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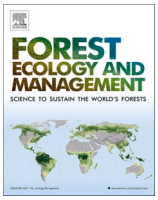

Individual-level variation in reproductive effort in chestnut oak (*Quercus montana* Willd.) and black oak (*Q. Velutina* Lam.)

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ABSTRACT

Masting is a population-level reproductive strategy, where individuals synchronize large but intermittent seed production. Despite the high degree of synchrony at the population level, there can be considerable variation in reproduction among individuals (intraspecific variation). Here, we use 18 years of acorn production data from individual chestnut oak and black oak from control and thinned stands, to understand what factors influence individual differences in reproductive effort and variability. We included a variety of tree-level measurements, environmental characteristics, and measurements from tree cores to determine if certain characteristics were associated variations in reproduction. We considered both mean annual acorn production per m^2 crown and interannual variation in acorn production (CV) as response variables. We also classified individuals as super producers (i.e., those that consistently produce more acorns than others), good, fair and poor producers (i.e., those that consistently produce less or have a higher number of failure years). In chestnut oak, 14% of the individuals were classified as super producers and contributed 34% of the total acorns, while poor producers made up 35% of the trees and contributed only 16% to total acorn production. In black oak, super producers (14% of the individuals) contributed 31% of total acorns and poor producers (24% of the individuals) contributed only 9% of the acorns. Diameter at breast height (DBH) was the most consistent variable for explaining intraspecific variation in reproductive effort and variability (i.e., larger individuals had higher mean acorn production for both chestnut oak and black oak, and lower CV for black oak). Other variables that influenced reproduction and variation included elevation and clay content for chestnut oak, and slope for black oak. We found no significant effect from the thinning treatment on acorn production. Our results illustrate how tree-level and environmental characteristics can distinguish acorn production groups, which can be used to inform management and selective harvesting decisions.

1. Introduction

By definition, masting is a population-level reproductive strategy in plants characterized by high inter-annual variability in seed production (Koenig et al., 2003; Pearse et al., 2016). How individuals synchronize their reproductive effort, and the relative roles of weather, resources and pollination success has been the focus of many previous studies (e.g., Sork, 1993; Buonaccorsi et al., 2003; Koenig et al., 2003; Pearse et al., 2014; Bogdziewicz et al., 2017b). While most of the variation occurs between years for masting species, there can be a considerable amount of reproductive variability between individuals within a year (i.e., intraspecific variation; Greenberg, 2000; Pérez-Ramos et al., 2014; Bogdziewicz et al., 2020), where some individuals rarely produce seed and other individuals consistently produce seed every year. The term 'super producer' has been used to refer to these individuals with high mean seed production and low interannual variation because they consistently produce large seed crops (Healy et al., 1999; Greenberg, 2000; Pérez-Ramos et al., 2014; Minor et al., 2017; Patterson, 2020). These super producers are often responsible for most of the seeds being produced each year. For example, during a 4-year study, 10% of *Fagus grandifolia* individuals contributed 56% of the total beech nuts produced (Minor et al., 2017). In different 10-year study on *Quercus alba*, 11% of the individuals produced 31% of the acorns (Brooke et al., 2019). Despite their influence on masting at the population-level and the importance of these super producers to plant population dynamics, the causes of intraspecific reproduction are uncertain (Pérez-Ramos et al.,

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2014).

While a portion of intraspecific variability in plant reproduction is no doubt derived from genetics, individual variation in resources is likely to play an important role for determining individual reproductive effort. Eastern deciduous forests are highly heterogeneous landscapes, where individual trees experience differences in resources due to position on the landscape (i.e., slope, aspect, and elevation), stand density, and water and nutrient availability (Hutchinson et al., 1999). Individuals located in areas where resources are limiting (e.g., nutrient poor sites or areas with high competition from neighbors) should have higher interannual variability and lower overall reproductive effort. This prediction was supported by a study by Pérez-Ramos et al. (2014), who found increased soil moisture and alkaline soils were associated with individuals that had lower interannual variability and larger seed crops in cork oak (*Quercus suber* L.) and Algerian oak (*Q. canariensis* Willd.). The conclusion was that individuals with increased reproduction were in areas with greater access to resources. Studies using mechanical techniques like thinning have also been used to determine how competition and resources affect interannual variability. Healy et al. (1999) compared acorn production in northern red oak (*Q. rubra* L.) between thinned and un-thinned stands and found that individuals in the thinned stands had lower interannual variability in acorn production. This decrease in interannual variability was assumed to be from decreased competition and increased light availability. Similarly, Minor et al. (2017) found that trees with low inter-annual variability in fruit production were located in areas with higher soil nitrogen, available phosphorus, and had fewer neighbors.

In addition to resource heterogeneity, tree-level characteristics can influence intraspecific variation in reproduction (e.g., Greenberg, 2000; Viglas et al., 2013; Minor et al., 2017; Bogdziewicz et al., 2020). Tree-level characteristics such as canopy size, diameter at breast height (DBH), height, age, and basal area increment (BAI) have all been shown to influence reproductive effort (it is important to note that all of these characteristics are often highly correlated; Thomas, 2011). Most commonly recorded is a positive relationship between mean annual seed production and size (Greenberg, 2000; Minor et al., 2017; Bogdziewicz et al., 2020). Radial growth, also known as BAI, can also provide insight into resource availability, resource storage, and the influence of competition on an individual (Korner, 2003). For example, trees with higher BAI have been shown to have greater stores of carbon (Hoch et al., 2003; Genet et al., 2009; Stephenson et al., 2014). Years with thicker growth rings typically reflect years with ample resources, while thinner rings are found when resources are limited or allocated to other functions like maintenance or reproduction (Drobyshev et al., 2010; Speer, 2010; Martín et al., 2015).

For some masting species, comparing annual seed production to measures of annual vegetative growth have provided additional support for the hypotheses that resources limit reproduction (Yasumura et al., 2006; Sánchez-Humanes et al., 2011; Żywiec and Zielonka, 2013; Martín et al., 2015). For example, Martín et al. (2015) found a trade-off between growth and reproduction in holm oak (*Q. ilex* L.), while Yasumura et al. (2006) found that Japanese beech (*Fagus crenata* Blume) also showed decreased growth during a mast year, supporting the hypothesis that increased reproductive effort shifts resources from one function to another (i.e., resource switching). However, not all species demonstrate this negative relationship between growth and reproduction (e.g., Santos-del-Blanco et al., 2014; Koenig et al., 2020). Intraspecific variation has also been identified by comparing BAI with reproduction between individuals (Healy et al., 1999; Greenberg, 2000; Minor et al., 2017). Healy et al. (1999) created a metric for comparing different groups of producers within a population. Super producers are hypothesized to have little or no trade-off between growth and reproduction (i.e., high BAI with increased reproduction) while poor producers are hypothesized to show a large trade-off between growth and reproduction (i.e., low BAI with increased reproduction), especially during mast years (Greenberg, 2000; Sánchez-Humanes et al., 2011; Żywiec and Zielonka, 2013). Understanding how tree-level and environmental characteristics may distinguish super producers from moderate and poor producers (e.g., Healy et al., 1999; Greenberg, 2000; Minor et al., 2017) is critical for forest management and oak recruitment.

