



Acorn production, climate, and tree-ring growth of five oak species in southern Appalachian forests

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ABSTRACT

Oak (*Quercus*) are a dominant and important tree genus in the Central Hardwood Region (USA) due to their commercial timber value, and food value of their protein-rich seed – acorns – to wildlife. Acorn production is characteristic of masting, with highly variable crop sizes that are synchronized within populations, but with consideration variation among individual trees. Critical to acorn masting studies are longitudinal datasets, which are often difficult to maintain due to a host of constraints. One possible approach to extending mast datasets involves the use of dendrochronology, where tree-ring-width variability serves as a proxy for annual acorn production. In this study, we addressed the future utility of mast reconstructions by examining relationships between acorn production, climate, and tree-ring data from five common oak species in southern Appalachian hardwood forests (Bent Creek Experimental Forest). We found little evidence to suggest that acorn production influences seasonally resolved tree-ring data, even when we considered early and latewood growth separately, or when we analyzed trees with substantially higher overall investment in acorn production (i.e., super producers). Monthly climate (temperature, precipitation) correlated to acorn production was strongest when lagged, which could indicate weather conditions were more important for phases of flower production and fertilization than acorn maturation. However, relationships were relatively weak, indicating limited potential for the forecasting of acorn crops, or for reconstruction methods that combine observed weather data and tree-ring responses to masting. Overall, our findings provide some support for the role of resource dynamics in regulating masting in oaks, but relationships between radial growth and acorn production are not sufficiently strong, at least in this location, to permit tree-ring based reconstruction of masting in these oak species.

1. Introduction

Oak (*Quercus*) are a dominant and important tree genus in the Central Hardwood Region (USA) due to their commercial timber value, and food value of their protein-rich seed – acorns – to wildlife (Brooke et al., 2019). Acorns are considered a keystone forest food resource, as crop size affects the survival and reproductive success of seed-consuming animals that in turn, influence populations of their predators (Wolff, 1996). For example, acorn crops affect populations of many game species including white-tailed deer (*Odocoileus virginianus*) that affect forest composition and structure by selective browsing when population levels are high (Feldhamer, 2002). Acorn production also directly affects oak regeneration (Loftis and McGee, 1993). Acorn crop sizes are highly erratic, with considerable variation among oak species, years, locations,

and even individual trees (Rose et al., 2012).

Acorn production patterns are often characterized as “masting” to describe large interannual fluctuations in crop sizes due to synchronized fruiting or nonfruiting across oak individuals within a population (Koenig and Knops, 2013; Pearse et al., 2016). Long-term studies indicate that a strict masting paradigm (Koenig and Knops, 2000) is not an accurate characterization of eastern oaks; “boom” and “bust” years of acorn production occur, but a gradient of crop sizes between those extremes is common (e.g., Greenberg and Warburton, 2007; Rose et al., 2012). At the population level, acorn crop sizes are a function of both the proportion of oak trees fruiting and the density of acorns on their crowns, which are strongly positively correlated (Greenberg and Warburton, 2007; Greenberg, 2020). Thus, heavy crop years are characterized by more oak trees fruiting and a higher density of acorns per crown;

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this strong relationship allows for prediction of within-year crop size based solely on the proportion of fruiting trees within a population (Greenberg and Warburton, 2007; Greenberg, 2020).

In addition to annual variability in the population-level proportion of oak trees producing acorns, individual trees differ in their frequency of acorn production and the number of acorns they produce. Rose et al. (2012) reported that 78% of oak trees ($n = 475$) produced no acorns in $\geq 25\%$ of 10 years sampled, and nearly 40% produced none in $\geq 50\%$ of the 10 years sampled. Greenberg (2000) reported that frequency of acorn production ranged from never to annually among individuals. Individual trees that produce acorns most years also tend to produce more acorns than their poor-producing counterparts (Greenberg, 2000), setting them apart as superior, or “super producers”. Several studies indicate that super producers compose a relatively small proportion of oak trees (14–46% depending on the species) but contribute disproportionately to the acorn crop in moderate and heavy crop years (Healy et al., 1999; Greenberg, 2000; Smith et al., 2022).

In many masting species the interannual variability and synchrony of seed production are linked to weather conditions during key phenological phases, although the mechanisms linking weather and seed production remains poorly understood (Pesendorfer et al., 2021; Bogdziewicz et al., 2023; Fleurot et al., 2023). In oaks, the red (*Erythrobalanus*) and white oak (*Leucobalanus*) subgenera may show contrasting responses to weather due to differences in the length of time between flowering and acorn maturation. For species in the white oak subgenus, flowers are fertilized in April, and acorns mature by autumn of the same year. In contrast, for species in the red oak subgenus, flowers are fertilized in April, but acorns do not mature until autumn of the following year. In both subgenera, floral primordia are initiated the year prior to flower production. Thus, the full cycle from development of floral primordia to acorn maturation is two years for the white oak subgenus and three years for the red oak subgenus (Sork et al., 1993). Some studies in oak forests of the Central Hardwood Region indicate that April wind and humidity (e.g., Sharp and Sprague, 1967) can affect wind pollination, whereas April frosts and summer drought can negatively affect acorn production by killing flowers or developing fruits (Sork et al., 1993; Fearer et al., 2008).

Long-term, well-replicated research on annual fruit production is uncommon due to the time and resources it requires (Hackett-Pain et al., 2022). In some conifers, cone scars can be used to reconstruct past cone production and the occurrence of mast years (Bouchard and Pernot, 2020; Crone et al. 2011). Alternatively, differences in annual tree-ring-widths could potentially be used as a proxy for annual mast production, if indeed tradeoffs between diameter growth and seed production occur; this would allow for multi-decadal to multi-century mast reconstructions. In addition to understanding natural spatiotemporal variation in masting (Mundo et al., 2021), tree-ring-based reconstructions of masting would enable researchers to establish the relationship between masting and weather where long observational records of masting were absent, and subsequently facilitate the development of masting forecasts (Journé et al., 2023; Pearse et al., 2021). *Dendromastecology* (e.g., Speer, 2010) studies have revealed relationships between total annual ring growth, climate, and masting events for some species (e.g. *Fagus* spp., *Pinus* spp.), and used these relationships to reconstruct annual mast production from ring growth (e.g. Drobyshev et al., 2014; Hackett-Pain et al., 2015; Rodríguez-Ramírez et al., 2019; Mundo et al., 2021). However, results of mast reconstructions from radial growth are equivocal for oaks. Speer (2001) found a growth-masting relationship in only 7% of all sampled eastern oak trees, indicating over 90% of trees had no relationship between radial growth and mast production. Similarly, Koenig et al. (2020) was unable to reconstruct masting events from total radial growth using five oak species in California. Recent research suggests that seasonally resolved ring-width, rather than total ring-width, is generally a superior metric for climate sensitive tree species of the southeastern US (Mitchell et al., 2019; Soulé et al., 2021; Catherwood et al., 2023), but season wood

analyses are largely absent in past studies of the relationships between masting and oak tree-ring growth.

