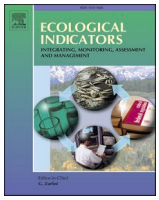
Ecological Indicators 192 (2026) 115726



Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Infrequent, high-volume rainfall events modulate acorn production for two common oak species in Western North Carolina, USA

Thomas W. Patterson [a,*], Cathryn H. Greenberg [b], Avery C. Catherwood [c], Paul A. Knapp [c], Andrew Hacket-Pain [d]

[a] F.D. Bluford Library, North Carolina Agricultural and Technical State University, Greensboro, NC 27411, USA
[b] USDA Forest Service, Southern Research Station, Upland Hardwood Ecology and Management Research Work Unit, Asheville, NC 28806, USA
[c] Carolina Tree-Ring Science Laboratory, Department of Geography, University of North Carolina Greensboro, Greensboro, NC 27402, USA
[d] Department of Geography and Planning, School of Environmental Sciences, University of Liverpool, Liverpool, UK

ARTICLE INFO

Keywords:
Acorns
Rainfall
North Carolina
Reproduction
Masting

ABSTRACT

Variations in landscape-scale acorn production have been studied across the *Quercus* genus to understand its role in ecosystem ecology and forest regeneration. Multiple weather conditions may influence annual acorn production, especially the positive influence of seasonal rainfall. Prior studies have assessed the effects of rainfall measured over monthly and seasonal scales, but have not focused on the potential influence of daily rainfall events (e.g., frequency and volume) on acorn production. Here, we examined 19 years of daily rainfall data with annual acorn data collected from *Quercus montana* and *Quercus alba* at the Bent Creek Experimental Forest, North Carolina, USA to understand how daily rainfall modulates acorn production. We organized daily rainfall data into three percentile thresholds (50th, 90th, and 99th) and examined how well linear models were able to explain variations in mean annual acorn production with and without previous-year high-volume daily rainfall (i.e., the highest volume rainfall days). We discovered model strength remained strong, and sometimes improved, when removing the frequent, low-volume rain events, and daily rainfall at or above the 90th percentile (21.9 mm/day) was crucial for establishing statistical relationships with annual acorn production. Our results indicate the importance for high-volume daily rainfall events to explain precipitation-acorn production relationships for two common oak species in North Carolina. Further, our results provide insights into the importance of daily high-volume rainfall for above average acorn production, which could have implications under future climate change.

1. Introduction

Annual acorn production in eastern US oak species (*Quercus* spp.) expresses a range of variability that includes differences in output between individual trees, locations, and years. High- and low-yield years are spatially synchronized as is typical for masting (Bogdziewicz et al., 2024; Kelly, 1994). However, many oak species express a wide range of acorn yield, which makes a strict masting characterization problematic (Patterson et al., 2023; Rose et al., 2012). This difficulty arises because acorn crops often include many intermediate (moderate) years, and because forest stands frequently contain both white oaks (one-year acorn development) and red oaks (two-year development), leading to asynchrony at the stand level(Patterson et al., 2023). In addition, many individual trees are chronic low acorn producers with a small proportion of heavy producers that can be characterized as "super producers" (Healy et al., 1999; Patterson et al., 2023; Smith et al., 2021). Despite this range of complexity, some signal in coordinated acorn production exists that has prompted research examining the influence of weather and climate patterns on synchronized acorn yield.

Research examining the influence of weather on acorn production for eastern US oak species has had mixed success in diagnosing common variables or periods important to synchronized acorn yield. Composites of daily, monthly, and seasonal climate variables have been important for acorn yield in white (*Quercus alba*), black (*Quercus velutina*) and red (*Quercus rubra*) oak in Missouri (Cecich and Sullivan, 1999; Sork et al., 1993), white and red oak in Virginia and Maryland (Fearer et al., 2008), black and chestnut (*Quercus montana*) oak in Ohio (Smith et al., 2021), and for five oak species in Florida (Abrahamson and Layne, 2003) and North Carolina (Patterson et al., 2023). These studies have revealed temperature and precipitation variables are linked

* Corresponding author at: F.D. Bluford Library, North Carolina Agricultural and Technical State University, Greensboro, NC 27411, USA.
E-mail address: twpatterson@ncat.edu (T.W. Patterson).

https://doi.org/10.1016/j.ecolind.2026.115726
Received 9 July 2026; Received in revised form 25 September 2026; Accepted 15 October 2026
Available online 22 October 2026
1470-160X/© 2026 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

to variations in acorn production (pollination, flowering, acorn maturity, etc.) throughout the acorn development cycle, and therefore serve as modulators for acorn production (Pearse et al., 2016). Extreme temperature values – maximum and minimum temperatures – as well as freeze events may modulate acorn production but this understanding is limited (Fearer et al., 2008; Patterson et al., 2023; Smith et al., 2021; Sork et al., 1993). While the influence of precipitation on acorn production factors into much of the eastern US acorn literature, relationships are commonly established using monthly and seasonal rainfall totals. At present, no research has examined how daily rainfall volume, or the frequency of extreme precipitation events (hereafter "frequency"), modulate these relationships in eastern US oak species.

Extreme precipitation events across the range of the eastern deciduous forest have become more variable in terms of magnitude and frequency (Davenport et al., 2021; Easterling et al., 2017; Feng et al., 2016; Powell and Keim, 2015; Singh et al., 2013) due to underlying climate change and surface temperature anomalies across the region (Armal et al., 2018). In the southeastern United States, precipitation events have become shorter in duration but more intense, with greater overall accumulation (Brown et al., 2019; Brown et al., 2020). The ecological impacts of extreme precipitation patterns are not well understood (van de Pol et al., 2017), and to our knowledge, no comparable work has been conducted for oaks. Here, we evaluate acorn production from two precipitation-sensitive species (Patterson et al., 2023) to examine the following research questions: 1) How do levels of daily rainfall at various percentile thresholds influence annual acorn production? And 2) How important is daily extreme rainfall for overall acorn production? Any information about the response of acorn yield to varying levels of daily precipitation will be vital to forest management in the 21st century.

