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Both weather and resources influence masting in chestnut oak (*Quercus montana* Willd.) and black oak (*Q. velutina* Lam.)

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Abstract Masting is the synchronous and highly variable production of fruit within a population. Although several hypotheses have been proposed to explain why and how masting evolved in plants as a reproductive strategy, the factors that trigger a large reproductive effort in a particular year are still not well understood. While both weather and resources have been proposed to play an important role, testing these hypotheses has been challenging due to a lack of long-term data and appropriate experimental designs. In this manuscript, we used 18 years of acorn production data to analyze the relationship between resources, weather, and masting in black oak (*Quercus velutina*) and chestnut oak (*Q. montana*). The data were collected in southeast Ohio as part of the Fire and Fire Surrogate (FFS) study, which applied silvicultural treatments (i.e., thinning and prescribed fires) to reduce competition and manipulate resources. We found species-specific responses to the thinning and fire treatments, with an overall increase in acorn production for chestnut oak in the thin + burn treatment and an increase for black oak in the thin-only treatment compared to the control. Chestnut oak reproduction also had strong positive relationships with warm spring temperatures, and a positive change in summer temperatures compared to the previous year (i.e., summer temperatures that went from cool to warm). For black oak, warm spring temperatures increased acorn production while later starts to spring warming the year before decreased acorn production. These results support the hypotheses that both resources and weather (as a cue and as a limiting factor) are important for masting in oaks. Thus, both factors should be included in predictive models for acorn production under current and future climate conditions.

Keywords Fagaceae · Hard mast · Tree reproduction · Eastern deciduous forests · Acorns

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Introduction

In eastern deciduous forests, oaks are considered foundational species that drive forest ecosystem dynamics by providing pulses of food resources

through masting (Fralish 2004; Koenig and Knops 2005; McShea et al. 2007; Ostfeld and Keesing 2000). Masting is the intermittent and highly variable production of seed by a population (Silvertown 1980). Hypotheses for why masting evolved as a reproductive strategy broadly include economies of scale, such as predator satiation and pollination efficiency (Janzen 1971; Koenig and Knops 2005; Norton and Kelly 1988; Silvertown 1980), while proximate drivers such as resources and weather are thought to affect masting on a yearly basis (reviewed in Pearse et al. 2016). Although masting has been studied in a multitude of species around the world, the common factors that trigger large reproductive effort in any one particular year are still not well understood (Koenig et al. 2016; Satake and Iwasa 2002). This is partly because the individual factors that lead to variation in reproduction are inconsistent across species and geographic regions (Kelly and Sork 2002; Koenig et al. 2016; Norton and Kelly 1988; Pearse et al. 2017). Identifying the factors that influence reproductive variability will be essential, if we are to predict how reproduction will be affected under future climate change.

Temperature can be an important cue for masting, as it can synchronize populations over large spatial scales. Spring temperatures in particular, are hypothesized to cue populations to begin flower initiation or fertilization. In European temperate forests, warm spring temperatures were positively correlated with large seed crops in both red oak (*Q. rubra* L.) and sessile oak (*Q. petraea* Matt. (Liebl.)) (Caignard et al. 2017). Sork et al. (1993) and Koenig et al. (2008) also found positive relationships between warmer spring temperatures and seed crop size in black oak (*Q. velutina* Lam.), northern red oak, white oak (*Q. alba* L.), and the California valley oak (*Q. lobata* Née) in North America. Warm spring temperatures also reduced microclimate variability for *Q. lobata*, which increased phenological synchrony leading to larger acorn crops (Koenig et al. 2015). Temperatures in years preceding masting events have also been shown to act as cues. For example, the positive change in mean summer temperature (ΔT) from the previous year compared to summer temperatures two years before seed crop, acted as a weather cue for several masting species in New Zealand by synchronizing populations, resulting in increased reproductive effort (Kelly et al. 2013).

Weather can also act as a limiting factor and reduce seed crop size when temperature or precipitation negatively impact flower production, pollination, fertilization, or fruit development (McCarthy and Quinn 1989). Northern red oak experienced reduced reproduction in years with late spring frosts the year prior, as these weather events damaged initiating flowers and developing ovules (Sork et al. 1993). Precipitation during flowering can also limit reproductive effort in northern red oak, as the likelihood of successful pollination decreased as precipitation increased (Kasprzyk et al. 2014). Similarly, Cecich and Sullivan (1999) found that the number of spring days with hail had a negative correlation with flower survival for white oak and black oak. Hail damaged male catkins and pistillate flowers, thus resulting in decreased acorn crops.