Studies showing that super producing individuals contribute disproportionately to acorn crops (Healy et al., 1999; Greenberg, 2000; Smith et al., 2022) suggest that acorn production-radial growth relationships could be more easily detected in this small subset of an oak population (Hackett-Pain et al., 2019). Smith et al. (2022) reported mixed relationships between acorn production and ring growth across individual trees within poor, moderate, and super producer acorn production classes. However, most dendromastecology studies do not examine differences in acorn production-ring growth relationships among acorn production classes. Here we comprehensively test for relationships between growth and acorn production in five common southern Appalachian oak species, evaluating the potential for tree-ring-based masting reconstructions. In particular, we test the potential for seasonally-resolved growth, and focus on super producing individuals to address previous challenges in identifying masting effects on oak radial growth. We also test the potential for a combined approach to reconstructing oak masting that integrates weather and tree-ring data (Drobyshev et al., 2014). To this end, we used 18 years of monthly climate data with seasonally-resolved tree-ring-width and acorn production data from 71 chestnut oak (*Q. montana*), 62 white oak (*Q. alba*), 11 black oak (*Q. velutina*), 36 northern red oak (*Q. rubra*), and 31 scarlet oak (*Q. coccinea*) (total 211 oak trees) to examine potential relationships between climate, annual tree growth, and acorn production. Our goal was to determine whether mast reconstruction based on tree rings was possible for these oak species, whether season wood could explain more than total wood ring-width in potential tradeoffs between radial growth and acorn production, and if potential relationships were more or less evident in regular vs super producer chronologies.

2. Methods

2.1. Study area

The Bent Creek Experimental Forest (BCEF) encompasses a 2,250-ha watershed (35.5°N, 82.6°W) within the Pisgah National Forest in the mountainous Blue Ridge Physiographic Province of western North Carolina, USA. Annual precipitation averages 140 cm (Owenby and Ezell, 1992), and elevation ranges from 650 m to 1070 m. Winters are short and mild, and summers are long and warm. Oaks compose approximately 47% of mature trees (Greenberg et al., 2014). Common tree species on subxeric sites include scarlet oak, chestnut oak, black oak, blackgum (*Nyssa sylvatica*), sourwood (*Oxydendrum arboreum*), and occasional shortleaf pine (*Pinus echinata*) and pitch pine (*P. rigida*). Tulip poplar (*Liriodendron tulipifera*), and northern red oak dominate moist slopes and coves. Red maple (*Acer rubrum*), hickory (*Carya* spp.), dogwood (*Cornus florida*), and white oak (*Q. alba*) are present on all sites (McNab and Greenberg, 2004).

2.2. Acorn production

We measured acorn production by five oak species in several areas within the BCEF watershed during 2000–2018. All study trees were georeferenced and numbered. Oak species included scarlet oak ($n = 31$), black oak ($n = 11$) and northern red oak ($n = 36$) in the red oak subgenus (*Erythrobalanus*), and white oak ($n = 62$) and chestnut oak ($n = 71$) in the white oak subgenus (*Leucobalanus*). We randomly selected trees to represent a wide range of size classes (12.7–108.0 cm diameter at breast height (dbh) at study establishment), elevations (646–1067 m), and topographic features (i.e., aspect, slope position, and percent slope). Most trees were 80–120 years old at study establishment and in dominant or codominant (a few were intermediate) crown positions. We collected acorns in circular, 0.46 m² traps placed randomly beneath the tree crowns. The number of traps per tree was approximately proportional to the basal area (2–14 per tree) until 2004, when we standardized

to three traps per tree for consistency. Acorns were collected at approximately 2-week intervals from mid-August through the completion of acorn drop in late fall. For the purpose of this study, we counted all well-developed acorns and did not distinguish between insect-damaged and sound acorns or between different acorn sizes. Crop size estimates probably were conservative as they did not account for acorns removed from traps or tree crowns by squirrels or other acorn predators. We used the mean number of acorns/m² of trap area as our metric of crop size for individual trees, species, and all oaks combined.

2.3. Tree-ring sampling

During summer 2018 we measured dbh, then removed two core samples at breast height from opposing sides of each study tree bole. Core samples were taken perpendicular to the slope to minimize the influence of reaction wood (Speer, 2010). We sleeved all samples in paper straws for safe transport and dried the core samples for a minimum of one week. All core samples were prepared using standard procedures (Stokes, 1996; Speer, 2010). Each was mounted in wooden core mounts and sanded using progressively finer sandpaper (105 – 10.6 μ) to reveal individual cells structures and ring boundaries. We visually crossdated samples using the list method (Yamaguchi, 1991) to ensure dates were assigned across contemporaneous growth rings. We scanned all samples to 1,200 DPI using an Epson flatbed scanner and measured annual growth rings using the computer program CooRecorder (Larsson, 2014). We delineated seasonwood on each sample and saved individual growth measurements as totalwood (TW), earlywood (EW), and latewood (LW) width. Season wood delineation was determined visually using the method proposed by Umebayashi et al. (2008) where the portion of the ring containing one or more rows of vessels was classified as earlywood and the remaining portion of the ring was classified as latewood. We compiled measured samples by species and crossdating accuracy was verified with the computer program Cofecha (Holmes, 1983). Finally, we standardized all samples using a 2/3rds cubic smoothing spline using the computer program Arstan (Cook, 1985; Cook and Holmes, 1996) to produce standardized chronologies with a mean index value of 1.0.

2.4. Climate data

Local climate data were obtained from a National Oceanic and Atmospheric Administration Applied Climate Information System (NOAA ACIS) station (Bent Creek; 35.504, –82.597) located within the BCEF watershed and ≤ 5 km away from study trees (ACIS, 2022). We used monthly temperature (maximum, minimum, mean) and total monthly precipitation for all available years of the climate data station (1949–2017, 68 years) in our analyses.

2.5. Data analyses

We used general descriptive statistics to explore the variability of acorn production within and among the five study species. We examined the mean and standard deviation (SD) of acorns produced for the full 18-year dataset and identified the frequency of zero-mast years (zero acorns) by individual trees. Additionally, we examined species-level synchrony during high acorn production years to understand if species within subgenera may be influenced by a common environmental cue. No definitive methods exist for defining a masting event (LaMontagne and Boutin, 2009), and data suggests that eastern oak species do not follow a strict masting model (e.g., Rose et al., 2012). Therefore we use a conservative method that defines a high acorn production year for a species as any year where it exceeds 0.5 standard deviations (SD) from its 18-year mean. Years that exceed the 0.5 SD threshold were defined as “high production” whereas all others were classified as “regular production”.