2. Methods

2.1. Acorn data

We obtained 19 years (2000–2018) of annual acorn yield data for two species within the white oak subgenus (Leucobabanus) from a long-term acorn monitoring experiment at the 2600 ha Bent Creek Experimental Forest (BCEF) in North Carolina, USA (Fig. 1). This dataset includes data from 82 *Quercus montana* (Chestnut oak, hereafter CO) and 77 *Quercus alba* (White oak, WO) individuals, distributed across eight stands: Boyd Branch (0 CO, 2 WO), Buell Plot (17 CO, 8 WO), Bike Trail (4 CO, 8 WO), Greenslick (21 CO, 12 WO), Hard Times (15 CO, 18 WO), Old Gate (9 CO, 3WO), Rice Pinnacle (0 CO, 19 WO), and South Ridge (16 CO, 7 WO). Elevation in the BCEF ranges from 612 to 2010 m above sea level (m.a.s.l.) with acorn sampling sites ranging approximately 683–908 m.a.s.l. Acorn sampling sites represent a range of elevation, slope, and aspect across the BCEF. Individual tree ages ranged from 80 to 120 years (Greenberg, 2021) and average (standard deviation) tree diameter at breast height was 54 (21) cm as of 2017. Annual rainfall in the BCEF averages 1230 mm and is evenly distributed throughout the year. Complete methods for site and tree selection as well as acorn measurement are summarized in Patterson et al. (2023). As before, our study quantified acorn production as average annual acorns/m2 of trap area for all trees for each species.

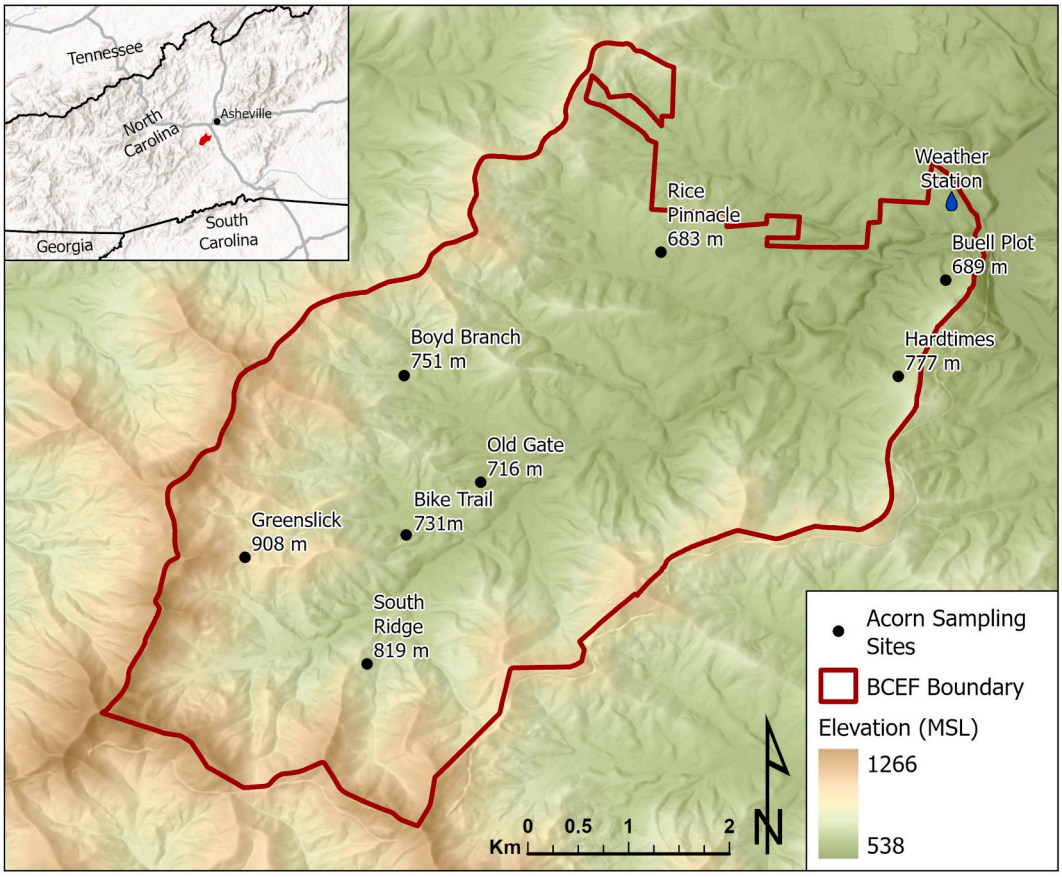


Fig. 1. Main map: Acorn sampling sites with average site elevation in m.a.s.l. and the NOAA weather station in the BCEF (NC One Map, 2019). Inset Map: the BCEF (red polygon) located southwest of the city of Asheville, North Carolina in the greater Southern Appalachian Mountain range. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Rainfall data

Daily station data were obtained from the National Oceanic and Atmospheric Administration Automated Surface Observing Systems station located within BCEF (35.504° N, 82.597° W). An earlier study showed that CO and WO acorn production by these trees was strongly correlated to the previous year's May–July rainfall (Patterson et al., 2023); therefore, we used daily precipitation data for the years (1999–2017, $n = 19$) that lagged our acorn data set by one year. Additionally, we examined trends in rainfall for all available years at the BCEF station (1949–2024) and analyzed these data separately from the years that overlapped our acorn dataset.

2.3. Data analyses

2.3.1. Rainfall partitioning

We rank-ordered all May – July daily rainfall events from 1999 to 2017 excluding zero values, and established daily accumulation thresholds for the 50th, 90th, and 99th percentiles. We partitioned daily rainfall above and below each percentile threshold and computed total May – July rainfall volume (sum of mm or rainfall) and the number of days experiencing rain for each classification: lower 50th – upper 50th, lower 90th – upper 10th, and lower 99th – upper 1. As a result, we created six classes of cumulative May – July rainfall totals that fell above or below the daily thresholds of increasing extremeness (50th, 90th, and 99th percentile) so that we could examine how the frequency of daily extreme rainfall could influence acorn production.