In this manuscript, we use 18-years of acorn production data from 68 individuals to identify potential drivers of intraspecific variation in reproduction of black oak (*Q. velutina* Lam.) and chestnut oak (*Q. montana* Willd.) in two eastern temperate deciduous forests. These species were selected because chestnut oak is in the white oak subgenus *Leucobalanus* and black oak is in the red oak subgenus *Erythrobalanus*. One major difference between them, is that chestnut oak matures their acorns within a single season, while black oak acorns mature over two seasons (pollination occurring in the first spring, with fertilization and acorn maturation in the second season). First, we consider how individual reproductive effort and CV_i relate to (i) variables that influence resource availability (e.g., slope, aspect, neighbor density), (ii) micro-environmental variability in soil nutrients (e.g., P, C:N, soil pH), and (iii) individual tree-level characteristics (e.g., DBH, height, BAI). We predicted that reproductive effort would be higher when resources are higher, either due to extrinsic or intrinsic properties. Second, we classified individuals as super producers, good producers, fair and poor producers. We predicted that super producers would be associated with a combination of traits, such as high resource availability, lower density of neighbors, and larger sizes. Finally, we used tree cores to compare potential trade-offs between growth and reproduction between individuals. If a growth-reproduction trade-off is evident, we predicted that this would be strongest in fair or poor producers and weakest in super or good producers.

2. Methods

2.1. Site history and description

Study sites were located in the unglaciated portion of the Allegheny Plateau, in Zaleski State Forest (39°35′5″ N, 82°37′0″ W) and Vinton Furnace Experimental Forest (39°20′0″ N, 82°39′0″ W), Vinton County, Ohio. Both sites are second growth forests that began regenerating from 1850 to 1900 after harvesting for iron furnaces ended. Elevation of these sites ranges from 200 to 310 m a.s.l. and are characterized by variable topography and heterogeneous microclimate gradients, from xeric ridgetops to more mesic slopes and valley bottoms (Albrecht and McCarthy, 2006; Lombardo and McCarthy, 2008). Ridgetops are dominated by white oak (*Quercus alba* L.), black oak (*Quercus velutina* Lam.), chestnut oak (*Quercus montana* Willd.), and hickory (*Carya* Nutt.). Mesic slopes are dominated by red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), and black gum (*Nyssa sylvatica* Marshall). The sites at Zaleski and Vinton are ~ 20 km apart, and experience similar weather throughout the year. The mean annual temperature is 12.4 °C and mean annual rainfall is 95.62 cm.

For the current study, we used annual acorn data for 34 chestnut oak and 34 black oak. Oaks were distributed across two treatments, a control and a thinning treatments, at both study sites (Iverson et al., 2008). Thinning treatments occurred from December 2000 to February 2001, preferentially retaining oak and hickory trees while removing maple and beech from the midstory (i.e., 15–30 cm DBH). Each oak tree had two 0.25 m^2 acorn collection traps permanently placed beneath the dominant canopy. Basket traps are elevated 1 m above ground to reduce seed predation. Acorn collection traps were set up in 2000 in the control sites and in 2001 in the thinning sites. Acorns are collected once per month from August until December (Lombardo and McCarthy, 2008; Smith et al., 2021). The sum of all fully formed acorns for each tree for each year were used in the analysis below (for control, 2000–2018 and for thinning, 2001–2018. No acorns were collected in 2016 for either treatment). Since each tree has the same number of seed traps, our response variable is acorn production per m^2 of crown, as in other studies (Healy et al., 1999; Rose et al., 2012; Brooke et al., 2019;

Greenberg, 2021).

2.2. Species of interest

Chestnut oak are in the white oak subgenus *Leucobalanus*. Staminate and pistillate flowers are produced in the spring and acorns mature within 6 months (Sharp and Chisman, 1961; Sharp and Sprague, 1967). Chestnut oak are mainly found on ridges and south and west facing slopes in sandy, rocky soils with low moisture holding capacity. They typically occupy xeric sites, as seedlings/saplings are outcompeted by faster growing species on more mesic sites (Mowbray and Oosting, 1968).

Black oak are in the red oak subgenus *Erythrobalanus*. Black oak also produces staminate and pistillate flowers in the spring. Pollination occurs this first spring, however the pollen tubes stop just short of the ovule. Fertilization occurs in the spring of the following year when the male cells complete the pollen tube and reach the ovule. Thus, it takes 18 months from pollination to acorn maturation for black oak (Sork et al., 1993). Black oak will grow on all aspects and slope positions, but prefer middle or lower slopes, with north or east facing aspects (Brinkman, 1965).

2.3. Field methods

In the summer of 2018, we measured canopy height (m), tree height (m), diameter at breast height (DBH in cm) and extracted two 5 mm tree cores with a Haglof increment borer from each study tree. Canopy and tree height were measured with a Halgof Vertex Laser Geo hypsometer, which automatically accounts for slope position.

To account for variations in the environment that could influence resource availability for each individual, we measured slope (%), elevation (m), aspect (°), and quantified their neighborhood to account for competition. Slope was measured with the Haglof Vertex Laser Geo hypsometer. Elevation readings were taken with a Garmin eTrex35 GPS that was calibrated for our study area. Aspect was determined by observing which way the landscape drained and a standard compass. Since aspect is a circular variable (i.e., from 0° – 360°), we calculated two variables to represent east/west ($\sin(\pi \cdot \text{aspect}/180)$) and north/south ($\cos(\pi \cdot \text{aspect}/180)$). Neighbors were defined as all trees within a 10 m radius of the target tree with DBH > 5 cm. For each individual, we calculated the sum basal area of neighbors as an estimate for competition.

To account for variations in soil nutrients, we took six soil cores for each tree located halfway between the drip line of the tree and the trunk. Soil cores were extracted with a PVC pipe that was 7 cm in diameter, to a depth of 10 cm. All six soil cores air dried and were sifted through 2 mm sieves to create a homogenized composite sample for each tree.

2.4. Laboratory methods

Soil texture, pH, carbon:nitrogen (C:N) ratio and phosphorus (P) concentration were measured for soil samples taken from each study tree. Lab analysis for C:N ratio and P concentration were outsourced to Spectrum Analytics, Washington Court House, Ohio. All nutrients are total nutrients in the soil, which is appropriate for long term patterns and matches the scale of our response variable (i.e., mean acorn production over 18 years). C:N was measured with a combustion analyzer, while total P concentration was measured using the Mehlich 3 extraction method. Soil texture was measured with the Bouyoucos (1961) method. Soil pH for each sample was measured by combining 10 g of soil with 20 mL of deionized water, mixed on a spin plate for 30 min and then let it rest for 10 min to equilibrate with atmospheric CO_2. pH was measured with an Oakton pH meter placed in the soil slurry. For the statistical analysis below, we used the log transformed pH.