Although previous studies have found support for weather as a cue or as a limiting factor, Pearse et al. (2016) proposed that resource availability, or stored resources, *in combination with weather* is likely what drives variability in seed production. This particular hypothesis can be challenging to test, as modifying resources can be logistically difficult and weather can have both a direct and indirect effect (i.e., a direct effect as a cue or limiting factor, or by indirectly influencing resources). This indirect effect of weather on resources is most clearly demonstrated by the influence of summer droughts on crop size. Across a seven-year study, Sork et al. (1993) found that years with the lowest acorn production in black oak, northern red oak, and white oak were associated with summer drought. Espelta et al. (2008) also saw a significant decrease in acorn crops with increased summer droughts for both holm oak (*Q. ilex* L.) and downy oak (*Q. humilis* L.) in the Mediterranean.

Although rare, experimental approaches can also be used to clarify the influence of weather and resources on reproductive effort. For example, Bogdziewicz et al. (2017) found that adding nitrogen fertilizer to northern red oak increased acorn production overall. Smaill et al. (2011) added nitrogen fertilization to New Zealand Mountain beech (*Nothofagus solandri* var. *cliffortiodes* (Hook f.) Pool) and found that seed production in unfertilized plots was determined by rainfall during the resource priming phase. In fertilized plots, seed production was more influenced by temperature during flower formation. Lombardo and McCarthy (2008) used a combination of thinning

and burning treatments established through the Fire and Fire Surrogate (FFS) Study, to modify stand structure, composition and resources. For chestnut oak only, they found that the treatments with burning showed a small increase in acorn production. Chestnut oak seed crops were also negatively correlated with summer drought and low minimum temperatures from May to June. Although black oak acorn production was insensitive to the treatments, crop size was negatively correlated with droughts during October of the first growing season and February of the second growing season. Thus, resource availability and weather may both play a role for masting in chestnut oak and black oak. However, masting is a multi-year phenomenon and precaution should be taken when drawing conclusions from this 5-year analysis.

In this manuscript, we present the results of 18 years of data from this same FFS study and re-examine the influence of resources and weather on masting. First, we examine the potential effect of resource limitation by comparing reproductive effort between silvicultural treatments. We hypothesized that the control treatment should have the lowest seed production, while the thin + burn treatment should have the highest production. All three treatments were effective at reducing density, and black and chestnut oak both showed substantial increases in basal area increment (BAI) following the treatments, while BAI in the control remained unchanged (Anning and McCarthy 2013b). Soil nutrient availability after the first fire in 2001 did not show a significant increase (Boerner et al. 2008); however, repeated fires in the same forest (but for a different study) found an increase in soil pH and Ca availability (Boerner et al. 2004). Second, we determine which weather parameters are associated with reproductive effort (weather parameters and their link to specific hypotheses are summarized in Table 1). If weather acts as a cue for masting, we hypothesized that warm springs will be positively correlated with reproduction (e.g., as this would trigger bud burst and flower development). If weather acts as a limiting factor for seed production, we hypothesized that freezing spring temperatures or heavy precipitation during pollination will be negatively correlated with reproductive effort. Finally, if weather indirectly affects resources that are important for seed production, then we would expect drought to be negatively correlated with reproductive effort.

Methods

Site history and description

Data collection for this study occurred in Zaleski State Forest (39° 35′ 5″ N, 82° 37′ 0″ W) and Vinton Furnace State Experimental Forest (39° 20′ 0″ N, 82° 39′ 0″ W), located in Vinton County, Ohio. Both sites are located in the unglaciated Allegheny Plateau region of Ohio and are composed of second growth forests that began regenerating between 1850 and 1900, after clearcutting for the charcoal iron furnaces ceased (Iverson et al. 2008; Lombardo and McCarthy 2008; Yaussy et al. 2013). The topography is deeply dissected which creates strong microclimatic gradients with dry west and south slopes and mesic north and east facing slopes (Albrecht and McCarthy 2006). Due to land use history, canopies in Zaleski and Vinton Furnace are oak dominated, with a mid/understory of shade tolerant species such as red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), and black gum (*Nyssa sylvatica* Marshall) (Albrecht and McCarthy 2006). This area has a mean annual temperature of 12.4 °C and mean annual rainfall of 95.62 cm.

In 2000, the FFS study was initiated to test potential management effects on regeneration of oak and hickory species (Iverson et al. 2008; Lombardo and McCarthy 2008; Yaussy et al. 2013). Four treatment areas were established within Zaleski and Vinton Furnace: control (C), thin-only (TO), thin and burn (TB), and burn-only (BO). Thinning occurred from December 2000 to February 2001, focusing on retaining oak and hickory while removing midstory trees from 15 to 30 cm DBH. Basal area in Zaleski was reduced from 25.5 to 18.5 m^2 ha^{-1}, overstory density was reduced from 192 to 142 stems per ha, and midstory density was reduced from 255 to 150 stems per ha. Basal area in Vinton Furnace was reduced from 28.0 to 22.6 m^2 ha^{-1}, while overstory and midstory densities were reduced from 133 to 103, and 239 to 194 stems per ha, respectively (Yaussy et al. 2013). Prescribed burns occurred approximately every 5 years, starting in early April 2001 before leaf-out and ending in early April 2016. During this time period, there have been a total of 4 burns (i.e., 2001, 2005, 2010, 2016).