2.3.2. Statistical analyses

We used general descriptive statistics and parametric correlative analyses to explore the behavior of the rainfall data. We tested the predictive power of previous year May–July rainfall on CO and WO acorn production using standard linear regression in the statistical program R with the ggplot2 package for graphics (R Core Team, 2024; Wickham, 2016). For each model, we assigned rainfall volume (total mm) within each percentile class as the predictor variable and mean annual acorn production as the response variable. We examined the strength of the explained variance in the response variable (r^2) to understand how different percentile thresholds of rainfall were able to explain the variation in the annual number of acorns produced (average annual acorns/m^2 of trap area) for each species. We also differentiated high acorn production years from regular years as any year where species-wide acorn production was greater than one standard deviation from mean acorn production (see LaMontagne and Boutin (2009) for discussion of quantitative mast-year classifications) and measured the number of 90th percentile rain events that occurred between high and regular acorn production years. Lastly, we examined trends in the full rainfall dataset (1949–2024, $n = 76$ years) by using linear regression to examine the frequency of May – July 90th percentile rainfall events as well as the mean and standard deviation of those 90th percentile rain events per decade.

3. Results

3.1. Rainfall data

Mean May–July rainfall was 376 mm ($\sigma = 162$ mm) while mean daily rainfall during this period was 8 mm ($\sigma = 12$ mm). All months recorded measurable rainfall during 1999–2017. Over the 19 years that overlapped the acorn data, rainfall was recorded during approximately half (50.3%) of all 880 calendar days (Table 1). The distribution of daily rainfall was right-skewed (Fig. 2) with a large number of days ($n = 384$, 43.6%) producing ≤1 mm of rainfall. In contrast, days with high-volume rainfall were infrequent and contributed disproportionally to the total volume of rainfall data (Fig. 2). For example, the 90th percentile represented only 10% of all rain days, but contributed approximately half (45.8%) of all rain volume in the dataset (Table 1). Daily rainfall experienced a slight (1.5 mm/month) monthly increase from May through July (Fig. 3).

Table 1
Distribution of daily rainfall for the percentage thresholds at BCEF (1999–2017).

Rainfall percentage thresholds	Days with rain (#)	Days with rain (%)	Rainfall volume (%)
All data	880	100%	100%
Lower 50th	450	51.1%	7.1%
Upper 50th	430	48.9%	92.9%
Lower 90th	792	90%	54.2%
Upper 10th	88	10%	45.8%
Lower 99th	869	98.75%	89.7%
Upper 1	11	1.25%	10.3%

The correlative relationships between total volume of May–July rainfall and volume of rainfall at various percentiles revealed two important findings: 1) the high contribution of high-percentile days to overall volume, and 2) the asynchrony of rainfall above and below each percentile threshold (Fig. 4 A). Specifically, strong, positive correlations occurred between rainfall above the 50th ($r = 1$, $p < 0.001$), 90th ($r = 0.94$, $p < 0.001$), and 99th ($r = 0.8$, $p < 0.001$), percentiles and total MJJ rainfall volume even though these percentiles had diminishing volumes of rainfall (e.g., rainfall at the 90th and 99th percentiles only contained 45.8% and 10.3% of all rainfall volume). Additionally, no significant relationships occurred between rainfall below or above the 50th, 90th, and 99th percentiles (Fig. 4 B). Thus, these findings reveal the importance of high-volume rain days for the overall contribution of total MJJ rainfall volume, and that these daily high-volume rain events are asynchronous from low-volume rain events.

3.2. Rainfall volume and acorns

The relationships between annual acorn production and previous May–July rainfall across the percentile thresholds revealed the importance of high-volume rainfall events on model skill (Fig. 5). Models that examined rainfall below the 50th and 90th percentiles produced r^2 values near zero and were not significant for both CO and WO. Conversely, models that examined the upper 50th, 10th and 1 percentile rainfall events were able to explain similar or greater variance as the model that examined all rainfall combined (Fig. 5). The strongest model was for WO when the upper 10th percentile of rainfall data were tested ($r^2 = 0.76$, $p < 0.001$). In this model, 90% of all daily rainfall events were eliminated, and the upper 10th percentile still contained 46% of the rainfall volume. Comparing all rainfall data vs only daily rainfall data above the upper 1 percentile, variance explained was reduced by 43.8% for CO and only 30% for WO. These final models eliminated 99% of all rain days and only contained 10% of the rainfall volume.

3.3. 90th-percentile rainfall events

90th percentile rainfall events varied between the year preceding regular and high production acorn years, and were less frequent during regular years. The mean number of 90th percentile rain events preceding high production years was 11 ($\sigma = 4.6$) whereas years preceding regular production years averaged 3.4 ($\sigma = 2.4$) (Fig. 6A). Differences also existed in the frequency of monthly 90th percentile rainfall events, and the largest difference preceding the regular and high production years was for May (Fig. 6B). The mean May 90th percentile rainfall events preceding high production years was 4.7 ($\sigma = 2.1$) whereas the May months preceding regular years averaged 0.7 ($\sigma = 1.1$).

3.4. Full data trends

There was no significant change in the frequency of May – July 90th percentile rainfall events over the 76-year time period ($r^2 = 0.01$, $p >$

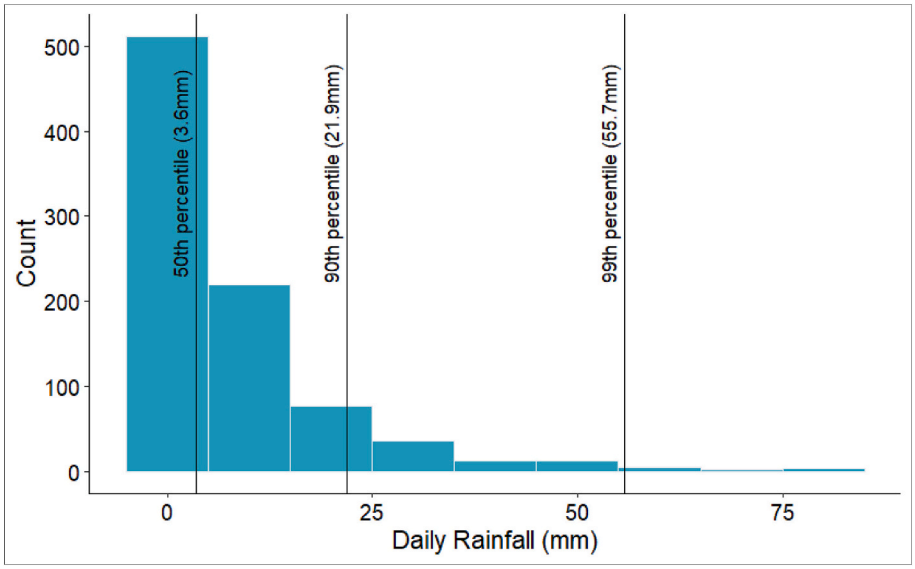


Fig. 2. Histogram of daily May–July rainfall data (n = 880) from the BCEF weather station (1999–2017).