Tree cores were mounted to 2.54 cm × 2.54 cm molding with Elmer's Glue, and then sanded on a belt sander with progressively finer sandpaper (i.e., 150, 240, 320, and 400 grit sandpaper). Cores were finished by hand with 30- and 15-μm paper to ensure ring boundaries were clear. For each species, tree cores were dot dated and then the list method was used to create a master chronology. All cores were measured on a Velmex Tree Ring Measuring System (Velmex Inc. Bloomfield, NY, USA) to 0.01 mm with JX2 Professional Software (Voortech Consulting Holderness, NH). Measurements were checked with COFECHA (Grissino-Mayer, 2001) to check intercorrelation of rings between cores. We had tree cores for all 34 chestnut oak individuals and 33 black oak individuals (one black oak tree was not cored). Since we took two cores per tree, the time series of annual increments from the same individual were averaged. From the tree cores, we estimated three variables for each individual: age, basal area increment (BAI) sum, and relative growth rate (RGR). For three chestnut oak individuals and eight black oak individuals, we were unable to reach the pith due to heart rot. For these individuals, we did not estimate age however we were able to still calculate BAI sum and RGR. The sum of BAI from 2000 to 2017 for each individual was calculated using the dplR package (Bunn et al., 2020). RGR was calculated as $(\text{basal area}_{2017} - \text{basal area}_{2000})/\text{basal area}_{2000}$ (Pommerening and Muszta, 2016). While the sum of BAI is positively correlated with DBH (black oak, Pearson's $r = 0.65$; chestnut oak, $r = 0.75$), RGR a size independent metric and had a fairly weak negative correlation with DBH (black oak, $r = -0.38$; chestnut oak, $r = -0.11$). After calculating the BAI sum and RGR, we then detrended each individual ring width series using a 20-year cubic spline with a frequency cut off of 0.5, to remove trends associated with size and gap-phase dynamics. The detrended annual RWI (ring width indices) were used to look for growth-reproduction trade-offs (see below).

2.5. Data and statistical analysis

All statistical analyses were conducted with the statistical software R version 4.1.0 (R Core Team, 2021). Acorns per m^2 of crown was the response variable. We calculated two metrics for each individual, (1) the mean annual number of acorns per m^2 of crown, and (2) the individual coefficient of variation (CV_i = SD/mean). The mean annual number of acorns represents mean reproductive effort for each individual, while CV_i represents annual variability in reproductive effort.

We used generalized linear models, with the mean annual number of acorns per m^2 of crown for each individual and CV_i as the response variables. Individual tree characteristics, environmental measurements and treatment (control or thinned) were the fixed explanatory variables. As some variables were highly correlated (e.g., DBH and sum of BAI) only one of these variables were included in the model at a time. Model selection was done using the lowest AICc score, as calculated from the R package MuMIn (Barton, 2020). Akaike information criterion (AICc) measures the fit of a model while correcting for the fact that models with a higher number of parameters will have an improved fit. When the difference in AICc between the top models was < 2, we chose the simpler model with the fewest parameters.

Once we had identified the top model, we tested if site needed to be included as a random effect. We fit two models using generalized least squares with REML using the R package nlme (Pinheiro et al., 2020). One model had site included as a random effect, and the other did not. We then compared models using AICc and the model.sel function in the library MuMIn (Barton, 2020). The model with fixed effects only was always chosen, and in every case, the variance for the random intercept was < 0.01 supporting the conclusion that almost no variance was attributable to site differences.

Assumptions of normality, linearity, homoscedasticity were checked by plotting the residuals. Leverage was checked by using the function influence measures in R. To meet assumptions of normality, mean annual acorns per m^2 crown was log transformed for both black and chestnut oak. The initial model for black oak CV_i had unequal variance issues with slope and P. We used a generalized least squares (GLS) model

and created models with different variance structures. We compared these models using AICc (Appendix Table S2), including a model without any variance structure. The final model for black oak CV_i included a fixed variance structure for slope, and P was removed as a fixed effect. Below, we report the results from the best model only (but see Appendix Tables S1 and S2 for a model comparison table).

2.5.1. Acorn production groups

We classified each individual into one of four groups: (1) Super producers, (2) Good producers, (3) Fair producers and (4) Poor producers. While there are a variety of methods to classify individuals (e.g., Hacket-Pain et al., 2019; Patterson, 2020), we chose to use a similar approach that Healy et al. (1999) and Brooke et al. (2019) used for red and white oaks. Super producers had mean acorns per m^2 of crown $\geq$ the population mean + 1 SD; good producers had a mean acorns per m^2 of crown $\geq$ the population mean but within 1 SD; fair producers had mean acorns per m^2 of crown less than the population mean but at least $\geq$ 60% of the mean, and poor producers produced < 60% of the population mean. After the initial classification, we calculated the frequency of fruiting for each individual (i.e., the number of years when 0 acorns were collected versus the number of years where > 0 acorns were collected). The goal was to ensure that super and good producers were also more consistent producers, while poor producers had a higher number of failure years. Upon consideration of this frequency of fruiting, there were four individuals that were assigned a new classification (one chestnut oak that went from Good to Fair, another chestnut oak that went from Fair to Good, and two black oaks that both went from Poor to Fair, see Appendix Fig. S1).

To determine if certain individual or environmental variables were associated with each group, we performed a principal component analysis (PCA) using the R package vegan (Oksanen et al., 2019). For each species, we ran a PCA that included all of the individual and environmental characteristics, as well as a second PCA that included only those variables from the top models. Since variables are in different units, the data was scaled and centered. A PERMANOVA was used to determine if the centroids of the groups were significantly different using the adonis function, and a post-hoc test to determine which group (s) differed was done using the R package pairwiseAdonis (Martinez Arbizu, 2020).

2.5.2. Relationship between growth and reproduction

For each individual, we created three linear models using annual seed production as the response variable and annual RWI as the explanatory variable. We used the RWI of the current year (i.e., is there evidence of a growth-reproduction trade-off?), the previous year (i.e., did growth the previous year predict seed production? Is there evidence of resource priming?) and subsequent year (i.e., is there a delayed reproductive cost?). If there was no relationship between growth and reproduction, then we would expect approximately half of the individual slopes to be positive and half to be negative. We used a binomial test (null hypothesis, proportion = 0.5) for each species. We then conducted a one-way ANOVA using the slope from each individual as the response variable and their category (i.e., super, good, fair or poor producers) as the predictor variable. If groups were significantly different, then a Tukey post-hoc test was conducted to determine which group(s) differed.

3. Results

3.1. Reproductive effort and CV_i in chestnut oak

On average, chestnut oak individuals (n = 34) produced 16.7 (SE ± 1.90) acorns per m^2 of crown, ranging from 2.8 to 54.3. The average coefficient of variation (CV_i) for individuals was 1.74, ranging from 1.23 to 2.82 (Figs. 1 and 4a). The best linear model for predicting the mean annual number of acorns per m^2 of crown included DBH and elevation (Fig. 2, Table 1). In general, individuals with the highest mean annual acorn production were larger (Fig. 2a) and located at higher elevations within the landscape (Fig. 2b). For predicting the CV_i of acorns per m^2 of crown, the only variable retained in the final model was the percent clay content of the soil which explained 14% of the variation (Table 2). Individuals with high CV_i had soils with a higher clay content (Fig. 2c).