We identified super producer trees by calculating the z-score of each

tree’s acorn contribution to total population-level acorn production for each species and all 18 years in the dataset (Patterson, 2020). Individual trees producing ≥ 1 SD of acorns relative to the population of that species were classified as super producers; trees producing < 1 SD were classified as regular producers. Data were first normalized at the sample-site level to control for possible differences in sample-site productivity, then aggregated to the population level.

We used simple linear regression to examine the relationship between population-level mean acorn production and population-level standardized ring growth (TW, EW, LW) for each species for all years (n = 18 years). We repeated these analyses separately for super producers. Analyses were performed for the current year (growth of the current year against acorn production of the same year) to examine the effect of acorn maturation on ring-width.

We also examined potential relationships between monthly climate variables and annual acorn production using Pearson product moment correlations. We specifically examined correlations between acorn production and monthly average mean temperature, average maximum temperature, average minimum temperature, and total rainfall.

3. Results

Acorn production varied among the five species during the 18 years examined (Fig. 1). Annual mean (SD) acorns/m² trap area was 4.9 (7.9) for chestnut oak, 21.4 (33.4) for white oak, 15.2 (16.3) for black oak, 12.9 (17.2) for northern red oak, and 13.2 (17.6) for scarlet oak. Modulating these mean acorns/m² trap values were frequent instances where individual trees produced zero acorns in a given year. Instances of no mast (zero acorns recorded) accounted for 35.6 % of all observations in the dataset including 45.1% for chestnut oak, 32.9% for white oak, 25.8% for black oak, 35.8% for northern red oak, and 27.1% for scarlet oak.

High production years (>0.5 SD) occurred 3–4 times per species during the 18-year period of study (Fig. 2). Four of the five study species produced heavy acorn crops in 2010 (all except scarlet oak) and 2014 (all except black oak). The white oak subgenus (chestnut oak and white oak) exhibited subgenus-level synchrony in three (2004, 2010, 2014) of their respective four high production years. This is evident in a strong, positive correlation between white oak and chestnut oak acorn production ($r = 0.883$, $p < 0.001$; Table 1). The red oak subgenus (black oak, northern red oak, and scarlet oak) showed less subgenus-level synchrony. High production years co-occurred for two of the three red oak subgenus species in 2009, 2010, and 2014 but never by all three

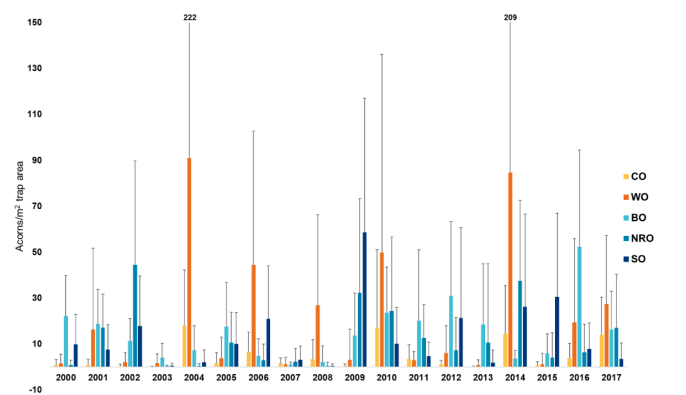


Fig. 1. Mean (SD) annual acorn production (acorns/m² trap area) for chestnut oak (CO), white oak (WO), black oak (BO), northern red oak (NRO), and scarlet oak (SCO) in the Bent Creek Experimental Forest, Pisgah National Forest, North Carolina. Species in the white oak subgenus are plotted in orange colors, and species in the red oak subgenus in blue colors. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

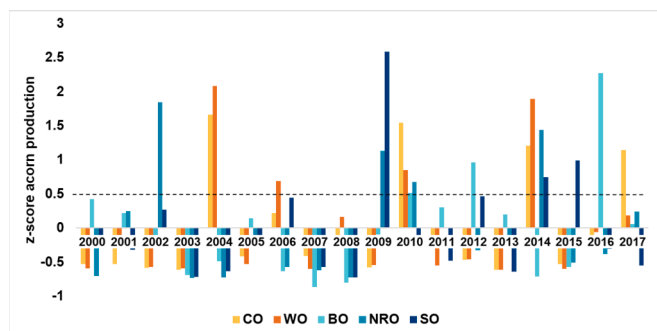


Fig. 2. Z-score acorn production (2000–2017) for chestnut oak (CO), white oak (WO), black oak (BO), northern red oak (NRO), and scarlet oak (SCO) in the Bent Creek Experimental Forest, Pisgah National Forest, North Carolina. High production years exceed the 0.5 Z-score dashed line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Correlation matrix for chestnut oak (CO), white oak (WO), black oak (BO), northern red oak (NRO), and scarlet oak (SCO) in the Bent Creek Experimental Forest, Pisgah National Forest, North Carolina. Bold values were statistically significant ($p < 0.05$).

| | CO | WO | BO | NRO | SO |
|-----|--------------|--------|--------|--------------|----|
| CO | – | | | | |
| WO | 0.883 | – | | | |
| BO | –0.079 | –0.199 | – | | |
| NRO | 0.159 | 0.128 | –0.004 | – | |
| SO | –0.148 | –0.054 | –0.057 | 0.490 | – |

species. These results are also reflected in the correlation matrix

between the red oak subgenus species (Table 1). Only scarlet oak and northern red oak produced a significant relationship ($r = 0.49, p = 0.039$), indicating poor acorn-production synchronicity between these three species. Super producers comprised 8.5 – 16.7% of the population and contributed 18 – 49.8% of all acorns per species over the 18-year study period (Fig. 3; Table 2). Within the white oak subgenus, super-producers at the species level produced 319 – 485% more acorns than regular producers; within the red oak subgenus, super-producers at the species level produced 121–235% more acorns than regular producers (Table 2). During high production years (>0.5 SD), chestnut oak and white oak super producer trees recorded a $> 1000\%$ increase in acorn production from their 18-year baseline mean, an order of magnitude greater increase than regular producers (Fig. 4). Within the red oak subgenus, black oak, northern red oak, and scarlet oak super producers also increased their acorn output during high-production years relative to regular producers (364 – 629% vs 78 – 130%), but less than their white oak subgenus counterparts. Finally, super producers were