Table 1. A subset of the weather parameters examined, with associated hypotheses about how they would influence reproductive effort

Variable	Description	Definition	Assoc. hypothesis
ΔT	Change in average summer temperature from year^{-1} to year^{0}	Summer was defined as June, July and August	Weather as a cue
Mean maximum spring temperature	Mean maximum spring temperature. Included one lag year	Chestnut oak: spring is defined as April 21–May 4 Black oak: spring is defined as April 14–May 8	Weather as a cue
Mean minimum spring temperature	Mean minimum spring temperature. Included one lag year		Weather as a limiting factor
Mean maximum spring precipitation	Mean maximum spring precipitation. Included one lag year		Weather as a limiting factor
Date of spring warming (mean < 5 °C)	Day of year after which frosts were unlikely. Included one lag year	Last day of spring with daily mean temperature < 5 °C	Weather as a limiting factor
SummerDaysNoRain	Total number of days without rain in summer. Included one lag year	Summer defined as June, July, August	Resource
Summer PDSI	Average PDSI for June, July, and August. Included two lag years	Palmer severity drought index	Resource
Full PDSI	Average PDSI for June, July, August, and September. Included two lag years		Resource

Current year = year^{0}, previous year = year^{-1}. See Table S2 for a complete list

Species of interest

Due to the differences in seed maturation time, a species from the white oak group and a species from the red oak group were chosen for the FFS study. Chestnut oak is in the white oak subgenus *Leucobalanus*. Male and female flowers are initiated in the spring and mature within 6 months (Sharp and Chisman 1961; Sharp and Sprague 1967). Black oak is in the red oak subgenus *Erythrobalanus*. Black oak produces staminate and pistillate flowers in the spring of the first summer, with pollination occurring in April; however, flowers are not fertilized until the following spring, thus taking 18 months for black oak acorns to mature (Sork et al. 1993). Both oaks are wind-pollinated; however, the difference in reproductive cycles should lead to differences in their response to weather and resource requirements. Black oaks in particular are expected to be more susceptible to environmental damage, due to this extended period between flower formation and maturation (Sork 1993).

Seed Collection

As part of the FFS study, 144 trees (72 chestnut oak and 72 black oak) were selected to observe if treatment had an impact on seed production (Lombardo and McCarthy 2008). Two 0.25 m^2 seed fall traps were placed under the dominant canopy of each tree. Seed fall traps were set out each year in August and acorns were collected monthly until December when seed fall ceased. For each tree, acorns were categorized as sound, aborted, weevil infested, or other (Lombardo and McCarthy 2008). Acorns that appeared sound were weighed and then broken open to check for weevil infestation. Acorn collection began in 2000 and continued every year in all four treatments, until 2015. Acorn collection resumed again in 2017, but only in the control and thin-only plots. The dataset for this analysis is composed of years 2000–2015 and 2017–2018 (data were not collected in 2016).

Data and statistical analysis

Weather data were provided by a local weather station, located inside Vinton Furnace Experimental Forest. Hourly temperature and precipitation data were aggregated into daily mean, minimum, and maximum values that were then used to calculate the various weather variables (Table 1). Monthly acorn data were summed per tree per year and included all sound, weevil infested, and other acorns (as these were fully developed acorns that had been partly eaten or infected by a fungus). Total acorn production for each species was summarized based on trap area (i.e., acorns per m^2 of seed trap) to adjust for differences between years in sample sizes, as more trees were added in the second and third years of the FFS Study. Acorn data were log transformed ($\ln(x + 1)$) to meet assumptions. The choice to use annual plot totals as our response variable for most of our analyses, is because this paper is analyzing the drivers of population-level variation in reproduction (not individual trees per se). A subsequent paper will be examining the drivers of individual-level variation in reproduction.

All data analyses used the statistical software R (v. 4.0.0, R Core Team 2020). To determine if there was a treatment effect (i.e., the effect on all of the trees within a treatment unit) on the production of seeds for each species, we used linear mixed effect models and the nlme library (v. 3.1-147, Pinheiro et al. 2020). The transformed seed data were used as the response variable while treatment and year were used as explanatory variables. Treatment and year were treated as factors. For this analysis only, the replicates were individual trees because we needed variation within a year and treatment, to run an ANOVA. Study site was included as a random effect because the FFS study was designed as a randomized complete block design, with all treatments replicated at each site. Since the limited number of levels in site can pose problems for random terms, we also tried site as a fixed effect. Site (as a fixed effect) was not significant and results for all other variables remained the same as for the presented analysis that includes site as a random effect. While acorn collection began in 2000, data for determining the effect of treatment on masting included years 2001–2015 because these years included all four treatments. We also looked for a potential lag effect on reproduction from the fire treatments. Due to the potential impact of weather, we used the final generalized linear weather models for each species (i.e., these models predicted acorn production based on weather parameters, see below). We ran the final weather model for each treatment separately, then extracted the residuals of acorn production for each year and plotted the residuals against time. If fire did provide delayed benefits by lowering competition and increasing resources, the residuals for the burn-only and thin+burn treatments should be higher than the thin-only and control treatments, especially the year after a fire (i.e., after accounting for weather, those treatments that included fire would have higher acorn production than the weather model predicts).