3.2. Reproductive effort and CV_i in black oak

On average, black oak individuals (n = 34) produced 22.1 (SE ± 2.47) acorns per m^2 of crown, ranging from 2.1 to 72.0. Average CV_i for individuals was a little lower than for chestnut oak, with a mean of 1.34 (ranging from 0.96 to 2.34; Fig. 1, Fig. 4b). For black oak, the best model for predicting the mean number of acorns per m^2 of crown only included DBH and explained 35% of the variation (Table 1), with large

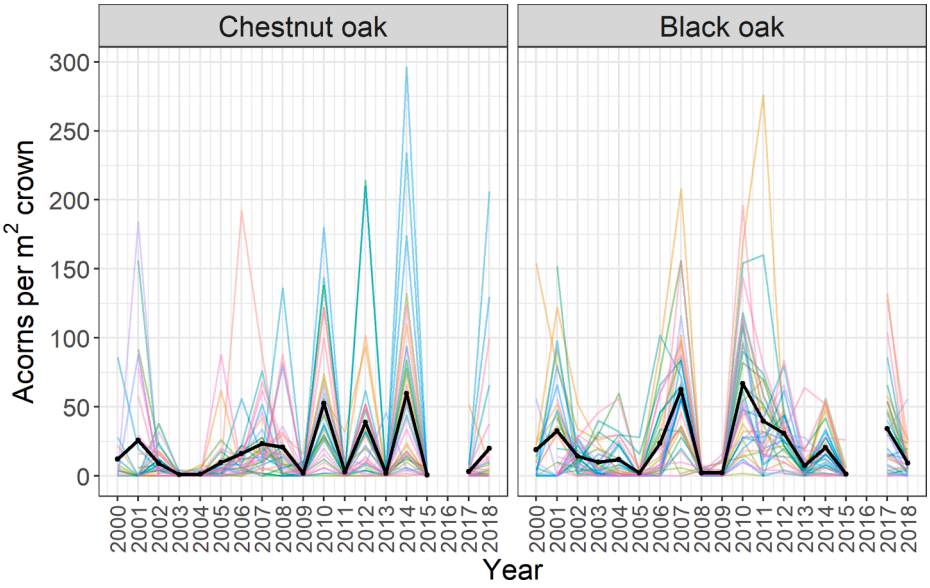

Fig. 1. Yearly acorn production per m^2 of crown for chestnut oak and black oak. The black line is the mean, and each colored line is a different individual (n = 34 for each species), demonstrating high variability between individuals within a population. Acorns were not collected in 2016.

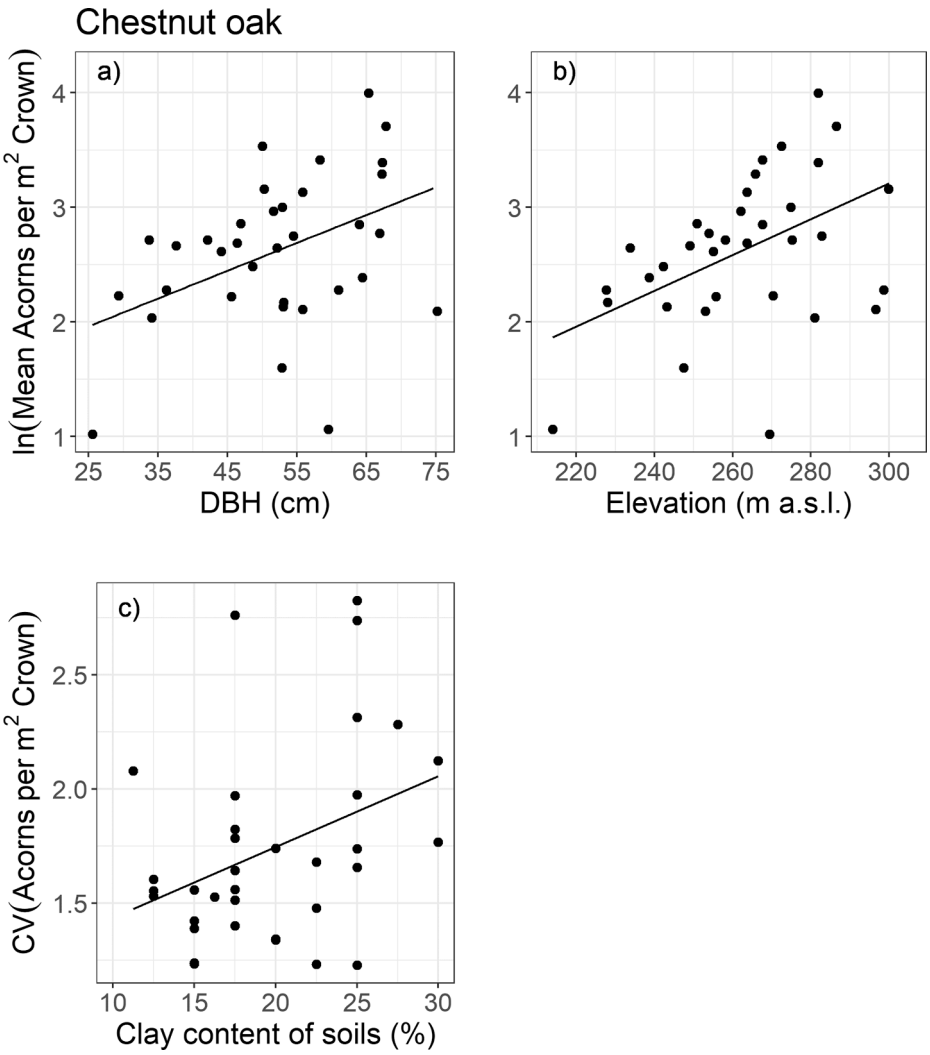

Fig. 2. Mean annual acorns per m^2 of crown (a and b) and the coefficient of variation (CV_i, panel c) for chestnut oak. Annual acorns per m^2 of crown is shown as a function of (a) diameter at breast height and (b) elevation. Mean annual acorns was based on 17 or 18 years of collections from seed traps, and was log transformed to meet assumptions. Dots represent individuals while the solid line is the predicted fit from a multiple general linear model (see Tables 1 and 2).

Table 1
Analysis from a general linear model, for predicting mean annual acorns per m^2 of crown for individual chestnut oak (n = 34) and black oak (n = 34). Acorns per m^2 of crown was log transformed (ln) to meet assumptions of normality. DBH is diameter at breast height.

	Estimate (±SE)	*F*	*df*	*P*	R^2
Chestnut oak					
DBH	0.024 ± 0.01	9.45	1, 31	0.004	0.34
Elevation	0.016 ± 0.005	11.70	1, 31	0.002	
Black oak					
DBH	0.037 ± 0.01	23.52	1, 32	< 0.001	0.42

Table 2
Analysis from a general linear model, for predicting the coefficient of variation (CV_i) for annual acorns per m^2 of crown for individual chestnut oak and black oak.