Table 2

Percentage of trees classified as super producers (SP), the percentage contribution of super producers to mean acorn density (acorns/m² trap) across the study site, and difference in total (18-year) acorn production by super producers (SP) vs. regular producers (RP) of chestnut oak (CO), white oak (WO), black oak (BO), northern red oak (NRO), and scarlet oak (SCO) in the Bent Creek Experimental Forest, Pisgah National Forest, North Carolina.

| | CO (n = 71) | WO (n = 62) | BO (n = 11) | NRO (n = 36) | SO (n = 31) |
|-----------------------------------|-------------|-------------|-------------|--------------|-------------|
| SP trees (%) | 8.5 | 14.5 | 9.1 | 16.7 | 16.1 |
| SP acorns/m ² trap (%) | 28.0 | 49.8 | 18.1 | 40.2 | 34.5 |
| SP vs RP Av total acorns (%) | 319.3 | 484.6 | 121.0 | 235.2 | 173.4 |

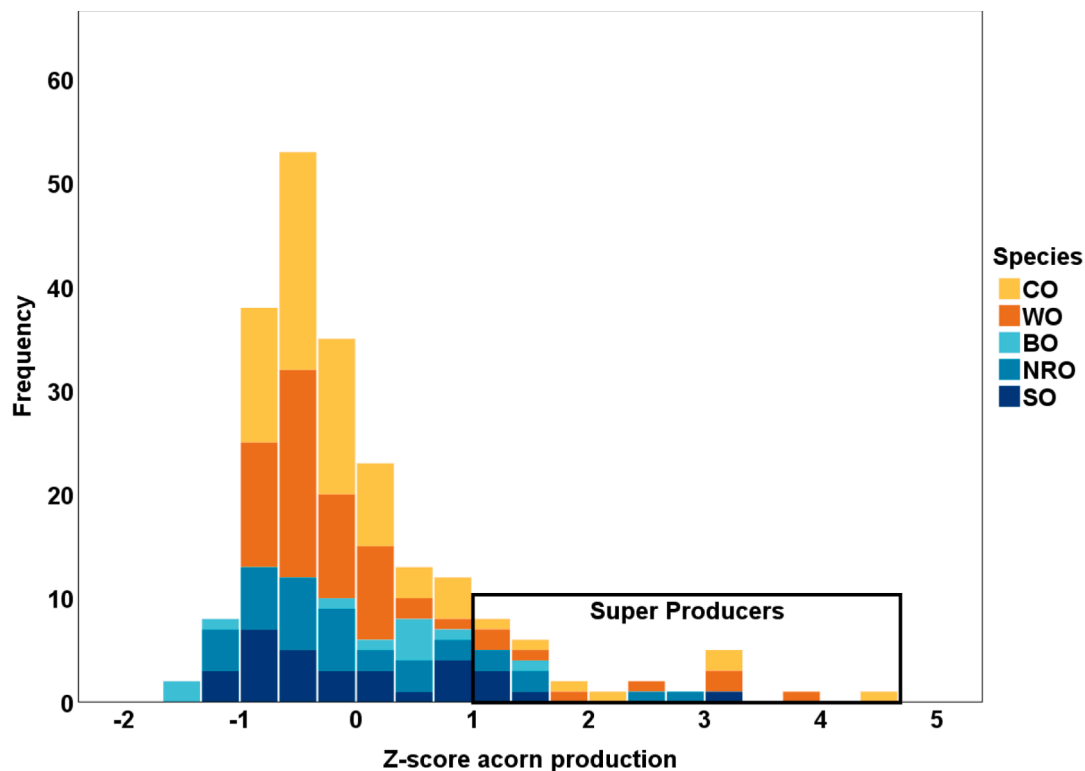


Fig. 3. Frequency histogram of z-score normalized acorn production for chestnut oak (CO), white oak (WO), black oak (BO), northern red oak (NRO), scarlet oak (SCO) and total oaks ($n = 211$) over 18 years at the Bent Creek Experimental Forest, Pisgah National Forest, North Carolina. Super producers are ≥ 1 z-score from the mean (identified in the box). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