To determine the relationship between weather and acorn production, we used generalized linear models with the total number of seeds produced per year as the response variable (i.e., the annual plot totals per m^2) and a variety of weather parameters as explanatory variables (Table 1, Table S2). We calculated different weather parameters based on our hypotheses about the processes that were most likely to affect flower development, pollination, and maturation. For chestnut oak, spring was defined based on the dates of flowering as reported by Sharp and Chisman (1961) and Sharp and Sprague (1967). For black oak, spring phenology dates were based on reports by Cecich and Haenchen (1995) and Cecich (1997). These studies represent the most comprehensive and recent studies for flowering phenology in these two species of oaks. However, it is important to acknowledge the potential uncertainty surrounding these dates, as they were recorded decades ago in Pennsylvania and Missouri, respectively.

Although we considered a comprehensive set of weather variables (Table S2), most had no relationship with seed production. We used the correlation coefficient between each weather parameter and seed production to identify potential weather variables (Pearson's $r > |0.4|$). This resulted in five weather variables for chestnut oak and black oak. We then created linear models based on this subset of variables. Model selection was done using the lowest AICc score, as calculated from the R package MuMIn (v. 1.43.17, Barton 2020), and the principal of parsimony when multiple models were equally ranked. Akaike information criterion (AICc) score measures the fit of a model while correcting for the fact that models with a higher number of parameters will have an improved

fit. We include the results from the best model only (see Tables S3 and S4 for additional models).

Results

Based on the total number of acorns caught per m^2 of seed trap, the three largest reproductive events for chestnut oak occurred in 2010, 2012, 2014, and the three largest reproductive years occurred in 2001, 2007, and 2010 for black oak (Fig. 1). Chestnut oak had larger variation in reproductive effort among years (coefficient of variation (CV) = 1.91) compared to black oak (CV = 1.52).

Resources

From 2001 to 2015, annual mean chestnut oak acorns per m^2 was 19.3 (± 5.7 SE) in the control treatment, 15.6 (± 4.3) in the thin-only treatment, 15.5 (± 4.0) in the burn-only treatment, and 28.0 (± 7.6) acorns per m^2 in the thin + burn treatment. Annual mean CV for chestnut oak in the control treatment was 1.81, 1.34 for thin + burn, 1.47 for thin-only, and 1.82 for burn-only. For black oak, acorn production across treatments was a little more even (from 2001 to 2015: mean annual acorns per m^2 was 19.5 (± 5.3 SE) in the control treatment, 23.3 (± 5.6) in the thin-only treatment, 18.5 (± 3.4) in the burn-only treatment, and 22.2 (± 5.1) in the thin + burn treatment). Annual mean CV for black oak in the control treatment was 1.41, 1.28 in the thin + burn, 1.26 in the thin-only, and 1.23 in the burn-only.

Treatment, year and the interaction between treatment x year all had a significant effect on acorn production for both species (Table 2). The effect of year on acorn production indicates high variability in acorn production among years (Fig. 2), which is expected for masting species. The effect of treatment on acorn production was also significant for both species (Table 2). When comparing across all years, chestnut oak produced significantly more acorns in the thin + burn treatment when compared to the other three treatments (Tukey post hoc comparisons averaged over year; TB to Control, $P = 0.001$; TB to BO, $P < 0.001$, TB to TO, $P = 0.002$). Mean annual chestnut acorn production in the control, thin-only and burn-only treatments were not significantly different from one another. For black oak, even though there was a significant treatment effect (Table 2), the only post hoc comparison that was approaching significance was the thin-only treatment producing more acorns than the control (Tukey post hoc comparisons averaged over year; TO to Control, $P = 0.07$). The treatment × year interaction was more difficult to interpret, as it implies that the order of the treatments differed and/or that there were not significant differences between treatments in some years (Fig. 2).

