independent climate variables on the occurrence of a mast year by means of a generalized mixed model, assuming a binomial distribution for data (binary response). The aforementioned variables entered the model as linear terms through a logit link function. A unit random effect was included to take into account correlation among measurements from the same unit. Variable selection was carried out sequentially, with the presence of any pattern in the residuals being checked at each step. All calculations were computed in R 3.0.1 (R Core Team, 2013). Significance for all analyses was determined at $\alpha = 0.05$.

Results and Discussion

Seed rain

Overall, 1,141 viable seeds were collected during the study period. Seed rain ranged from 500,411 viable seeds/ha (estimated for Unit 2 in 1985) to null crops of 1986 and 1987. In addition to the latter two years, the years 1989, 1990, 1991 and 1993 failed to reach the threshold of 50,000 viable seeds/ha. The mean value and standard error of the mean of those crops occurring beyond this threshold was 153,772 and 41,825 seeds/ha, respectively. Tukey's test on mast crops yielded significant differences between years 1985 and 1992 (p -value= 0.0056). The distribution of seeds among plots was 33% for Unit 1, 40% for Unit 2, and 27% for Unit 3. Spatially, seed dispersal was relatively homogeneous throughout the units, as illustrated by the low coefficient of variation across the traps (*e.g.*, in 1985

CV's for Units 1-3 were 0.56, 0.63 and 0.45, respectively)

For the mast year of 1985, or just one year from the completion of restoration treatments, the seed crop of the cut/no burn treatment unit (Unit 2) exceeded by threefold that of the cut/burn treatment (Unit 3). However, this trend reversed with the passage of time following the restoration treatments. During 1992 and 1994, seedfall was greater in the cut/burn unit (Unit 3) than in the cut/no burn unit (Unit 2) (Figure 1); seedfall in both treated units far exceeded that of the untreated control (Unit 1).

Cutting and burning treatments are commonly prescribed by managers in this region to simulate the historic disturbance regime of low-intensity, frequent surface fires under which ponderosa pine forest ecosystems developed and perpetuated (Agee, 1996). Commonly, the goal of these restoration treatments is to reverse the cumulative negative consequences of fire suppression on stand conditions; namely, development of great wildfire hazard, densification of low-vigor trees, and displacement of ponderosa pine by more shade-tolerant species (such as Douglas-fir). Treatment effectiveness in addressing the first two issues has been widely studied and well demonstrated (*e.g.*, Graham *et al.*, 2004; Jain *et al.*, 2012; McIver *et al.*, 2012), but few have studied the effects of restoration treatments on ponderosa pine seed production. Our findings contribute evidence that restoration treatments benefit seed production, but also suggest that the specific details of the treatment matters. At a nearby site in western Montana, similar restoration treatments (combinations of cutting and burning) improved ponderosa pine tree growth and physiological responses, but no difference among treat-

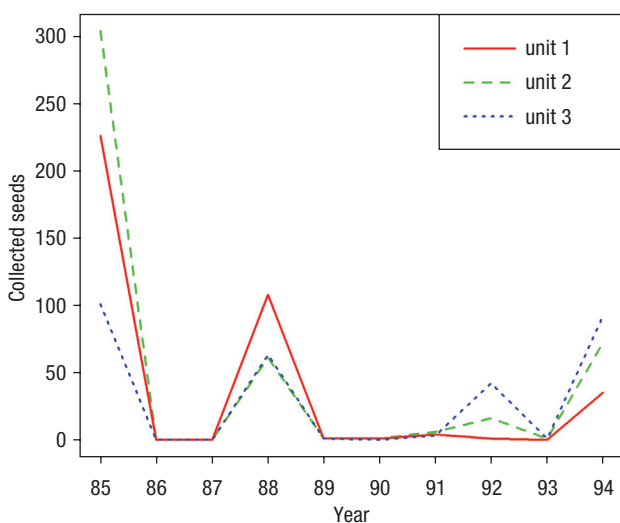


Figure 1. Total collected seeds over time from the three units (solid line, control; dashed line, cut/no burn; dotted line, cut/burn), with a synchronous seed production pattern evident.

ment combinations was evident (Sala *et al.*, 2005). A related study of reproductive output at the same site showed a similar treatment benefit, with all treatments producing a greater number of cones per tree than the control, but also revealed distinct differences among treatment combinations (Peters & Sala, 2008). Specifically, the viable seed mass, germination rate, and time to germination were all far lower for the cut and spring burn treatment than the cut-no burn treatment, the cut and fall burn treatment, and the control. More research is clearly needed to better understand the mechanisms for differing restoration treatment effects on these and other attributes of reproductive output.

Synchronic seed production, cyclical masting and crop depletion

Kendall's coefficient of concordance proved significantly different from zero (p -value < 0.0001) in all three units over the 10 study years, with high values of W (0.7965, 0.8014, 0.8087 for plot 1, 2 and 3, respectively). These results confirm the strong masting habit that has long been documented in ponderosa pine throughout the species' range, including the northern Rockies (Curtis & Foiles, 1961; Shearer & Schmidt, 1970), the central Rockies (Roeser, 1941; Shepperd *et al.*, 2006; Mooney *et al.*, 2011), the Pacific Northwest (Daubenmire, 1960; Dahms & Barrett, 1975), Arizona (Larson & Schubert, 1970), and California (Fowells & Schubert, 1956; Sundahl, 1971; McDonald, 1992).