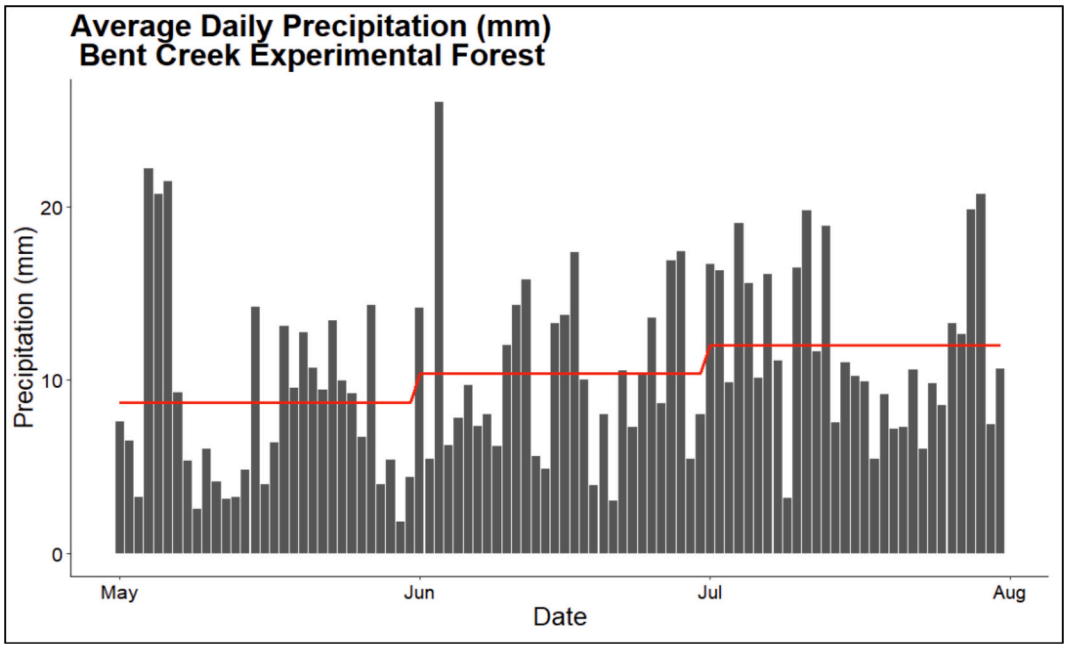


Fig. 3. Average daily rainfall in the BCEF (grey bars) with the daily average for each month in (red line). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

0.05). That said, decadal variations in 90th percentile rain events appear to increase in variance over the rainfall dataset, with decadal standard deviations increasing from 2.7 SD in the 1950s to 4.8 SD by the 2010s (Fig. 7).

4. Discussion

Our research revealed a new way to consider the relationship between rainfall and acorn production using two common US oak species in the BCEF. We have provided evidence for the key role of high-volume rainfall events on overall rainfall volume, and on the overall relationship between rainfall and acorn production. The following discusses our findings and contextualizes the big picture on how daily rainfall events may modulate acorn production for our study species.

We explored various thresholds that isolated the total volume of May–July rainfall, and found consistent results regarding strong, positive relationships between high volume rainfall (e.g., above the 90th percentile) and acorns produced the following year. Our results show that daily rainfall data were not normally distributed—the majority of the daily rainfall events were low in volume, while infrequent, high-volume rain days contributed to the majority of total MJJ rainfall. Thus, nearly half of the total MJJ rainfall volume was attributed to the majority of daily rainfall events (e.g., bottom 90%). Conversely, infrequent rain events had disproportionally large contributions to total MJJ rainfall and were statistically infrequent (e.g., top 10%). Taken as a whole, the largest driver of interannual variability in total MJJ rainfall were the infrequent, top 10% rainfall events that were not correlated (r = 0, Fig. 4a) with regular (bottom 90%) rainfall.

Our findings suggest high-volume rainfall is critical for modulating interannual variability in total MJJ rainfall, and thus has a strong