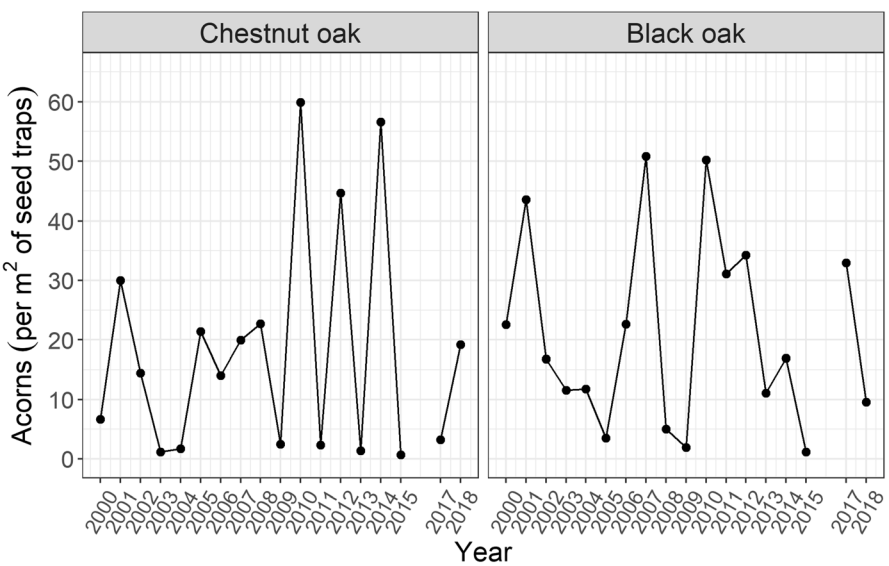

Fig. 1 Mature acorn production (per m^2 of seed trap) between 2000 to 2018 for chestnut oak and black oak, across both sites and all treatments. Seed traps were not set out in 2016

Table 2. Analysis from a linear mixed effects models determining the effect of silvicultural treatments on chestnut oak and black oak

Species		*df*	χ^2	*P*-value
Chestnut oak	Treatment	3	13.05	0.005
	Year	14	261.65	< 0.0001
	Treatment × year	42	74.80	0.001
Black oak	Treatment	3	14.84	0.002
	Year	14	172.43	< 0.0001
	Treatment × year	42	70.49	0.004

The four treatments included Control, Thin-Only, Thin + Burn, and Burn-Only. The response variable was the number of acorns collected per m^2 with fixed explanatory variables being treatment and year (year was treated as a factor). For this analysis only, the replicates were the individual trees (72 chestnut oak and 72 black oak). Acorn data were log transformed (ln $(x + 1)$) to meet assumptions, and site was included as a random effect

We extracted the residuals from the weather models (see below) to look for a lag effect of the prescribed fires. Time since fire was significant for both chestnut oak (Table S1, $F_{5,32} = 2.5$, $P = 0.05$) and black oak ($F_{5,36} = 19.9$, $P < 0.001$). However, since the residuals from all treatments went up or down in the years after a fire (Fig. S1), it cannot be a response to fire (since there was no fire in the Control or Thin-Only treatments). This was supported by the statistical analysis that found no effect of treatment and no interaction between treatment and time since fire for either species (Table S1). Thus, the effect of time since fire on the residuals likely reflects some other confounding factor or is just a coincidence.

Weather

Weather conditions in spring and summer had a significant effect on reproduction in chestnut oak