	Estimate (±SE)	*F*	*df*	*P*	R^2
Chestnut oak					
Clay content	0.03 ± 0.01	5.01	1, 32	0.03	0.14
Black oak		X^2	*df*	*P*	R^2
DBH	−0.012 ± 0.004	10.59	1	0.001	0.58
Soil pH	0.18 ± 0.10	3.62	1	0.057	
Slope	0.013 ± 0.003	27.80	1	<0.001	

individuals producing more acorns per unit of canopy (Fig. 3a). For analyzing CV_i, the final model was a GLS model with a fixed variance structure for slope (i.e., variance increased as slope increased), and included DBH, soil pH, and slope (Table 2). These three variables together explained 58% of the variation. Black oak individuals with the lowest inter-annual variability had the largest DBH and were growing on flatter parts of the landscape (Fig. 3b and d).

3.3. Acorn production groups

Five chestnut oak were classified as super producers, seven as good producers, 10 as fair producers and 12 as poor producers (Fig. 4a). Over the 18 years, 34% of the chestnut acorns collected were from these five super producers. Conversely, poor producers contributed just 16% of the chestnut acorns. When all tree-level and environmental characteristics were plotted within a PCA, many of the individual characteristics were positively correlated with each other (i.e., age, BAI sum, DBH, Height; Appendix Fig. S2a). Environmental characteristics, such as average clay content and elevation were also positively associated with each other (Fig. S2a). However, the PCA plots that included all the variables did not show separation of groups (PERMANOVA $F_{3,30} = 0.99$, $P = 0.45$). When we included just the variables from the top models for predicting either

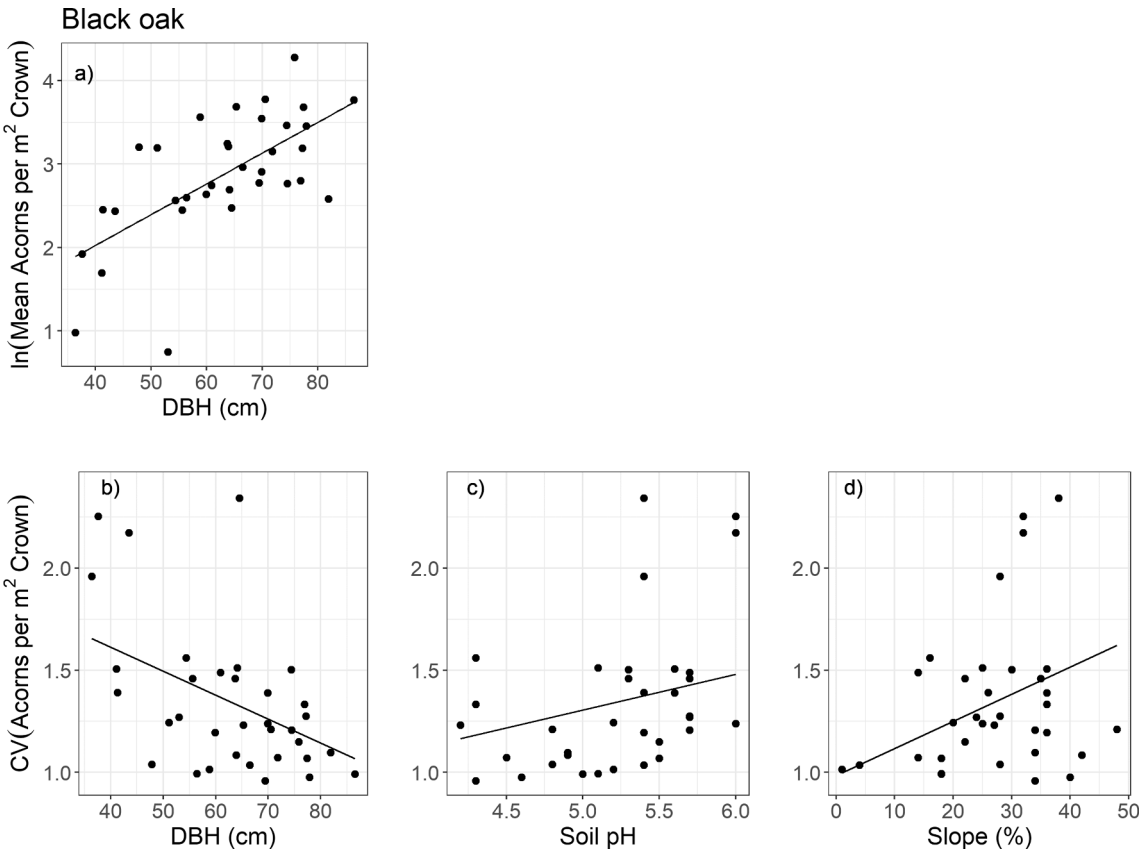

Fig. 3. Mean annual acorns per m^2 of crown (a) and the coefficient of variation (CV_i, panels b, c and d) for black oak. Mean annual acorns was based on 17 or 18 years of collections from seed traps and was log transformed to meet assumptions. Dots represent individuals while the solid line is the predicted fit from a multiple generalized linear model (see Tables 1 and 2).