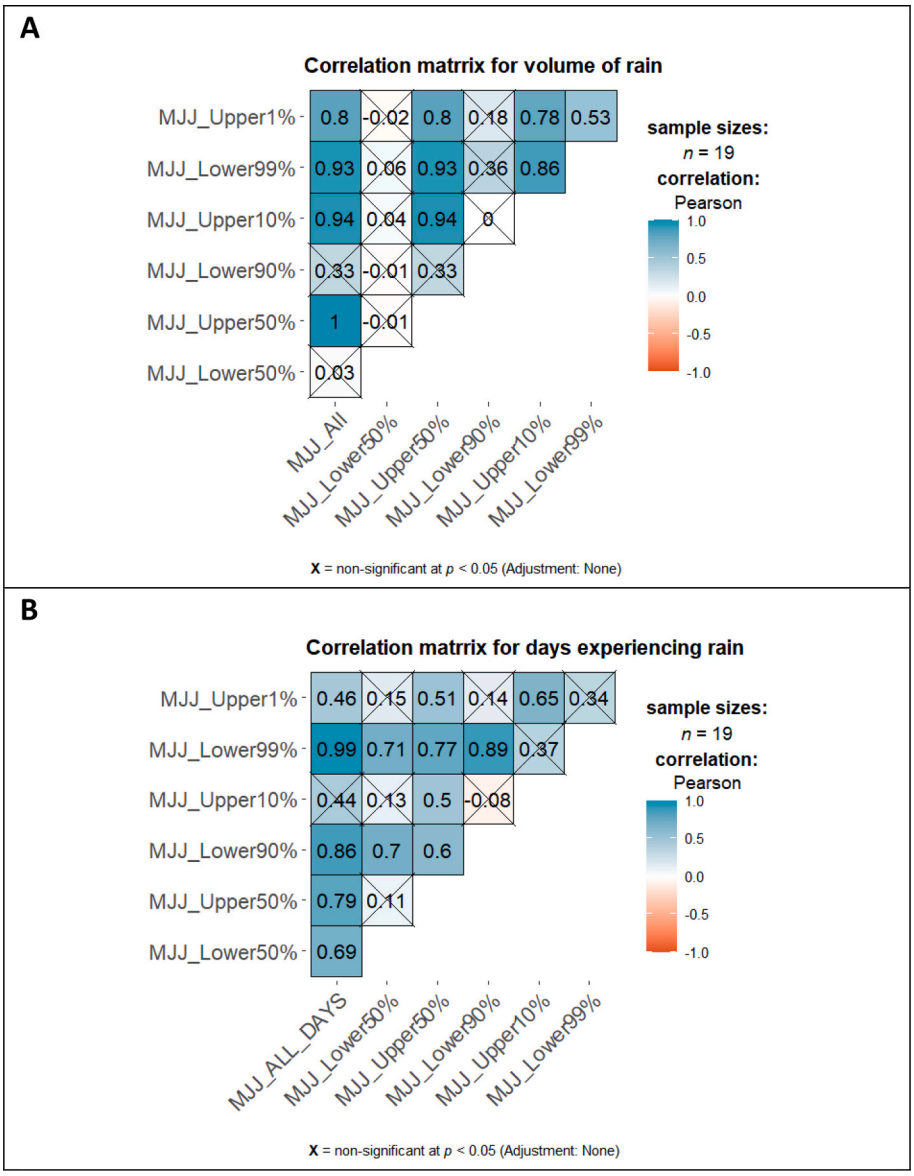


Fig. 4. Pearson correlation matrix of cumulative May – July (MJJ in figure) (A) daily rainfall volume and (B) daily rainfall frequency at the BCEF (1999–2017). Data include total May–July rainfall volume (MJJ_All) and rainfall encapsulated below and above the percentile thresholds.

influence on acorn-rainfall relationships in the BCEF. We posit the simplest explanation for our findings is that high-volume rainfall days have the largest impact on soil moisture, and subsequently years with frequent high-volume rain days likely improve reproductive conditions for acorn production the following year. Our findings are consistent with studies that have examined high-volume rainfall on acorn production for oaks species outside of the eastern US (Pérez-Ramos et al., 2010) as well as xeric upland oak species in Florida (Abrahamson and Layne, 2003). Abrahamson and Layne (2003) discuss the importance of exceptional rainfall that may strongly increase soil moisture availability in well-drained soils, hypothesizing that extremely wet growing seasons have the largest effect on acorn production in subsequent growing seasons. While outside of the *Quercus* genus, (Cannon et al., 2024) found hurricane rainfall during already wet growing seasons significantly increased longleaf pine cone production in subsequent years due to the likely abundance of available soil moisture. We posit a similar influence is operating in the BCEF, where years with frequent high-volume rain events provide suitable conditions for resource gain that WO and CO utilize for enhanced acorn production the following growing season. Nevertheless, the mechanism linking prior summer rainfall and acorn production remains unproven, as is the case for longleaf pine (Pearse and Wion, 2024).

Oak masting has often been linked to weather conditions prior and during flowering that influence pollination success, but recent research on European oaks has identified that flowering intensity is can also be an important regulator of acorn production(Fleurot et al., 2023; Fleurot et al., 2024). This raises the prospect that prior year rainfall may act as a cue for oak flowering. In southwestern Virginia, Merkle et al. (1980) were the first to isolate important months for flower primordia in white oak, finding staminate emergence occurring late May into summer months whereas pistillate emergence occurred as late as August. Conversely, two species in the red oak group (*Q. rubra* and *veultina*) from central Missouri cease flower primordia development as early as mid-May (Cecich and Haenchen, 1995). While we did not use red-oak group species in this study as our previous research showed these species contained no lagged relationships with rainfall (Patterson et al., 2023); we posit the strong, positive relationship between high volume rainfall and acorn production could relate to the difference in timing of flower-structure development between the two oak groups. If operable, white-oak group species that produce their flower structures throughout