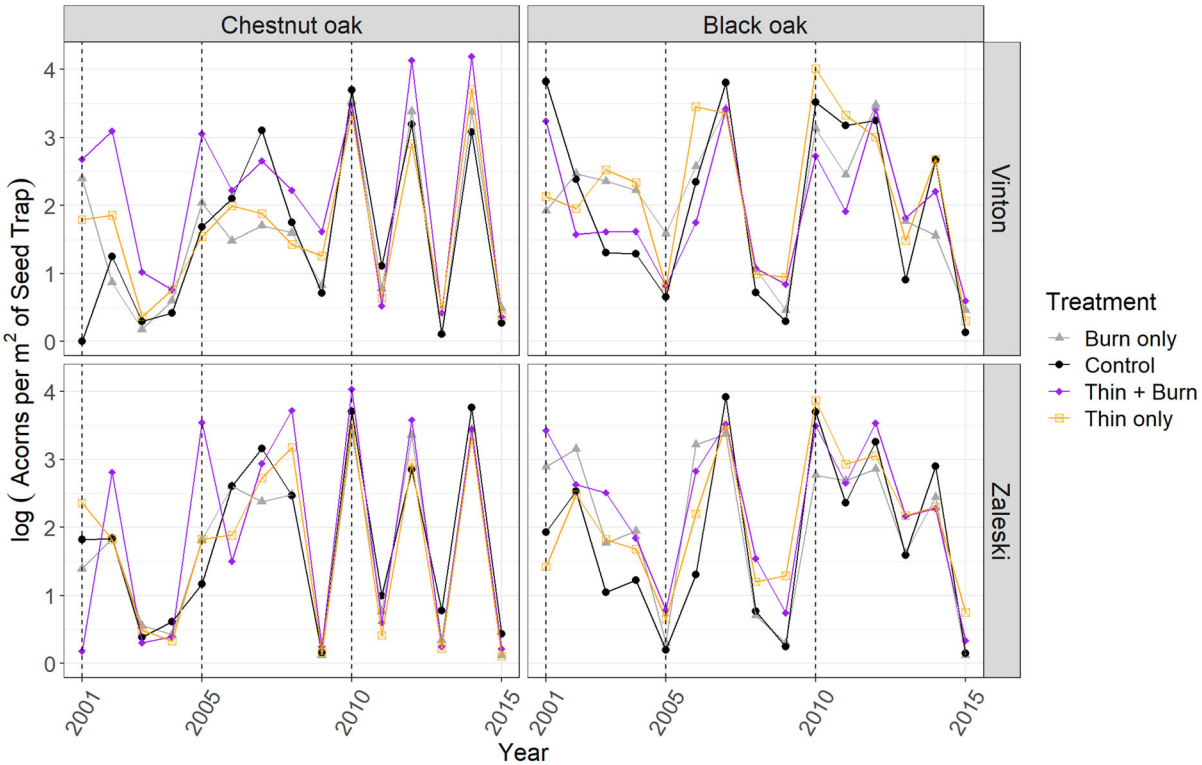

Fig. 2 Mean number of mature acorns collected per m^2 of seed trap for each treatment, at our two sites (Vinton and Zaleski). Treatments included Control (C), Burn-Only (BO), Thin-Only (TO), and Thin + Burn (TB). Black dashed vertical lines indicate years when prescribed fires took place. Thinning occurred at the start of the experiment in 2001. See Table 2 for accompanying model statistics

Table 3 Analysis from a generalized linear model for predicting the total number of seeds collected each year for the plot

Species	Weather variable	Estimate	SE	*SS*	*df*	*F*-value	*P*-value	R^2
Chestnut oak								
	ΔT	0.80	0.18	14.43	1	20.25	< 0.001	0.55
	Mean maximum spring temperature	0.22	0.10	3.41	1	4.79	0.048	
	Residuals			9.27	13			
Black oak								
	Mean maximum spring temperature	0.45	0.17	4.28	1	7.12	0.02	0.35
	Date of spring warming (mean < 5 °C) ($year^{-1}$)	-0.06	0.02	3.91	1	6.5	0.02	
	Residuals			9.01	15			

Seed collection data were log transformed (ln $(x+1)$) to meet assumptions. The ($year^{-1}$) refers to the date in the previous year. Additional variable definitions are listed in Table 1

(Table 3). The change in summer temperature from the previous year ($year^{-1}$) to the current year ($year^{0}$) had a significant positive relationship with number of acorns produced, while mean maximum spring temperature also had a significant positive relationship (Fig. 3). Acorn production increased, when difference in summer temperatures was positive (i.e., a cool summer to a warmer summer). For example, from 2009 to 2010, summer temperatures increased by 2.66 °C and a total of 2126 chestnut oak acorns were caught in seed fall traps in 2010 (Fig. 3a). However, from 2014 to 2015, summer temperatures cooled by 0.06 °C and only 25 chestnut oak acorns were caught in seed fall traps in 2015 (Fig. 3a). Other possible weather models included minimum spring temperature and annual precipitation (Table S3); however, minimum and maximum spring temperatures are highly correlated (Pearson's $r = 0.76$, $df = 20$, $P < 0.001$). This model explained 55% of the variance in annual chestnut oak seed production (Table 3).

For black oak, the best model for predicting reproduction included the mean maximum spring temperature and the day of spring warming the previous year ($year^{-1}$) (Table 3). Warmer springs also had a significant positive relationship on seed production for black oak (Fig. 4a). While the day of spring warming had a significant negative relationship, with reduced reproduction when spring warming occurred later the previous year (Fig. 4b). For example, 2015 was a year with very low acorn production (only 43

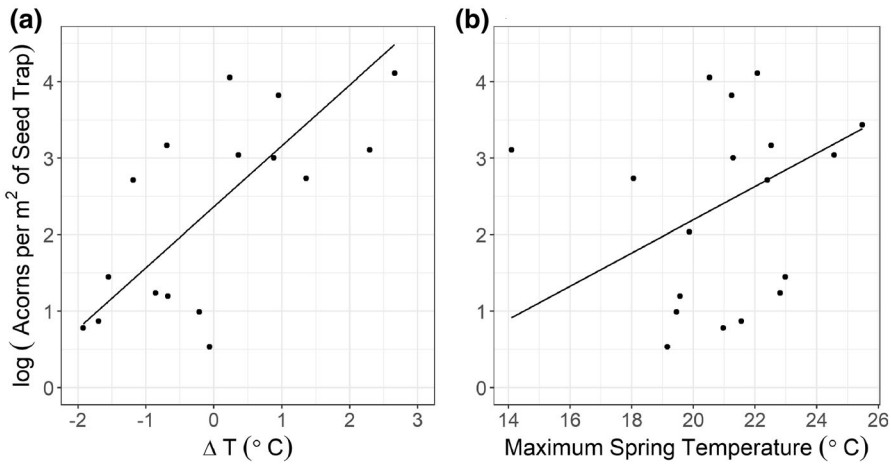

Fig. 3 Annual chestnut oak acorns collected per m^2 of seed trap, as a function of (**a**) the change in summer temperatures from the previous year to the current year, and **b** the mean maximum spring temperature (from April 21 to May 4). Dots represent years (2000–2015, 2017–2018), while the solid line is the model prediction. See Table 3 for accompanying model statistics