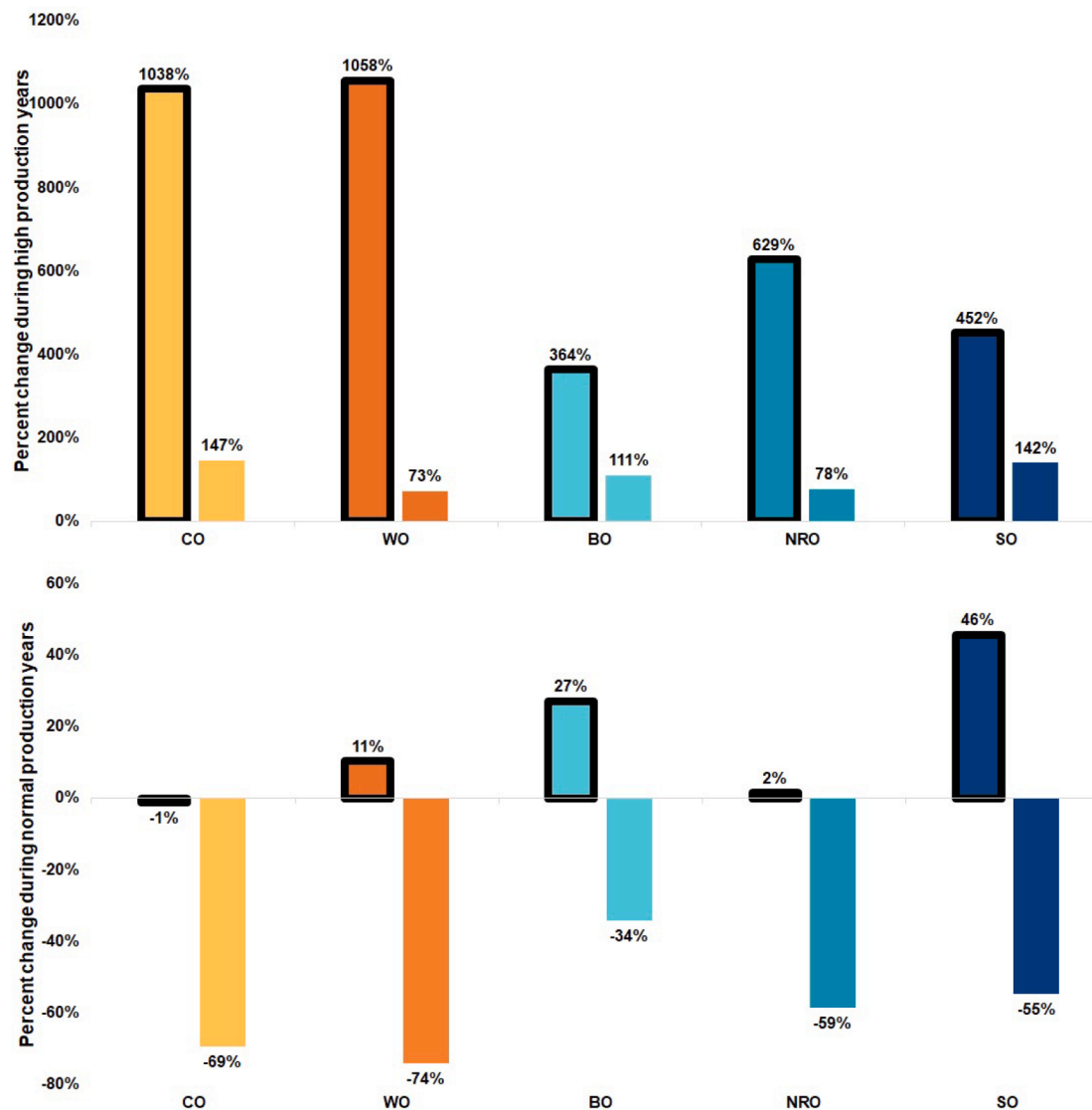


Fig. 4. Percentage increase or decrease from mean acorn production for super producers (outlined bars) and regular producers (non-outlined bars) during high-production years (top) and regular-production years (bottom) for in the Bent Creek Experimental Forest, Pisgah National Forest, North Carolina.

significantly larger in diameter for three of the five study species (chestnut oak, white oak, and scarlet oak; Fig. 5). Acorn production was weakly associated with monthly temperature and precipitation (Fig. 6). Acorn production in the white oak subgenus was positively correlated with precipitation in the previous May and July—the year of flower primordia development for white oak subgenus species. Additionally, mean minimum temperature during August of the previous year was positively correlated with chestnut oak acorn production and mean minimum temperature during October of two years prior was positively correlated with white oak acorn production. For the red oak subgenus, there were no significant correlations with precipitation, but there was some evidence of a negative effect of monthly mean minimum temperature during the two years of red oak subgenus acorn development. Black oak acorns were negatively correlated with January mean minimum temperature of two years prior (year of flower primordia development) and February of the previous year (year of flowering). Northern red oak was only correlated with one month, March of the current year, and scarlet oak acorn production was negatively correlated with July and November of the previous year as well as February and March of the current year.

All five oak species produced seasonally resolved, crossdatable chronologies that varied in length depending on the species (Table 3).

Mean series length was < 100 years for all species; older individuals (>150 years) advanced into each chronology but were only 3% of the sampled trees. Interseries correlation values were modest and never exceeded 0.5, indicating a common signal sufficient for cross-dating, but a lack of strong congruent growth signal between individuals of each species. Further, average mean sensitivity was low for all species (~0.2) indicating a lack of year-to-year ring-width variability. In general, LW chronologies presented higher interseries correlation and average mean sensitivity values than EW chronologies (Table 3).

We tested relationships between mean acorn production (acorns/m² trap area) and standardized ring-width for the three (TW, EW, and LW) ring-width measurements of each species (Fig. 7). We found limited evidence of relationships between mean acorn production and standardized ring-width for any of the five species or three ring-width measurements; all relationships were weak and statistically insignificant ($p > 0.05$). Analysis of relationships between mean acorn production and standardized ring-width for super producing trees also revealed limited evidence of relationships between growth and acorn production; we found one significant negative relationship between LW RWI and acorn production, noting this result does not correct for multiple comparisons ($p = 0.035$; Fig. 8).

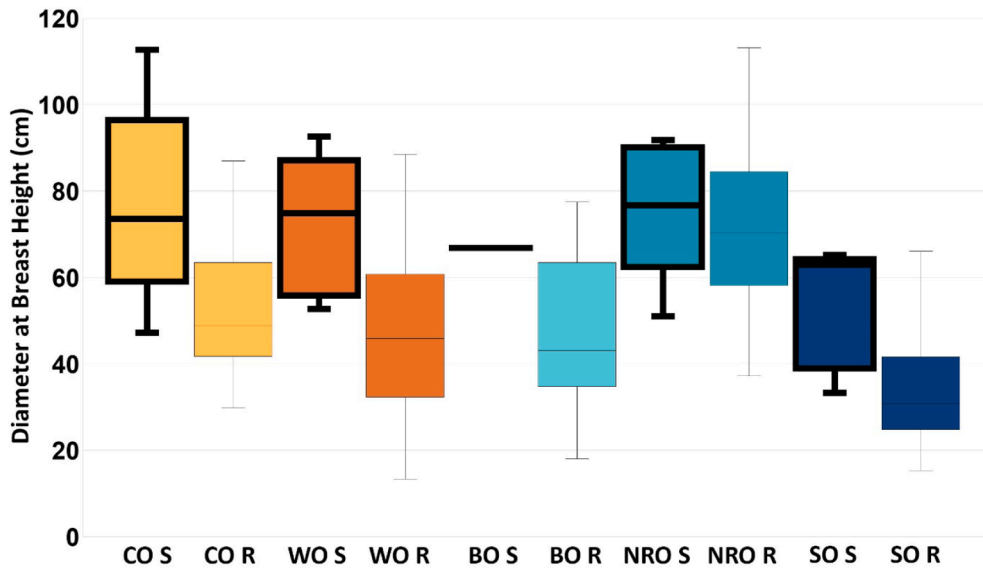


Fig. 5. Box and whisker plots of median (center line), interquartile range (box), and maximum and minimum (whiskers) diameter at breast height (cm) of super producers (bold outline) and regular producers (regular outline) of chestnut oak (CO), white oak (WO), black oak (BO), northern red oak (NRO), and scarlet oak (SCO) in the Bent Creek Experimental Forest, Pisgah National Forest, North Carolina. S and R appended to each species abbreviations denote super producer (S) and regular producer (R) groups. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