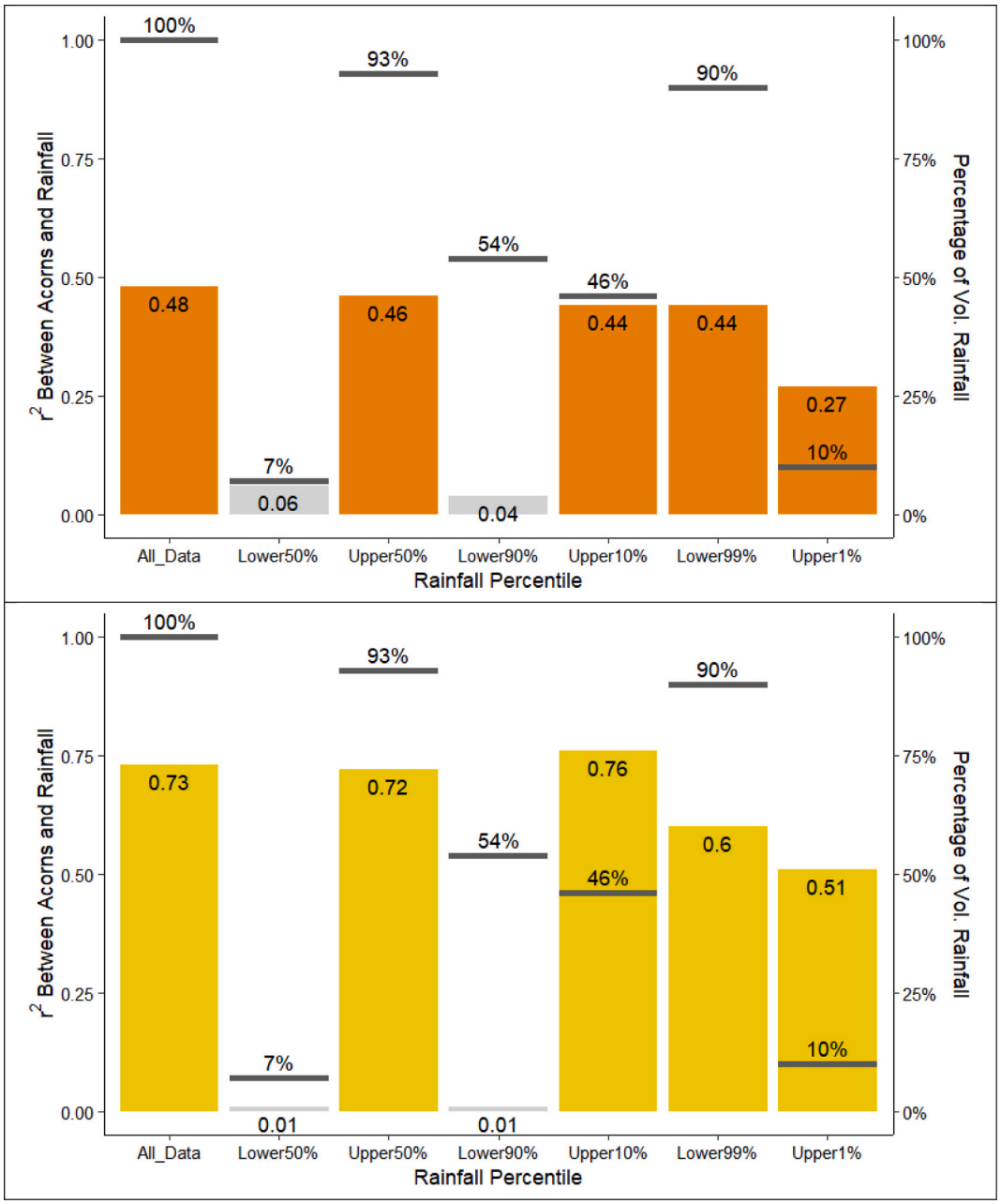


Fig. 5. Bar plots showing the relationship strength (r^2) between CO (top) and WO (bottom) acorn production and May – July rainfall across percentage classes. Colored vertical columns represent statistically significant ($p < 0.05$) models whereas grey columns indicate non-significant ($p > 0.05$) models. Horizontal dark grey bars represent the percentage of rainfall volume between each percentage comparison (50–50%, 90–10%, and 99–1%).

the growing season could benefit from frequent, high-volume rain days whereas red oak group species will have emerged before any summer rainfall occurs, and thus not respond to May – June rain events.

Infrequent, high-volume rainfall days that are critical for acorn production may change the magnitude and frequency of high acorn production years at the BCEF if the trend towards more variability in 90th percentile rainfall events continues. For example, we found no statistically significant relationships between previous year May–July rainfall and acorn production without the inclusion upper 10th percentile rainfall events. This finding has important implications in the context of forecasted precipitation trends in the southeastern US, suggesting more extreme and high volume precipitation events (Kim et al., 2023; Singh et al., 2013), albeit with a range of spatial variability (Brown et al., 2019; Brown et al., 2020; Powell and Keim, 2015; Skeeter et al., 2019). Our research findings indicate that future changes in rainfall intensity may positively influence acorn production, but we caution that our analysis was based on a 19-year dataset from a limited geographic region. A longer-term evaluation is needed to confirm the fidelity between extreme rainfall event frequency and acorn productivity over larger spatial and temporal scales.

5. Conclusion

Chestnut oak and White oak acorn productivity is significantly and positively influenced by previous year May – July high-volume rainfall, and our data suggest that these infrequent events have a major influence on annual acorn production. Further, changes in the frequency of high intensity rainfall events, particularly since the 21st century, suggest that this aspect of climate change may affect the seed production patterns of common white oak group species in the southeastern US. We believe this

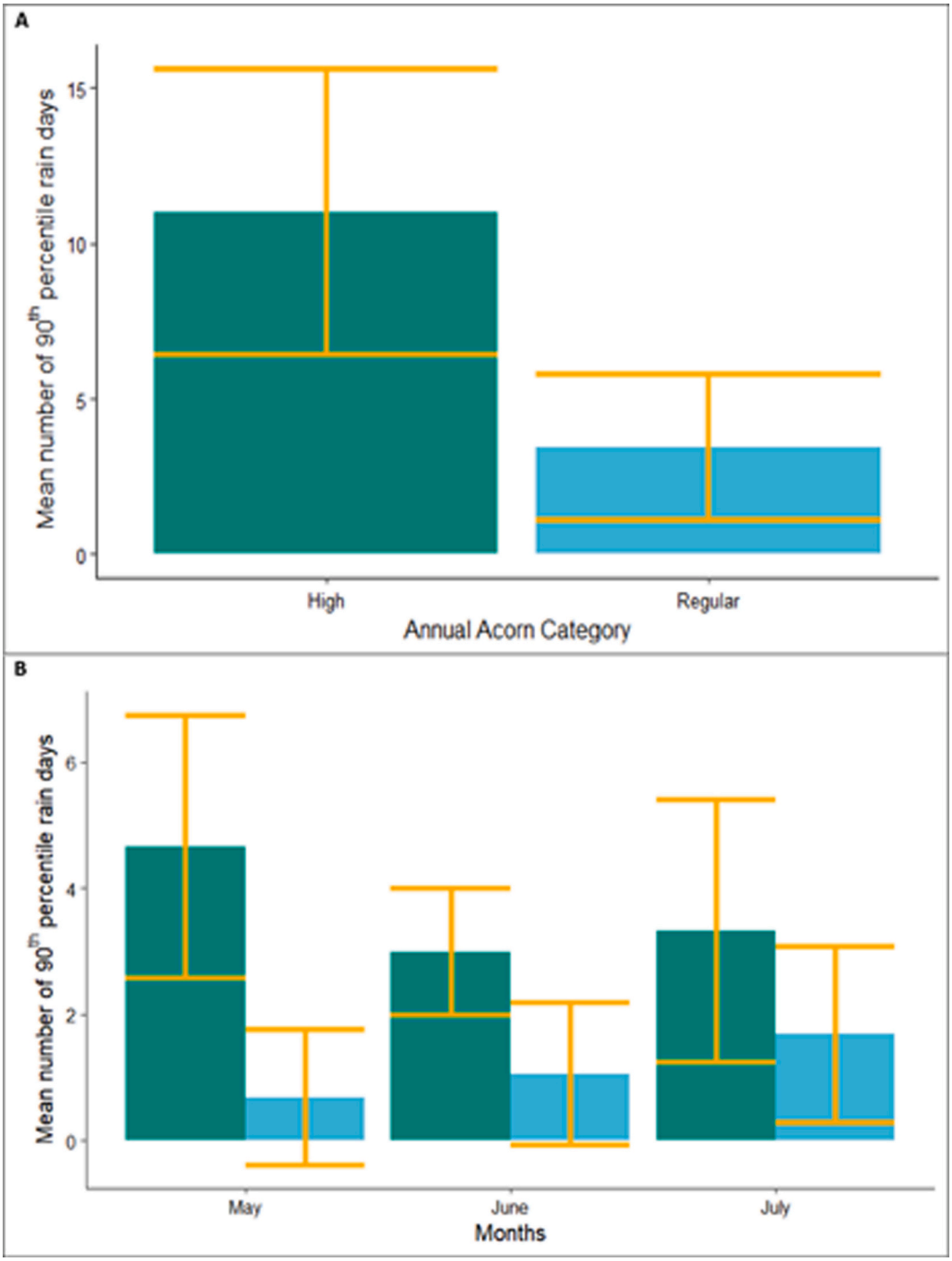


Fig. 6. Fig. 6A shows the total number of 90th percentile rainfall events in years preceding high vs. regular production, while Fig. 6B breaks this down by month (May, June, July)." Orange error bars are 95% confidence intervals.