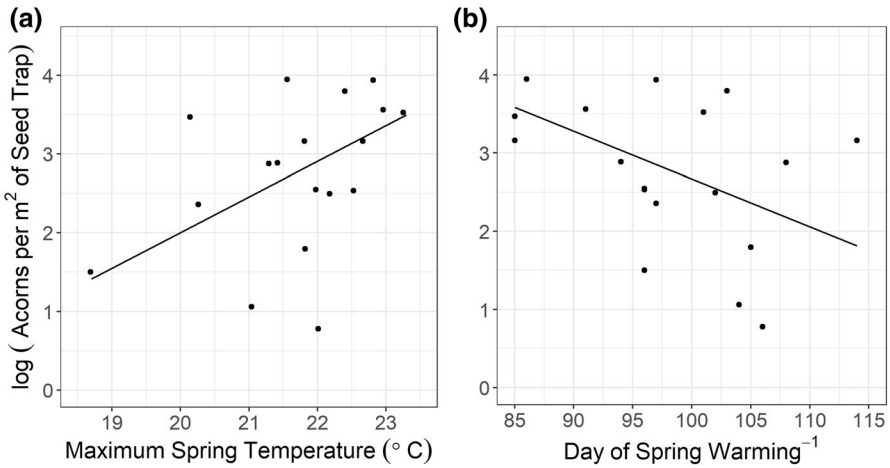

Fig. 4 Annual black oak acorns collected per m^2 of seed trap, as a function of (**a**) the mean maximum spring temperature (from April 14 to May 8), and **b** the Julian day of the previous year when spring warming started (defined as the last day when mean daily temperature < 5 °C). Dots represent years (2000–2015, 2017–2018), while the solid line is the model prediction. See Table 3 for accompanying model statistics

black oak acorns were collected from seed traps). In 2014, the last day that mean temperatures were < 5 °C was relatively late in the spring, on April 16th (DOY = 106). Alternatively, 2007 was a year with very high reproductive output (1881 black oak acorns were collected). In 2006, the last day that mean temperatures were < 5 °C occurred much earlier in the year (DOY = 86, March 27th). This model explained 35% of the total variance in acorn production (Table 3).

Discussion

The goal of this study was to identify the role of resources and weather for acorn production in two species of oak. Our results support the hypotheses that both resources and weather were important for black oak and chestnut oak. Interestingly, temperature was both a cue and a limiting factor—i.e., temperature was a cue for chestnut oak and a limiting factor for reproduction in black oak. Below, we will discuss in more detail the influence of resources and weather, as well as potential climate change impacts on masting.

Resources

Masting requires a substantial investment of resources (Pérez-Ramos et al. 2014; Yasumura et al. 2006; Żywiec and Zielonka 2013). Previous silvicultural experiments by Healy (1997) and Healy et al. (1999) found that thinning increased acorn production in northern red oak. The silvicultural treatments in our study were designed to reduce competition and increase the availability of light and resources to encourage oak regeneration. Lombardo and McCarthy (2008) analyzed the first 5 years of the FFS study, from 2001 to 2005 and found that the thin + burn treatment increased acorn production for chestnut oak only, but overall did not influence the patterns of inter-annual variation in reproductive effort. Our conclusions from 2001 to 2015 were similar, with chestnut oak showing an overall increase in acorn production in the thin + burn treatment but inter-annual synchrony among treatments was maintained. The thin + burn treatment also had the lowest CV of treatments for chestnut oak, suggesting that increased resource availability may also lower variability. Lombardo and McCarthy (2008) did not detect a treatment effect on black oak during the first 5 years of the experiment. However, our longer term dataset did find that the thin-only treatment had higher acorn production. The CV for black oak was also reduced in all silvicultural treatments compared to the control. Although resources were not directly measured, a dendrochronology study done by Anning and McCarthy (2013a) examined growth responses of trees to the treatments in these same study sites. They found that all trees (including black oak and chestnut oak) in the thin-only and thin + burn treatments showed a

significant increase in basal area increment post-treatment compared to the control, due to the reduced competition, and subsequent increase in resources and canopy space. Thus, we feel that it is reasonable to conclude that the reduced CV and the increased reproductive effort of chestnut oak in the thin + burn treatment and black oak in the thin-only treatment reflects an increase in resources.