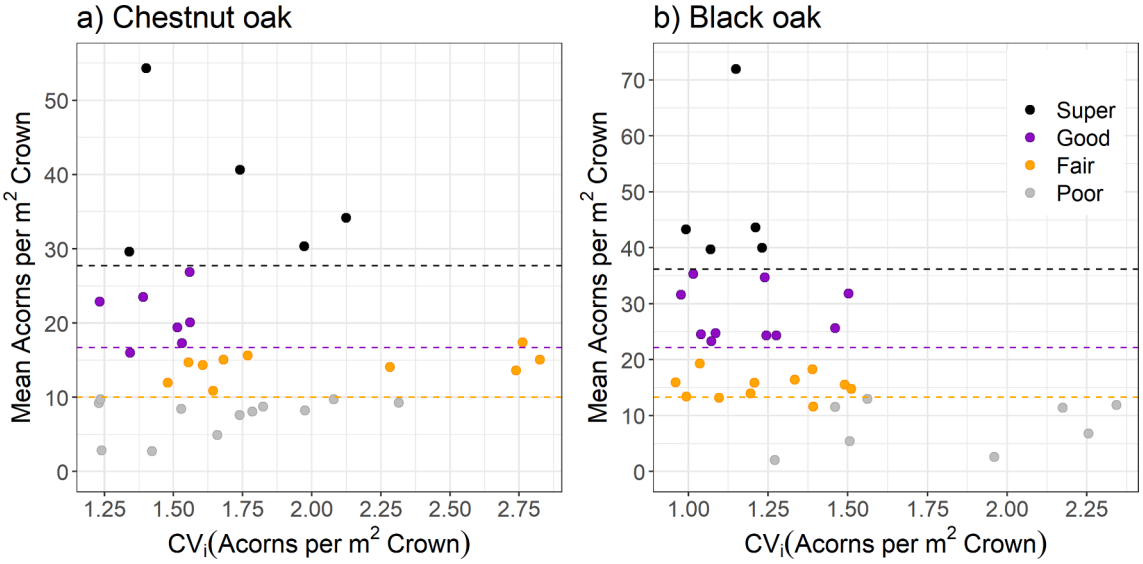

Fig. 4. Mean and CVi for each individual tree. Individuals with mean acorns per m^2 of crown ≥ mean + 1 SD (black dashed line) were classified as super producers, individuals with mean acorns per m^2 of crown ≥ mean (purple dashed line) were classified as good producers. Individuals that produced below the mean, but ≥ 60% of the mean (yellow dashed line) were classified as fair, and poor producers were those that produced < 60% of the mean. Fair and poor producers also had higher variability between years, which is shown as higher CV_i and a higher number of failure years (see Appendix). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the mean annual acorns per m^2 canopy or the CV_i, there was a still not a significant separation of groups (PERMANOVA $F_{3,30} = 1.31$, $P = 0.20$). Fair and poor producers tended to be associated with sandier soils and steeper slopes while super and good producers were associated with more of the individual tree-level characteristics (e.g., large DBH, sum BAI; Fig. 5a)

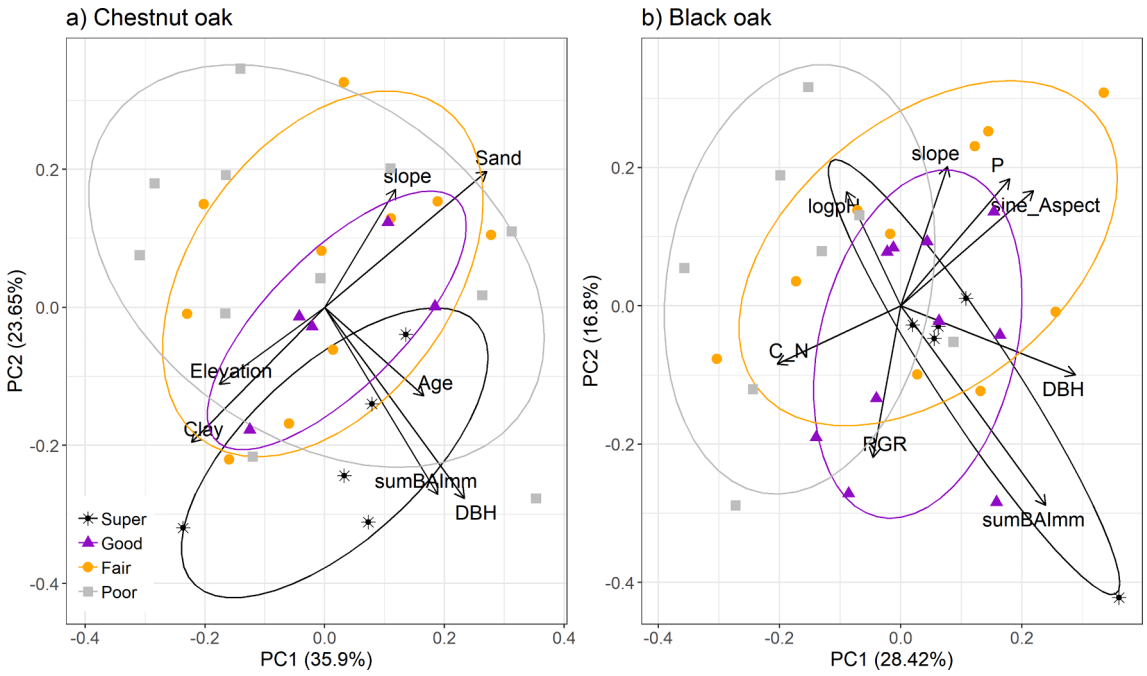

Fig. 5. Principal Component Analysis (PCA) for (a) chestnut oak and (b) black oak individuals, for the combined influence of selected tree-level and environmental characteristics on acorn production (only variables that were included in the top models for either mean acorns per m^2 crown or CV_i were included, see Appendix). Each point represents an individual tree, which were classified into groups based on their reproductive effort (see Methods). Ellipses represent the 68% confidence intervals. Reproductive groups were compared with a PERMANOVA (P = 0.20 for chestnut oak, and P = 0.001 for black oak).

For black oak, there were five super producers, 10 good producers, 11 fair and eight poor producers (Fig. 4b). Over the 18 years, 31% of the black oak acorns collected were from these five super producers while the eight poor producers only contributed 9% of the acorns. Similar to chestnut oak, when all tree-level and environmental characteristics were plotted within a PCA, many of the same individual characteristics and environmental characteristics were positively associated with each other (Appendix Fig. S2b). At least one reproductive group was significantly different from the others when all variables were included together (PERMANOVA $F_{3,29} = 1.44$, $P = 0.046$), the post-hoc analysis identifying a significant difference between the super producers and the poor producers only ($P = 0.036$; all other comparisons were $P > 0.1$). When we ran a PCA with just the variables from the top models for predicting either mean annual acorns per m^2 of canopy or the CV_i for black oak, there was again a significant separation of groups (PERMANOVA $F_{3,29} = 1.95$, $P = 0.007$; Fig. 5b). The post-hoc analyses identified a significant difference between the super producers and the poor producers ($P = 0.01$), and good producers and poor producers ($P = 0.02$; all other comparisons had $P > 0.1$). Super and good producers tended to be larger, and have higher BAI and RGR, while poor producers smaller and were associated with higher soil pH (Fig. 5b).

3.4. Relationship between growth and reproduction

The majority of the individual slopes between RWI and acorn production were not significantly different from zero (Fig. 6). For example, only one chestnut oak individual and seven black oak individuals had significant negative relationships between current years RWI and acorn production (Fig. 6b, e). For chestnut oak, 59% of the individuals had negative slopes when using the current year RWI and 67% of the individuals had positive slopes using the RWI from the previous year, however neither proportion is significantly different from the null expectation of 50% (Table 3). When comparing acorn production with the following years ring width index, the majority of individuals (76%) had positive slopes, which was significant (Table 3). There was also a significant difference in slopes between chestnut oak reproductive groups for the following year RWI (Fig. 6c; $F_{3,30} = 4.48$, $P = 0.01$). Super producers typically had negative slopes while the fair and poor producers typically had positive slopes (Super to Fair, $P = 0.03$; Super to Poor, P 0.01). There were no significant differences in slopes between chestnut oak reproductive groups for the previous year RWI ($F_{3,30} = 2.79$, $P = 0.06$), or the current year RWI ($F_{3,30} = 0.77$, $P = 0.52$).

For black oak, 82% of the individuals had a positive slope when using the RWI of the previous year (Fig. 6d), and 85% of individuals had a negative slope between acorn production and current year RWI (Fig. 6e). Both proportions are significantly different from the null hypothesis of 50% (binomial test, Table 3). There was also no significant differences between black oak reproductive groups for the previous year RWI ($F_{3,29} = 1.64$, $P = 0.20$) or the current year RWI ($F_{3,29} = 0.26$, $P = 0.85$), implying that this relationship between growth and reproduction was the same regardless of their reproductive category. 36% of individuals had a negative slope when using the RWI from the following year (Fig. 6f) which is not different from a null hypothesis of 50% (Table 3). However there were significant differences between black oak reproductive groups ($F_{3,29} = 4.50$, $P = 0.01$). The post-hoc analysis identified a significant difference between super and fair producers ($P = 0.01$), where super producers tended to have this negative relationship between seed production and growth the following year (i.e., a potential delayed cost of reproduction) while fair producers had mostly positive slopes (Fig. 6f).