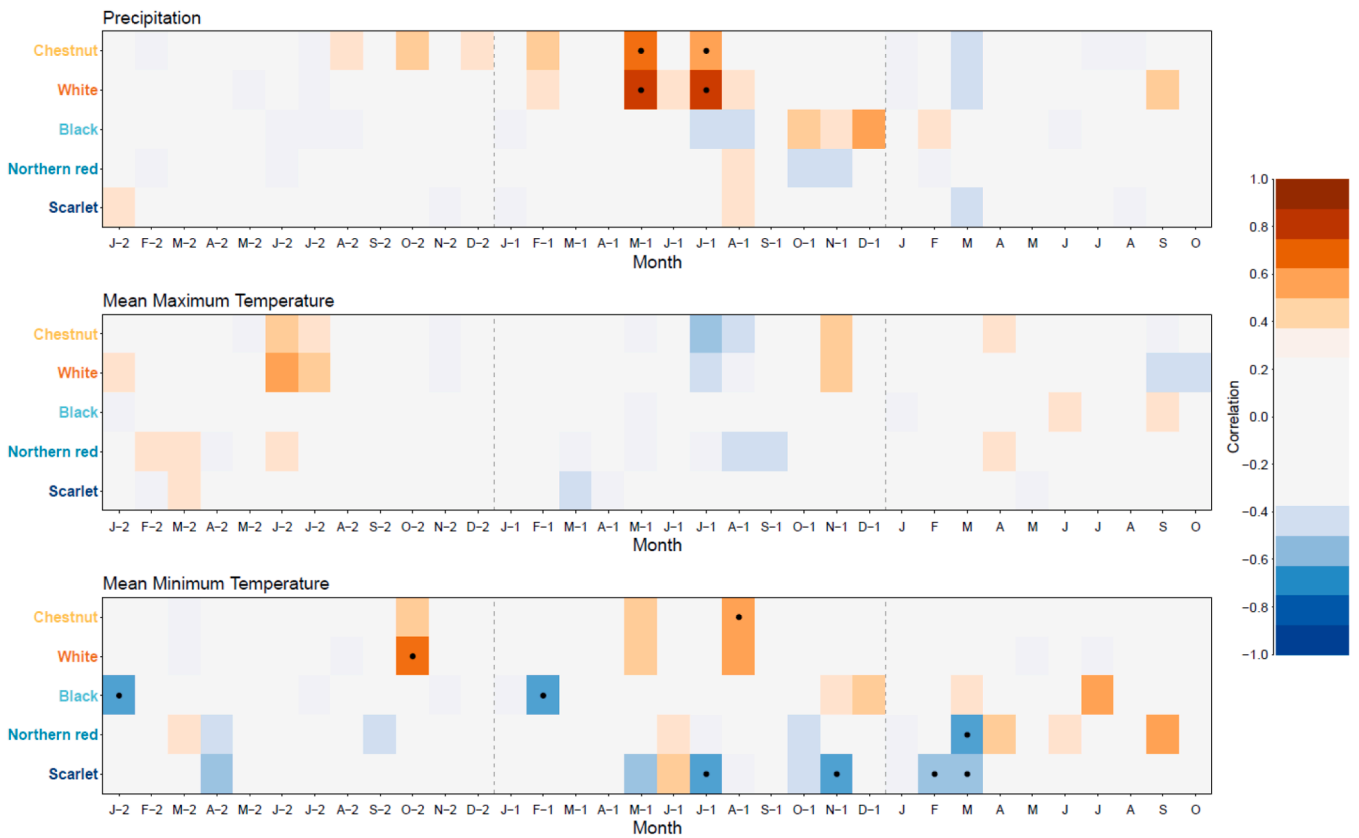


Fig. 6. Pearson product moment correlations between acorn production (number/m² trap area) by five oak species and monthly total precipitation (top panel), monthly average daily maximum temperature (middle panel) and monthly average daily minimum temperature (bottom panel) in the Bent Creek Experimental Forest, Pisgah National Forest, North Carolina. Correlations with $p < 0.01$ are indicated with a black point. Month abbreviation with -1 and -2 indicate conditions of the previous year and two years prior, respectively.

4. Discussion

We examined 18 years of tree-ring, monthly climate, and acorn-production data from 211 oak trees of five common species within the BCEF watershed to understand whether eastern-deciduous oak species

allocate resources between masting and growth, and how climate may modulate these potential relationships. A principle aim of our study was to evaluate the potential for tree-ring based reconstructions of masting in these oak species. Our research was guided by previous dendromastecology studies that examined relationships between annual

Table 3

Tree-ring chronology statistics for five common oak species in the Bent Creek Experimental Forest, Pisgah National Forest, North Carolina. Ring measure includes totalwood (TW), earlywood (EW) and latewood (LW). Interseries correlation measures the common signal of the chronology; mean sensitivity measures the year-to-year variability.

| | Ring measurement | Master Series (yrs) | Mean Length (yrs) | Interseries Correlation | Mean Sensitivity |
|------------------------|------------------|---------------------|-------------------|-------------------------|------------------|
| White Oak (n = 126) | TW | 238 | 96 | 0.46 | 0.2 |
| | EW | * | * | 0.21 | 0.19 |
| | LW | * | * | 0.47 | 0.3 |
| Chestnut Oak (n = 143) | TW | 178 | 80 | 0.45 | 0.2 |
| | EW | * | * | 0.19 | 0.2 |
| | LW | * | * | 0.46 | 0.28 |
| Black Oak (n = 21) | TW | 111 | 82 | 0.47 | 0.19 |
| | EW | * | * | 0.27 | 0.18 |
| | LW | * | * | 0.50 | 0.30 |
| Scarlet Oak (n = 60) | TW | 118 | 52 | 0.46 | 0.19 |
| | EW | * | * | 0.25 | 0.21 |
| | LW | * | * | 0.48 | 0.3 |
| N. Red Oak (n = 72) | TW | 134 | 66 | 0.37 | 0.18 |
| | EW | * | * | 0.23 | 0.19 |
| | LW | * | * | 0.42 | 0.29 |

mast and radial growth (e.g., Speer, 2001; Knops et al., 2007; Żywiec and Zielonka, 2013; Drobyshev et al., 2014; Martín et al., 2015; Patterson and Knapp, 2016; Hackett-Pain et al., 2019; Koenig et al., 2020; Hadad et al., 2021; Smith et al., 2022), but we incorporated a new approach by examining potential relationships between seasonally resolved growth (i.e., EW and LW), as well as total wood, and annual acorn production. Whereas some studies have successfully reconstructed multi-decadal to multi-century mast fruiting events from tree-ring variability (e.g., Speer, 2001; Drobyshev et al., 2014; Rodríguez-Ramírez et al., 2019; Mundo et al., 2021) others were unable to detect the strong relationship between masting and tree-ring-width needed for mast reconstructions (Żywiec and Zielonka, 2013; Koenig et al., 2020; Smith et al., 2022). For example, Koenig et al. (2020) did not find a strong relationship between acorn production and radial growth for five oak species in California. Similarly, Smith et al. (2022) found no consistent, significant relationships between acorn production and ring-width for two *Quercus* species in Ohio. Our results corroborate their findings, showing few detectable relationships overall between annual radial growth and acorn production for our five study oak species.