Weather

Weather has been shown to cue large reproductive years in masting species (e.g., Kelly et al. 2013; Koenig and Knops 2014; Pearse et al. 2014), as well as, limit reproduction (Espelta et al. 2008; Sork and Bramble 1993; Sork et al. 1993). Our results support both hypotheses, in that weather acts as a cue for chestnut oak and a limiting factor for black oak in southeast Ohio. For chestnut oak, a positive change in summer temperatures compared to the previous year and warm spring temperatures were associated with large reproductive effort. These variables have independently been found to act as cues for several masting species in other studies (Kelly et al. 2013; Koenig et al. 2016; Koenig and Knops 2014; Pearse et al. 2014; Sork et al. 1993). The notion that the change in summer temperature (ΔT) could be used as a cue for masting was originally posed by Kelly et al. (2013). They found increased reproductive effort was associated with the change in temperature from the previous two summers for the masting grass species *Chionochloa pallens* Zotov. and the masting tree species *Nothofagus fuscus* (Hook.f.) Oerst. We did not find a correlation with a lag of two years; however, we did find a significant relationship between reproductive effort and the change in summer temperatures from the year before. The ΔT cue as an explanatory variable is novel in that it may account for similar mast production over large spatial areas and may explain why consecutive episodes of large reproductive effort are rare, as the second summer will have a low ΔT resulting in a small acorn crop. The ΔT cue could also suggest that chestnut oak may respond positively or be unaffected by climate change. If summer temperatures continue to gradually increase, Kelly et al. (2013) makes the prediction that masting will be unaffected because the ΔT cue will be unaffected.

Using ΔT cue for predicting increased reproductive effort in masting species has some limitations. Pearse et al. (2014) proposed two potential problems with interpreting ΔT as a weather cue. They argue that using the effect of weather on pollination success and resource limitation on acorn production is a more mechanistic way of explaining masting than ΔT. They also argue that the ΔT cue requires a perceived memory of weather conditions of years past by populations and a response to the memory (although see Samarth et al. (2020) for a hypothetical epigenetic model to explain memory). Despite their theoretical objections to the ΔT cue, Pearse et al. (2014) did find that the change in spring temperatures from the previous two years was able to predict acorn production in the California valley oak, when also combined in a model with the previous year's acorn crop and the current spring temperature. Pearse et al. (2014) also disagreed with Kelly et al. (2013) prediction about how climate change will affect masting, specifically noting that climate change will have a negative effect on the California valley oak because of mechanistic relationships between flowering and weather.

However, there are biological reasons why weather conditions in previous years are important to consider for reproduction. The determination of reproductive tissues in oaks is made the year before—both pistillate and staminate buds are initiated in the late summer, and staminate buds are structurally mature by the time dormancy occurs in October (Merkle et al. 1980; Pearse et al. 2014). This strategy for preparing the next years flowers makes weather conditions in the year prior important for flower investment and seed set. Weather in previous years could also affect resource storage. Summer droughts during bud development could shift resources away from bud formation and toward maintenance or resource storage (Willson 1983). Thus, ΔT may not solely be a cue but may also be tied to the mechanistic drivers of reproduction.

Warm spring temperatures have also been observed to be an important cue for multiple masting species, including species in the white and red oak groups (e.g., Koenig et al. 2016; Sharp and Chisman 1961; Sharp and Sprague 1967; Sork et al. 1993). Sharp and Chisman (1961) reasoned that warm spring temperatures increased reproductive effort due to successful pollination. Sork et al. (1993) also found that warm spring temperatures were important for black oak and northern red oak, expanding Sharp and Chisman's conclusions to include ovule development and fertilization.

For black oak, weather also acted as a limiting factor as late spring warming the previous year reduced seed crop size. Sork et al. (1993) also found

similar results. Black oak begin developing flowers in late March (Cecich and Haenchen 1995), and thus late spring frosts during the year of flower formation will damage developing flowers and reduce acorn crop size (Sork et al. 1993). Because black oak takes 18 months from pollination to seed maturation, stochastic events are likely to occur during this period, making it more difficult to identify the role of any single weather variable.

Conclusions

We examined the role of both weather and resources for reproductive effort in chestnut oak and black oak. Resources were found to be important for both species, as there was a significant treatment effect (all treatments had lower inter-annual variability in seed production as measured by CV, the thin + burn treatment had the highest acorn production for chestnut oak, the thin-only treatment had higher acorn production than the control, for black oak). We also found that weather acts as a proximate driver of reproduction by either cuing or limiting successful seed development. We did not find any evidence to support the hypothesis that weather can act to limit resource acquisition (e.g., summer droughts). Although we found support for both resources and weather, a limitation of our study is that we were not able to quantify their relative influence (i.e., which factor is the most important for reproductive effort?). It might appear that weather is more important in our study, since inter-annual variation in reproduction was largely explained by weather (and population-level synchrony remained consistent among treatments). However, it is likely that both are critical and interact with each other, and parsing out their relative roles will remain a challenge. Ultimately though, determining the factors that influence masting has important implications for predicting climate change impacts, and subsequent changes in food resources for wildlife and forest-level trophic dynamics.

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Data availability All data and the associated R script are archived in the Environmental Data Initiative (DOI: https://doi.org/10.6073/pasta/2ee69498e7bbd2784267b9f8c6bfa668).

Code availability The R script used for data analysis is also archived in the Environmental Data Initiative (see DOI link above).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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