new insight into the relationship between rainfall and acorn production will encourage research that examines the influence that infrequent and extreme events have on plant reproduction and how these patterns operate at regional scales. Future research should also examine the mechanisms in operation between rainfall and ultimate seed count (e.g., soil nutrient flux, carbohydrate storage, flower counts, etc.) that may be influenced by infrequent but influential weather conditions that are projected to amplify with a changing climate. As the distribution of weather conditions shifts to include more extreme events, it will be critical to understand how plant reproduction is impacted in order to make informed forest management plans.

CRediT authorship contribution statement

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

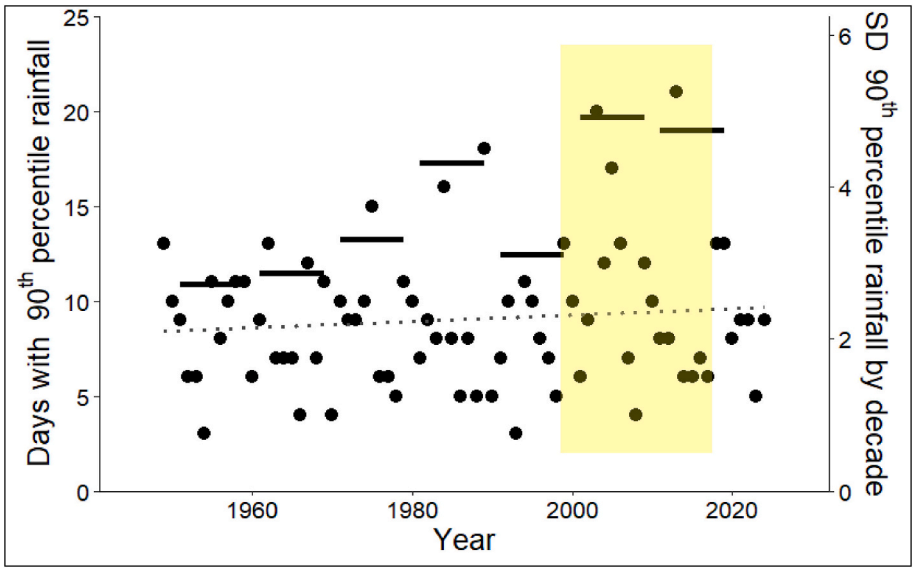


Fig. 7. Scatter plot of the number of days experiencing 90th percentile rain events by year from 1949 to 2024 (black dots, primary Y axis). Annual average line presented as grey dotted line (not significant). Decadal standard deviation of the number of days experiencing 90th percentile is presented as black bars on the secondary Y axis. Yellow highlight is the years of rainfall data that overlap the acorn dataset (1999–2017). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Investigation.

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.

Funding

This study was funded in part by the United States Department of Agriculture Forest Service, Southern Research Station, Bent Creek Experimental Forest.

Acknowledgements

Special thanks to T. Roof, K. Frick, J. Adams, V. Gibbs, and B. Benz for project management and fieldwork, and many other forestry technicians and volunteers for collecting and processing acorns.

Data availability

Data will be made available on request.

References

Abrahamson, W.G., Layne, J.N., 2003. Long-term patterns of acorn production for five oak species in xeric Florida uplands. Ecology 84, 2476–2492. https://doi.org/10.1890/01-0707.

Armal, S., Devineni, N., Khanbilvardi, R., 2018. Trends in extreme rainfall frequency in the contiguous United States: attribution to climate change and climate variability modes. J. Clim. 31, 369–385. https://doi.org/10.1175/JCLI-D-17-0106.1.

Bogdziewicz, M., Kelly, D., Ascoli, D., Caignard, T., Chianucci, F., Crone, E.E., Fleurot, E., Foest, J.J., Gratzer, G., Hagiwara, T., Han, Q., Journé, V., Lé, Keurinck, Kondrat, K., McClory, R., LaMontagne, J.M., Mundo, I.A., Nussbaumer, A., Oberklammer, I., Ohno, M., Pearse, I.S., Pesendorfer, M.B., Resente, G., Satake, A., Shibata, M., Snell, R.S., Szymkowiak, J., Touzot, L., Zwolak, R., Zywiec, M., Hacket-Pain, A., 2024. Evolutionary ecology of masting: mechanisms, models, and climate change, 39, pp. 851–862. https://doi.org/10.1016/j.tree.2024.05.006.

Brown, V.M., Keim, B.D., Black, A.W., 2019. Climatology and trends in hourly precipitation for the Southeast United States. J. Hydrometeorol. 20, 1737–1755. https://doi.org/10.1175/JHM-D-19-0004.1.

Brown, V.M., Keim, B.D., Black, A.W., 2020. Trend analysis of multiple extreme hourly precipitation time series in the Southeastern United States. J. Appl. Meteorol. Climatol. 59, 427–442. https://doi.org/10.1175/JAMC-D-19-0119.1.

Cannon, J.B., Rutledge, B.T., Puhlick, J.J., Willis, J.L., Brockway, D.G., 2024. Tropical cyclone winds and precipitation stimulate cone production in the masting species longleaf pine (Pinus palustris). New Phytol. 242, 289–301. https://doi.org/10.1111/nph.19381.

Cecich, R.A., Haenchen, W.W., 1995. Pollination biology of northern red and black oak, 197.

Cecich, R.A., Sullivan, N.H., 1999. Influence of weather at time of pollination on acorn production of Quercus alba and Quercus velutina. Can. J. For. Res. 29, 1817–1823. https://doi.org/10.1139/x99-165.