Most dendromastecology studies used total ring-width metrics to examine relationships between tree radial growth and mast production (e.g., Speer, 2001; Żywiec and Zielonka, 2013; Drobyshev et al., 2014; Martín et al., 2015; Patterson and Knapp, 2016; Hackett-Pain et al., 2018; Koenig et al., 2020; Hadad et al., 2021; Smith et al., 2022). Yet, recent research suggests that seasonally resolved ring-width is generally a superior metric for climate sensitive tree species of the southeastern US including chestnut oak (Mitchell et al., 2019; Soulé et al., 2021; Catherwood et al., 2023). Additionally, in ring-porous species, earlywood might be insensitive to a potential trade-off with reproduction because it forms before flowering and acorn maturation. In our study, we examined seasonally resolved tree-ring-width to determine whether latewood produced stronger relationships with acorn production than earlywood

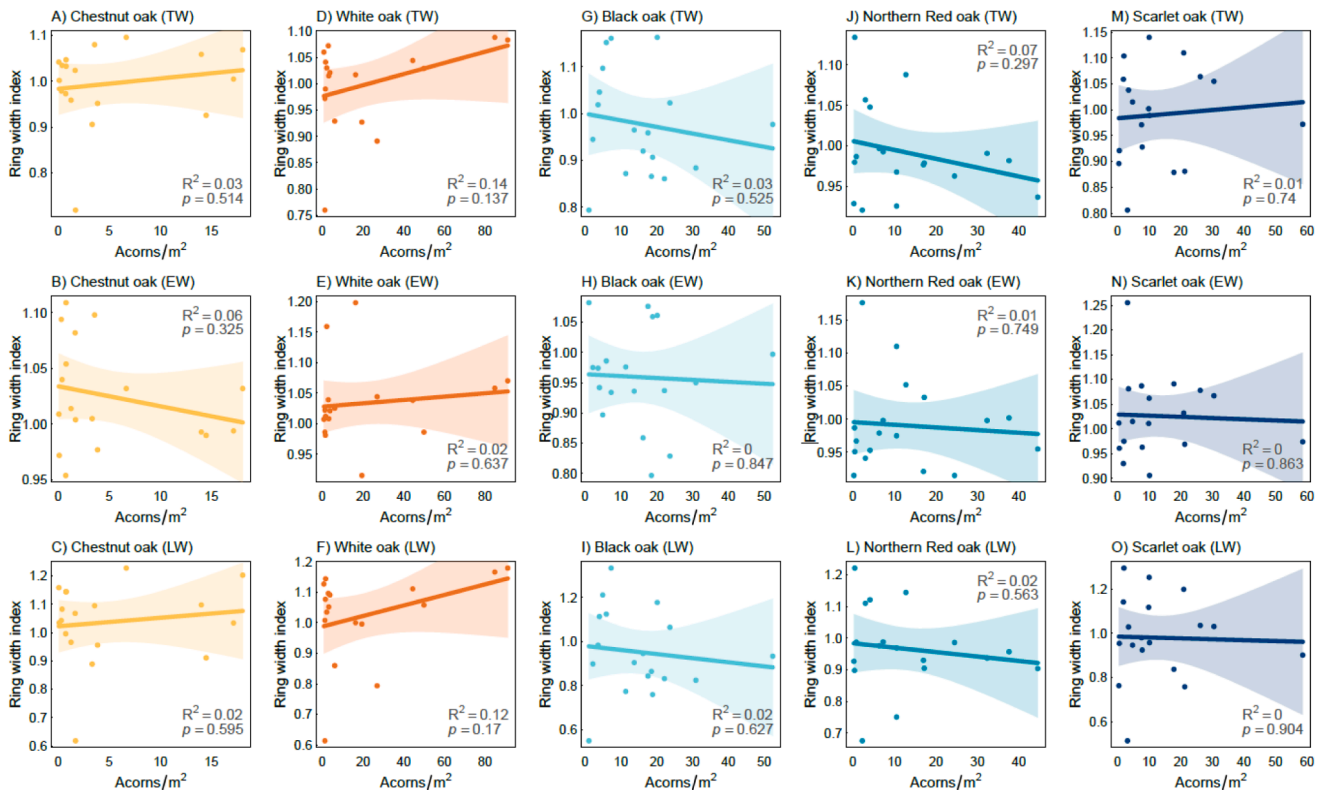


Fig. 7. Regression plots of the relationship between mean annual acorn production and ring-width for five oak species in the Bent Creek Experimental Forest, Pisgah National Forest, North Carolina. Plots are arranged by species (columns) and ring-width indices (rows). TW = Total wood, EW = Earlywood, LW = Latewood. n = 18 (2000–2017).