Understanding the factors contributing to temporal variation in tree seed production remains a compelling research problem for ponderosa pine and other North American tree species. The questions concern both the possibilities of cyclical masting, where it is believed that mast crops are produced at roughly regular intervals (as was concluded by Sork *et al.* (1993) for *Quercus* species), and resource depletion, where it is believed that the resource demand associated with producing large seed crops invariably results in depauperate crops during the year immediately afterwards (*e.g.*, Piovesan & Adams, 2001). In their comprehensive study of seed production records of 22 tree species, Greene & Johnson (2004) observed no evidence of cyclical production patterns, but did find a modest, seldom-significant tendency for years of high seed crops to be immediately followed by low seed production years. Our data support both of those conclusions. Graphical analysis of crop series over time indicated a clear synchronous pattern in seed production (Figure 1), but Spearman rank correlation coefficient assessments failed to show strong evidence for a 2-year, 3-year or 4-year cyclical masting pattern in annual seed counts (Table 1). Inter-

estingly, the Spearman coefficient was much higher for the 3-year lagged yields than for the other cases; Unit 3 arose as the only (slightly) significantly related series. Recognizing the limitations of our dataset, we believe that the results for the 3-year lag may reflect the occurrence of strong mast events in 1985 and 1988. Weak correlations among 1-year lagged seed counts failed to provide statistically significant evidence for crop depletion after a mast event, yet the ρ statistic was negative for all three plots, which suggests indeed a tendency for lower crops to follow a mast event. This trend may be partly attributed to resource depletion following mast events, as was observed in whitebark pine (*Pinus albicaulis* Engelm.) (Sala *et al.*, 2012). In that empirical study, researchers observed the depletion of stored nitrogen and phosphorous in wild trees during mast years; depletion began during the masting year within reproductive branches only, and subsequently spread to all terminal branches during the year afterward.

Table 1. Spearman rank correlation test results for 1-year to 4-year lagged crops across each Unit. S is the Spearman statistic, ρ is the Spearman rank correlation coefficient, and n is the number of observations.

Unit	Lag (yr)	S	ρ	p -value	n
1	1	171.429	-0.429	0.250	9
2	1	160.174	-0.335	0.378	9
3	1	153.391	-0.278	0.468	9
1	2	141.418	-0.683	0.062	8
2	2	118.225	-0.407	0.316	8
3	2	127.559	-0.519	0.188	8
1	3	13.728	0.755	0.050	7
2	3	14.785	0.736	0.060	7
3	3	12.020	0.785	0.036	7
1	4	43.754	-0.250	0.633	6
2	4	33.906	0.031	0.953	6
3	4	38.234	-0.092	0.862	6

Climate influence on masting habit

Due to the modest size of our dataset, the model failed to converge when more than one variable was included during the selection process. Therefore, we fitted one model for each variable showing a clear pattern in regard to mast occurrence. The quadratic form of T1 and T2 proved significant or nearly significant in their respective models (Table 2). This fact suggests that mast events are promoted by the occurrence of optimum mean temperatures promoting mast events in the beginning of spring during both the first year (11 °C) and the second year (9 °C) of cone development. PP1 exhibited a significant positive trend in regard to bumper crops (Table 2). FD2 was also significant (negative, signifying a suppressive effect on mast production); however, it seems to be strongly correlated with T2. All other variables were non-significant. The variance of the random effect was very low in all cases, indicating a negligible influence of the silvicultural treatments on seedfall.

Our findings support the hypothesis of climate-based masting in ponderosa pine. Climatic control of key cone development processes has already been identified in other *Pinus* species (*e.g.*, Calama *et al.*, 2011). Flowering in particular seems to be strongly affected by temperature and precipitation, which would explain the observed synchronous pattern in cone production. Working in Colorado, Mooney *et al.* (2011) claimed that cool weather at the pollen formation stage supports masting in ponderosa pine. The difference with our quadratic formulation of temperature may simply be due to the colder temperatures associated with our higher-latitude sites in Montana. The fact that temperature is also influential at the cone formation stage in Montana seems to confirm this circumstance.

Table 2. Main statistics for masting occurrence models, using T1, T2, PP1 and FD2 as explanatory variables; σ_u^2 is the variance related to the unit random effect.

variable	Model T1		Model T2		Model PP1		Model FD2	
	param. estimate	p -value	param. estimate	p -value	param. estimate	p -value	param. estimate	p -value
Intercept	-25.3835	0.0575	-35.7943	0.0275	-4.8808	0.0221	0.8717	0.01688
T1	4.7138	0.0526	–	–	–	–	–	–
T1 ²	-0.2116	0.0529	–	–	–	–	–	–
T2	–	–	5.2996	0.0375	–	–	–	–
T2 ²	–	–	-0.18400	0.0531	–	–	–	–
PP1	–	–	–	–	0.6086	0.0391	–	–
FD2	–	–	–	–	–	–	-0.2665	0.0125
σ_u^2	~ 0	–	~ 0	–	~ 0	–	~ 0	–
AIC	33.73		27.46		39.14		39.95	

Conclusions

For our analyses of 10-year seedfall and climate records in western Montana, we observed that ponderosa pine seed production pattern was non-cyclical, synchronous, and independent of silvicultural treatment history. A mast-depletion effect was evident but was not statistically significant. The non-cyclical occurrence of seed mast years was influenced by climate determinants. Specifically, mast events were promoted by the occurrence of optimum mean temperatures at the beginning of spring during both the first (11 °C) and second (9 °C) years of cone maturation. The probability of a mast year was also affected by precipitation amount (positive effect) during the first year, and late frosts (negative effect) during the second year. These factors seem to explain the synchronous pattern of seed production observed for this species. As a result, we conclude that fluctuations in mean early spring temperatures, late frost events, and water availability are likely to produce concomitant fluctuations in *P. ponderosa* seed production in this region.

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