4. Discussion

The goal of this study was to quantify intraspecific variation in reproduction in chestnut oak and black oak and to identify individual or environmental characteristics that were associated with acorn production. The individuals producing the highest number of acorns per m^2 crown on average and with the lowest CV_i, were the largest individuals for both chestnut oak and black oak. For chestnut oak only, being located at higher elevations also increased acorn production, while low clay content of soils decreased reproductive variability. Slope was also important for black oak, as reproductive variability increased on steeper

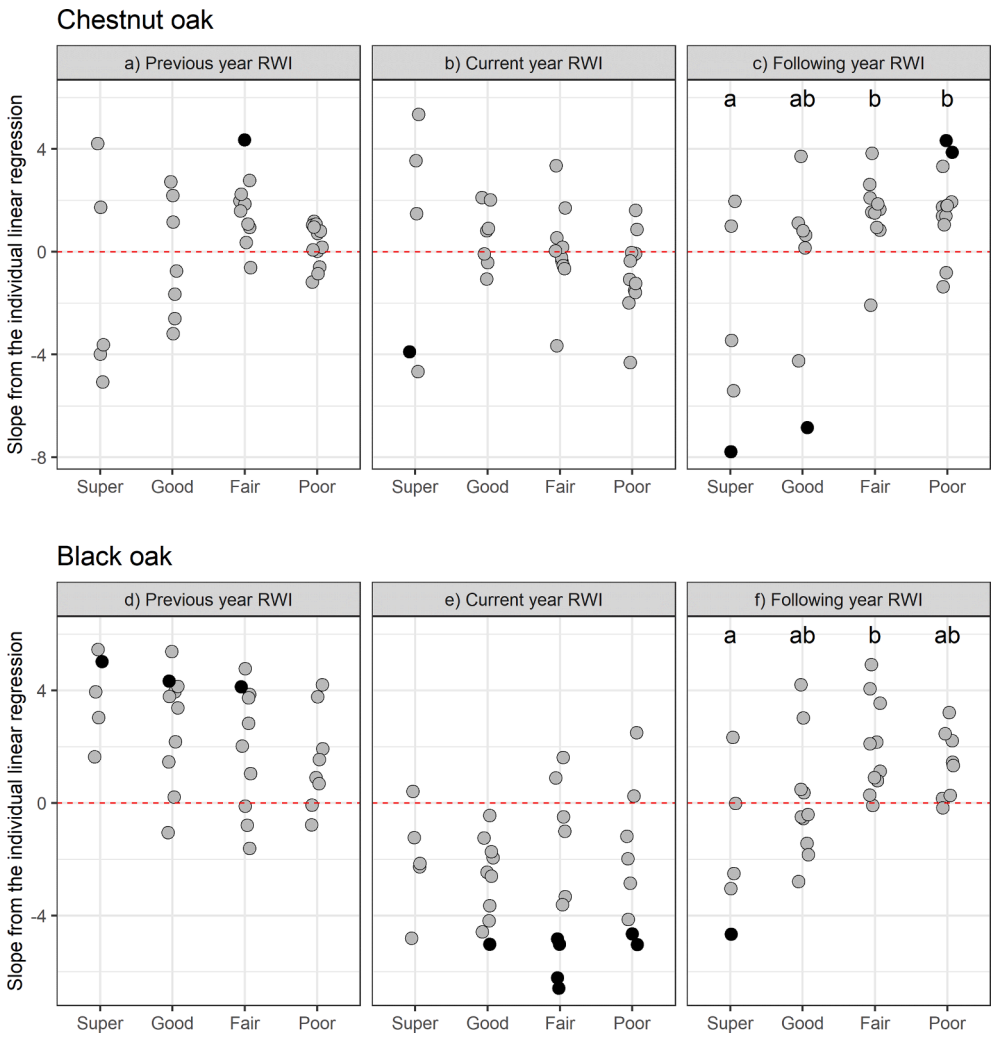

Fig. 6. Slope from linear regression; annual seed production ~ ring width index (RWI), for each chestnut oak individual (n = 34) and black oak individual (n = 33). Linear regressions used the RWI of the previous year (a, d), the RWI of the current year (b, e) and the RWI of the following year (c, f). The dotted red line indicates whether the slope of an individual is positive or negative (i.e., above 0 slope is positive and there is no trade-off between growth and reproduction, below 0 slope is negative and there is a trade-off between growth/reproduction). Most of the slopes for individuals were statistically not significant (shown as grey symbols), while the few individuals with statistically significant slopes are as black symbols. There were no differences between groups except in panels (c and f). Letters are from Tukey-Kramer post-hoc comparisons, groups that are significantly different from each other do not share letters. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Summary of negative and positive slopes, for individuals (see Fig. 6). The expected proportion of positive and negative slopes was 0.5 and was tested with a binomial test.

	Negative slopes	*Positive slopes*	*% Negative*	*% Positive*	*P*
Chestnut oak					
Previous year RWI	11	23	0.32	0.68	0.06
Current year RWI	20	14	0.59	0.41	0.39
Following year RWI	8	26	0.24	0.76	0.003
Black oak					
Previous year RWI	6	27	0.18	0.82	< 0.001
Current year RWI	28	5	0.85	0.15	<0.001
Following year RWI	12	21	0.36	0.64	0.16

slopes. Below we discuss in more detail (1) the individual and (2) environmental characteristics that influenced reproductive effort and variability for both chestnut oak and black oak, (3) super producers, and (4) the trade-off between growth and reproduction.

4.1. Individual characteristics

Diameter at breast height (DBH) was significant for both chestnut oak and black oak and was found to influence both reproductive effort and variability. Consistent with previous studies (e.g., Rose et al., 2012; Minor et al., 2017), we also found that the largest individuals had increased reproductive effort and lower variability. For example, Greenberg (2000) found that chestnut oak and black oak trees ≤ 25 cm DBH consistently produced less seed when compared to larger individuals and Bogdziewicz et al. (2020) also found that larger individuals had higher fecundity and were less likely to have a high proportion of years with low seed crops. The size of an individual has also been shown to have a linear relationship with crown size and root biomass (Petersson and Ståhl, 2006; Tobin et al., 2007). Thus, larger individuals likely have more above and below ground biomass, for producing seeds, photosynthesizing, and mining resources (Tobin et al., 2007; Rose et al., 2012). That being said, we analyzed acorns per m^2 of canopy so larger individuals are still producing more acorns per unit area, compared to smaller individuals.