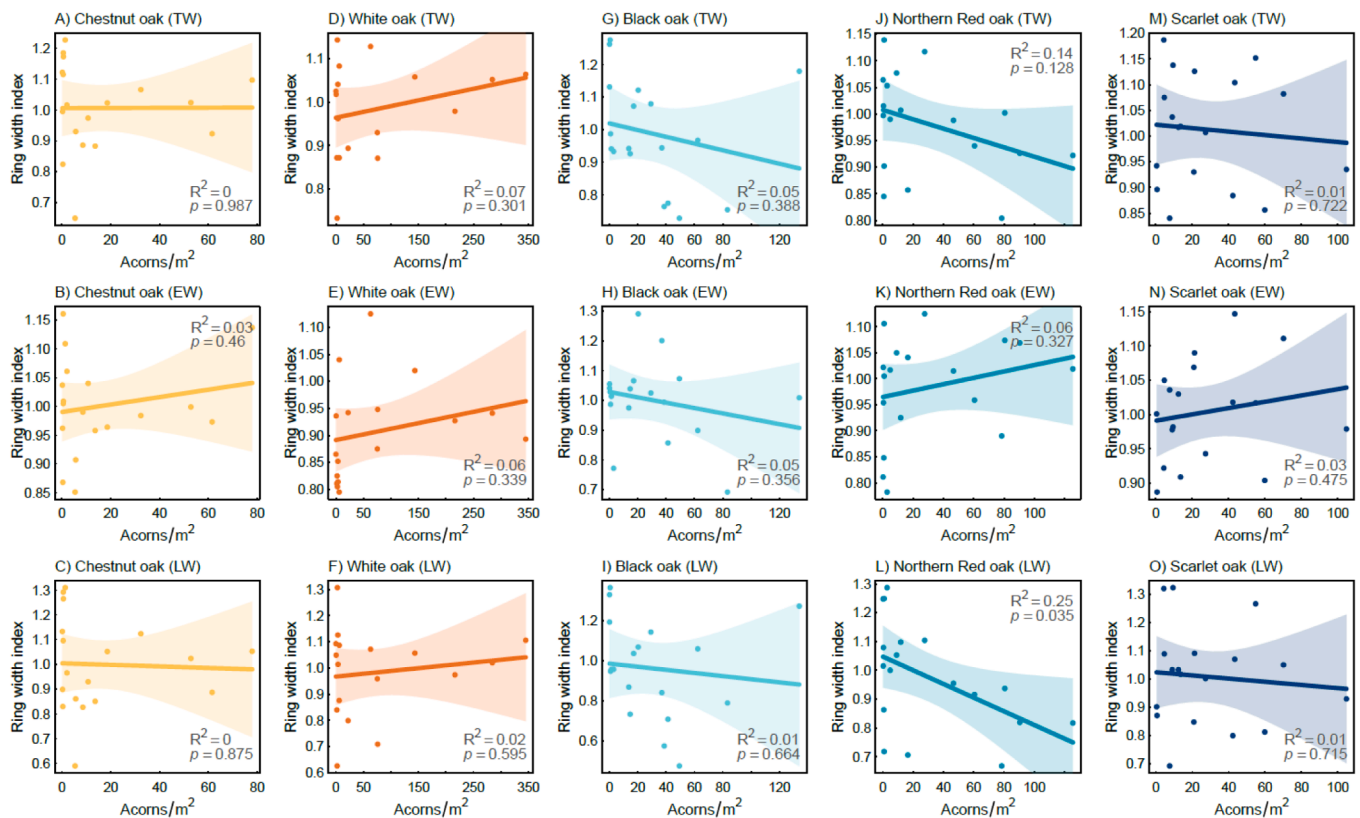


Fig. 8. Regression plots of the relationship between mean annual acorn production and ring-width for super producer individuals of five oak species in the Bent Creek Experimental Forest, Pisgah National Forest, North Carolina. Plots are arranged by species (columns) and ring-width indices (rows). TW = Total wood, EW = Earlywood, LW = Latewood. $n = 18$ (2000–2017).

or total ring-width. In general, we found no clear or consistent relationships to suggest that season wood produces a stronger relationship than traditional total ring-width measurements in our study species. We found negligible differences in chronology metrics such as interseries correlation—a measure of synchronicity between individual trees in a chronology—between total ring-width and season wood chronologies. Similarly, mean sensitivity—a measure of year-to-year ring-width variability—decreased for EW yet meaningfully improved for LW. Even though the LW chronologies exhibited a larger degree of year-to-year variability, we detected no clear improvements for season wood's relationship with acorn production for our five study species. Taken as a whole, our study indicates that seasonally resolved radial growth does not provide an avenue to improve the potential of tree-ring based reconstructions of oak masting. Despite large year-to-year variation in allocation to acorn production, we found little evidence of trade-offs between growth and reproduction. The lack of relationship between radial growth and acorn production in *Quercus* contrasts with numerous reports from other genera. *Quercus* are typically considered fruit maturation species, and the lack of relationship could be related to shared weather correlates of growth and acorn maturation success, but this remains to be tested.

Our tree-ring chronologies utilized all trees combined, but separate analysis of super producers – tree that invest more heavily in acorn production, also failed to identify significant relationships between growth and acorn production in species. It should be noted that our super producer chronologies had small sample sizes (1 for black oak; 5–8 for other species). Nevertheless, our results are consistent with past studies showing little evidence for differences in ring growth across acorn production classes (Żywiec and Zielonka, 2013; Smith et al., 2022).

Our results corroborate previous research that shows the influence of

weather on acorn production by eastern deciduous forest oak species (e.g., Sork et al., 1993; Cecich and Sullivan, 2011; Fearer et al., 2008; Smith et al., 2022). In our study, white and chestnut oak each had single-month precipitation relationships with the year prior to acorn production, and some evidence of relationships with previous summers temperatures. Taken together, prior-growing season conditions appear to be more influential than current year conditions for these white oak subgenus species, consistent with the results of Cecich and Sullivan (2011) and Smith et al. (2022). For red oak subgenus species, late winter (February and March) minimum temperature negatively affected acorn production. Fearer et al. (2008) reported similar results for species from the red oak subgenus in the mountains of southern Virginia. Sork et al. (1993) and Smith et al. (2022) both found a detrimental effect of cold spring temperatures of the previous year on red and black oak acorn production, a result we observed only for scarlet oak. Overall, weather effects on acorn production were relatively weak, and in some cases, difficult to interpret biologically, indicating that it would be challenging to use weather data to fore- or hindcast acorn production by our five study species in the southern Appalachians. Consequently, our results also indicate that a combined approach to mast reconstruction combining weather data and tree-ring data (Drobyshev et al., 2014) cannot be used to successfully forecast or reconstruct past masting events in our study system.

5. Conclusions

The appeal of reconstructing mast events using tree-ring data has been sustained by the temporal limitation of extant masting datasets (Hackett-Pain et al., 2022). Rarely do annual mast surveys extend for more than a few decades—a timespan that limits opportunities for longitudinal analyses. An overarching goal of tree-ring science is to

reconstruct environmental variables of interest. Thus, if mast production can be reconstructed from tree-ring-width variability, opportunities for centennial-scale mast analyses become possible (Mundo et al., 2021). Our study did not set out to reconstruct acorn production for the BCEF, but rather, to test new methods that could aid future dendromastecology studies in the southeastern US. We were unable to detect a clear and coherent signal between acorn production and ring growth for five common oak species, even when we focused on seasonally resolved radial growth. Our results therefore reinforce the most recent findings of similar studies using oak acorn and tree-ring data in North America (Koenig et al., 2020; Smith et al., 2022). Our findings contribute to the growing body of research that shows the limitations of tree-ring based mast analysis in *Quercus* species, and in particular, the inability to easily reconstruct mast production from tree-ring-width variability. We cannot conclude with confidence that future masting reconstructions are impossible for oak species in North America, but we feel compelled to assert that our results should guide future investigations into ring-width based mast analysis. Aside from ring-width analyses, our results indicated basic monthly climate variables are not overly influential on annual acorn production. While we used masting data and local climate data in the BCEF, we believe that future studies analyzing masting time-regions from across eastern North America could produce more insight into the relationship between climate and acorn production.

CRedit authorship contribution statement

Thomas W. Patterson: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing. **Cathryn H. Greenberg:** Conceptualization, Investigation, Methodology, Resources, Writing – original draft, Writing – review & editing. **Andrew Hacket-Pain:** Formal analysis, Visualization, Writing – review & editing.

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.

Data availability

Data will be made available on request.

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