Davenport, F.V., Burke, M., Diffenbaugh, N.S., 2021. Contribution of historical precipitation change to US flood damages. Proc. Natl. Acad. Sci. U. S. A. 118, e2017524118. https://doi.org/10.1073/pnas.2017524118.

Easterling, D.R., Arnold, J.R., Knutson, T., Kunkel, K.E., LeGrande, A.N., Leung, L.R., Vose, R.S., Waliser, D.E., Wehner, M.F., 2017. Precipitation change in the United States 1. https://doi.org/10.7930/J0H993CC.

Fearer, T.M., Norman, G.W., Pack Sr., J.C., Bittner, S., Healy, W.M., 2008. Influence of physiographic and climatic factors on spatial patterns of acorn production in Maryland and Virginia, USA. J. Biogeogr. 35, 2012–2025. https://doi.org/10.1111/j.1365-2699.2008.01960.x.

Feng, Z., Leung, L.R., Hagos, S., Houze, R.A., Burleyson, C.D., Balaguru, K., 2016. More frequent intense and long-lived storms dominate the springtime trend in central US rainfall. Nat. Commun. 7, 13429. https://doi.org/10.1038/ncomms13429.

Fleurot, E., Lobry, J.R., Boulanger, V., Debias, F., Mermet-Bouvier, C., Caignard, T., Delzon, S., Bel-Venner, M., Venner, S., 2023. Oak masting drivers vary between populations depending on their climatic environments. Curr. Biol. 33, 1117–1124. e4. https://doi.org/10.1016/j.cub.2023.01.034.

Fleurot, E., Lé, Keurinck, Boulanger, V., Debias, F., Delpierre, N., Delzon, S., Lobry, J.R., Mermet-Bouvier, C., Bel-Venner, M., Venner, S., 2024. Reconciling pollen limitation theories. Insights From Temperate Oak Masting 27, e70009. https://doi.org/10.1111/ele.70009.

Greenberg, C.H., 2021. Oak growth and acorn production in southern Appalachian mature forests and shelterwood with reserves regeneration harvests. For. Ecol. Manage. 481, 118691. https://doi.org/10.1016/j.foreco.2020.118691.

Healy, W.M., Lewis, A.M., Boose, E.F., 1999. Variation of red oak acorn production. For. Ecol. Manage. 116, 1–11. https://doi.org/10.1016/S0378-1127(98)00460-5.

Kelly, D., 1994. The evolutionary ecology of mast seeding. Trends Ecol. Evol. 9, 465–470. https://doi.org/10.1016/0169-5347(94)90310-7.

Kim, J., Amodeo, M., Kearns, E.J., 2023. Atlas of probabilistic extreme precipitation based on the early 21st century records in the United States. J. Hydrol. Reg. Stud. 48, 101480. https://doi.org/10.1016/j.ejrh.2023.101480.

LaMontagne, J.M., Boutin, S., 2009. Quantitative methods for defining mast-seeding years across species and studies. J. Veg. Sci. 20, 745–753. https://doi.org/10.1111/j.1654-1103.2009.01068.x.

Merkle, S.A., Feret, P.P., Croxdale, J.G., Sharik, T.L., 1980. Development of floral primordia in white oak. For. Sci. 26, 238–250. https://doi.org/10.1093/forestscience/26.2.238.

NC One Map, 2019. North Carolina Department of Information Technology, Government Data Analytics Center, Center for Geographic Information and Analysis. www.nconemap.gov.

Patterson, T.W., Greenberg, C.H., Hacket-Pain, A., 2023. Acorn production, climate, and tree-ring growth of five oak species in southern Appalachian forests. For. Ecol. Manage. 546, 121310. https://doi.org/10.1016/j.foreco.2023.121310.

Pearse, I.S., Wion, A.P., 2024. Hurricanes: an unexpected mechanism linking disturbance and seed production in trees. New Phytol. 242, 8–9. https://doi.org/10.1111/nph.19559.

Pearse, I.S., Koenig, W.D., Kelly, D., 2016. Mechanisms of mast seeding: resources, weather, cues, and selection. New Phytol. 212, 546–562. https://doi.org/10.1111/nph.14114.

Pérez-Ramos, I.M., Ourcival, J.M., Limousin, J.M., Rambal, S., 2010. Mast seeding under increasing drought: results from a long-term data set and from a rainfall exclusion experiment. Ecology 91, 3057–3068. https://doi.org/10.1890/09-2313.1.

Powell, E.J., Keim, B.D., 2015. Trends in daily temperature and precipitation extremes for the southeastern United States: 1948–2012. J. Climate 28, 1592–1612. https://doi.org/10.1175/JCLI-D-14-00410.1.

R Core Team, 2024. R: A Language and Environment for Statistical Computing.

Rose, A.K., Greenberg, C.H., Fearer, T.M., 2012. Acorn production prediction models for five common oak species of the eastern United States. J. Wildl. Manag. 76, 750–758. https://doi.org/10.1002/jwmg.291.

Singh, D., Tsiang, M., Rajaratnam, B., Diffenbaugh, N.S., 2013. Precipitation extremes over the continental United States in a transient, high-resolution, ensemble climate model experiment. J. Geophys. Res. Atmos. 118, 7063–7086. https://doi.org/10.1002/jgrd.50543.

Skeeter, W.J., Senkbeil, J.C., Keellings, D.J., 2019. Spatial and temporal changes in the frequency and magnitude of intense precipitation events in the southeastern United States. Int. J. Climatol. 39, 768–782. https://doi.org/10.1002/joc.5841.

Smith, S.J., McCarthy, B.C., Hutchinson, T.F., Snell, R.S., 2021. Both weather and resources influence masting in chestnut oak (*Quercus montana* Willd.) and black oak (*Q. velutina* Lam.). Plant Ecol. 222, 409–420. https://doi.org/10.1007/s11258-021-01115-7.

Sork, V.L., Bramble, J., Sexton, O., 1993. Ecology of mast-fruiting in three species of North American deciduous oaks. Ecology 74, 528–541. https://doi.org/10.2307/1939313.

van de Pol, M., Jenouvrier, S., Cornelissen, J.H.C., Visser, M.E., 2017. Behavioural, ecological and evolutionary responses to extreme climatic events. challenges and directions 372, 20160134. https://doi.org/10.1098/rstb.2016.0134.

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.