4.2. Environmental characteristics

Slope, clay content, and elevation were the only environmental characteristics that were found to be significant, however their influence on reproduction was species-specific. Mean acorn production increased in chestnut oak at higher elevations. In our particular study area, this

implies that the chestnut oak individuals with the highest mean reproduction were found on the ridge-tops. Landscape position has been shown to be a significant variable in predicting oak recruitment (e.g., Borchert et al., 1989; Iverson et al., 2008), as slope and aspect modulate moisture availability. However, we are not familiar with previous studies that found an effect of topography on individual seed production in forested ecosystems. We hypothesize that differences in landscape position are modifying temperature conditions for individual trees, which is influencing phenology and synchrony. Microclimate, specifically spring temperatures, influenced bud burst and flowering phenology in *Q. lobata*, which in turn increased population synchrony and overall acorn production (Koenig et al., 2015). Chestnut oak individuals located on the ridge tops may be experiencing more similar microclimatic conditions to each other, leading to increased flowering synchrony and pollination efficiency, which could explain the increased acorn production for these individuals located on ridgetops. Bogdziewicz et al. (2020) also hypothesized that super producers could have greater synchrony and this allowed these individuals to harness the advantages of masting through pollination efficiency.

Individual CV_i in chestnut oak was the lowest when soils had lower clay content. Clay content is related to soil moisture variability, with higher variability in soil moisture when clay content is high (Vereecken et al., 2007). For black oak, CV_i was the lowest in the flattest parts of the landscape (i.e., higher variability on steeper slopes) which could also relate to soil moisture. We did not find any significant relationships between total soil nutrients and mean acorn production nor CV_i. This is consistent with Leeper et al. (2020), who also found no relationship between plant available soil nutrients and mean cone production or CV_i for white spruce. However, other studies have demonstrated an impact of nutrients on seed production (Smaill et al., 2011; Bogdziewicz et al., 2017a). For example, nitrogen fertilization experiments increased seed production for red oak (Bogdziewicz et al., 2017a), and red and black oak super producers were located in areas with higher soil nutrient availability (Minor et al., 2017).

4.3. Super producers

Super producers often represent only a small percentage of individuals within a population (Healy et al., 1999; Greenberg, 2000; Minor et al., 2017; Bogdziewicz et al., 2020; Patterson, 2020); however, their impact on population-level reproduction is disproportionally large. Of the individuals sampled, 14% of chestnut oak and 14% of black oak were classified as super producers, and they produced 34% and 31% of total acorns respectively. Super producers also had lower CV_i and a lower frequency of failure years. Minor et al. (2017) hypothesized that the lower interannual variability of super producers could result from being located in areas with higher resource availability, which would decrease the amount of time needed to replenish stored resources after reproduction. Oaks that remained after a shelterwood harvest, responded by increasing their crown size and producing up to 80% more acorns per m^2 of crown, when compared to the controls (Greenberg, 2021). White oak individuals were found to have increased acorn production following crown release, especially poor producers (Brooke et al., 2019). This same study found no effect of fertilization on acorn production (Brooke et al., 2019), suggesting that light availability and competition may be more critical than nutrients. In our study, we found no effect from the thinning treatment on mean acorn production per m^2 crown nor CV_i. Our previous work had found thinning and burning was the only silvicultural treatment that increased acorn production in chestnut oak (Lombardo and McCarthy, 2008; Smith et al., 2021), however we did not quantify changes in crown sizes which has been shown to increase after thinning in oaks (Greenberg, 2021).

Our PCA models with all of the individual and environmental characteristics showed some systematic differences between groups of producers, but super producers were not exclusively associated with a certain combination of environmental or individual traits. Our models indicated that the most consistent pattern was that super and good producers were larger. However, distinguishing between the cause and effect of size is difficult, due to size being a potential consequence of available resources (i.e., being located in a resource-rich microsite) and resource acquisition (i.e., larger individuals can acquire more resources).

4.4. Growth-reproduction trade-off

The proposed trade-off between growth and reproduction assumes that resources are limiting and must be allocated between reproduction, growth, and maintenance (e.g., Sánchez-Humanes et al., 2011; Hacket-Pain et al., 2015). For oaks and other masting species, the exceptionally large but rare reproductive events may have an even larger trade-off. However, studies to determine the so-called "cost of reproduction" have been mixed. For example, in holm oak in the Mediterranean, Martín et al. (2015) found the expected negative correlation between holm oak acorn production and growth during masting years. However, other studies have found no evidence for a growth reduction during mast years (Żywiec and Zielonka, 2013; Koenig et al., 2020). Hacket-Pain et al. (2019) found a very weak negative relationship between stand-level cone production and ring width index in Norway spruce. There was a lot of variation between individuals and however the heavy cone producers were more likely to have a negative growth-reproduction trade-off.

In our study, there was minimal support for a growth-reproduction trade-off. For most individuals, there was not a statistically significant relationship between acorn production and RWI. The one chestnut oak individual that did have a significant negative relationship was also a super producer, however this could be a coincidence. In addition, the seven black oak individuals that had significant negative relationships were distributed across the different reproduction categories (one good producer, four fair producers and two poor producers). Even though most of the individual slopes were not statistically significant, we think that it is biologically significant that the vast majority of black oak individuals (85%) showed a negative relationship between acorn production and ring width index (i.e., growth is reduced when reproduction is higher). Interestingly, there was an equally strong positive response between acorn production and the previous years' ring width index (i.e., higher reproduction with larger rings the year before). This supports the resource budget model (Crone and Rapp, 2014), which posits that individuals need to acquire enough resources in prior years to support a large reproductive effort. Finally, we found some evidence that suggests a delayed cost for reproduction for super producers only. While previous studies found super producers to have little or no trade-off between growth and reproduction in the current year (e.g., Sánchez-Humanes et al., 2011; Żywiec and Zielonka, 2013), we are not aware of any previous studies that looked for a cost of reproduction the following year at the individual level (but see Drobyshev et al., 2010 for a stand analysis). This is a question that requires additional research, however could be answered by reanalyzing existing data (e.g., from Żywiec and Zielonka, 2013; Martín et al., 2015; Hacket-Pain et al., 2019; Koenig et al., 2020).

5. Conclusions

The results of this study demonstrate the high degree of intraspecific variation in acorn production, and the disproportionately large contribution from super producers. Diameter at breast height (DBH) was the most consistent variable for explaining intraspecific variation in reproductive effort and variability (i.e., larger individuals had higher mean acorn production for both chestnut oak and black oak). We also found that the thinning treatment did not impact mean acorn production or CV_i for either species. For forest managers interested in maximizing acorn production at the stand level, we would therefore recommend selective harvesting practices that retain the largest individuals.

CRediT authorship contribution statement

Sarah J. Smith: Conceptualization, Formal analysis, Investigation, Visualization. **Brian C. McCarthy:** Conceptualization, Methodology. **Todd F. Hutchinson:** Investigation, Resources. **Rebecca S. Snell:** Conceptualization, Formal analysis, Visualization, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120029.

Data availability

All data and associated R scripts are archived in the Environmental Data Initiative (https://doi.org/10.6073/pasta/a37fc0e58fb3e46aa9566e0c990681de).

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