Dendroecological investigation of red-cockaded woodpecker cavity tree selection in endangered longleaf pine forests

April L. Kaiser[a,*], Peter Soulé[b], Saskia L. van de Gevel[b], Paul Knapp[c], Arvind Bhuta[d], Jeffrey Walters[e], Evan Montpellier[f]

[a] *Department of Geography, University of Idaho, Moscow, ID 83844, USA*
[b] *Department of Geography and Planning, Appalachian State University, Boone, NC 28608, USA*
[c] *Department of Geography, Environment, and Sustainability, University of North Carolina-Greensboro, Greensboro, NC 27412, USA*
[d] *National Headquarters, USDA Forest Service, Washington, D.C. 20250, USA*
[e] *Department of Biological Sciences, Virginia Tech, Blacksburg, VA 24061, USA*
[f] *Department of Geography, University of Minnesota, Minneapolis, MN 55455, USA*

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ABSTRACT

Old-growth longleaf pine (*Pinus palustris*) is a keystone/foundation species for 29 threatened or endangered species in the Coastal Plain of the southeastern United States. The endangered red-cockaded woodpecker (*Dryobates borealis*; RCW) and endangered longleaf pine have an established ecological association. Here, we explore differences in climate/growth response and radial growth disturbance events in trees with RCW cavities compared to non-cavity trees in the Sandhills Gameland Reserve in North Carolina, USA. Using standard dendrochronological techniques, we collected and analyzed core samples from trees selected by RCW for their cavities (RCWC) and adjacent control trees (RCWCo) that had no visible cavity. We developed RCWC and RCWCo tree-ring chronologies that allowed us to examine if climate vulnerability is a component of the RCW selection process for their nests. Specifically, we investigated climate/growth responses, radial growth suppressions, and physical characteristics of both tree types through a comparison of tree age, latewood radial growth measurements, and number of resin ducts. For long-term climate response (1910–2018), we found no significant differences between RCWC and RCWCo trees. However, we identified temporal differences in climate/growth relationships between RCWC and RCWCo as well as significant differences in the number of suppression events and spatially-grouped suppression events. For tree physiology, we found more resin ducts during 1950–2018 in RCWC trees. Our dendroecological-based investigation examines multiple factors in addressing the question of why RCWs select specific longleaf pine trees for cavities, which may help improve conservation efforts for RCW and longleaf pine.

1. Introduction

Longleaf pine (*Pinus palustris*) and red-cockaded woodpecker (*Dryobates borealis;* RCW) species reside throughout the southeastern United States. Although RCW uses additional southern pines such as loblolly pine (*Pinus taeda*) and shortleaf pine (*Pinus echinata*) for foraging and excavating cavities, old-growth longleaf pine is their preference (Lennartz and Henry, 1985). These woodpeckers have a complex, cooperative breeding social structure, and each family of RCWs defends a set of tree cavities. These cavities include a roost cavity for each group member as well as cavities for nests (Walters et al., 1988). RCW are listed as near threatened and longleaf pine are listed as endangered by the International Union for the Conservation of Nature and

Natural Resources (IUCN; Farjon, 2013; Birdlife International, 2017). However, the United States Fish and Wildlife Service classify RCW as endangered (USFWS, n.d.). The RCW conservation status is attributed to decreased longleaf pine populations, habitat fragmentation, and habitat quality degradation primarily during the 1800s– mid-1900s (Lennartz and Henry, 1985; Conner et al., 2001). Longleaf pine habitat depends on frequent low-intensity fires that act as a thinning treatment, which facilitates longleaf pine and wiregrass regeneration and suppression of mixed hardwood forest development (Conner et al., 1991; Conner and Rudolph, 1991; Loeb et al., 1992; Waldrop et al., 1992; Conner and Rudolph, 1995; Gilliam and Platt, 1999; Conner et al., 2001; Glitzenstein et al., 2003; Loudermilk et al., 2011). Historically, fires often started from a lightning strike or by Native Americans.

Fig. 1. Photograph of Sandhills Gameland where frequent fire intervals facilitate a wiregrass-dominated understory with little to no mid-story development. Photograph taken by April Kaiser.

However, with the European settlement era along with a drastic decline in Native American populations, fire suppression became the norm (Van Lear et al., 2005). Longleaf pine historically ranged across 37.2 million hectares throughout the southeastern United States (Frost, 1993). Presently, longleaf pine distribution has decreased to < 1.7 million hectares, a 95% reduction, due to fire suppression, timber harvest, urban development, agriculture, and habitat fragmentation (Landers et al., 1995; Outcalt and Sheffield, 1996; Wear and Greis, 2002; Frost, 2007; Oswalt et al., 2012).

RCWs are unique in excavating cavities exclusively in living pine trees and typically select pine that are 90–100 or more years old (Ligon, 1970; Hovis and Labisky, 1985). This tree age preference is common because a cavity chamber must be constructed in heartwood rather than sapwood, and only old trees have developed enough heartwood to contain a cavity chamber (Conner et al., 2001). Cavity excavation is a lengthy process, requiring one to many years, rather than days to weeks as in other woodpecker species that excavate in dead wood. In our study area, the average excavation time in longleaf pine is 13 years (Harding and Walters, 2004). Intermittent excavation of the entrance tunnel through the sapwood, which is limited almost exclusively to the warmest months of the year, accounts for most of that time (Conner et al., 2001). Sapwood excavation is associated with a high risk that birds may become trapped in the sticky resin exuded from the damaged sapwood. Although cavities take a long time to excavate, once completed, they are used for an equal length of time (Ligon, 1970; Lay et al., 1971; Jackson, 1978; Conner et al., 2001; Harding and Walters, 2002, personal communication, Brady Beck). Thus, cavity trees are a valuable resource crucial for the survival of RCWs (Jackson et al., 1979); indeed, the population dynamics of the species revolve around acquisition and defense of this resource (Walters, 1991; Walters and Garcia, 2016).

Ornithologists and forest ecologists have explored which tree characteristics RCWs prefer for building cavities (Ligon, 1970; Locke et al., 1983; Field and Williams, 1985; Hooper, 1988; Rudolph and Conner, 1991; Loeb et al., 1992; Ross et al., 1997). In addition to requiring old trees, tree selection is also positively associated with heartwood decay (Hooper et al., 1991). This decay can be facilitated by the presence of red heart fungus (*Phellinus pini*) and other fungal species

(Jusino et al., 2015; Jusino et al., 2016), which makes cavity excavation easier (Walters, 1991). Longleaf pine cavity trees have an intermediate level of stress and the highest resin flow rates in comparison to other southern pine species (Ross et al., 1997). These species' specific characteristics facilitate increased RCW survival because woodpeckers chip into the sapwood around the cavity entrance daily to maintain resin wells that protect the cavity from snake predators (Jackson, 1974; Rudolph et al., 1990; Ross et al., 1997). Additionally, longleaf pine produce more resin for longer durations than other pines that contribute to a better resin barrier. These characteristics may attribute to longleaf pine's selection by RCW (Conner et al., 1998).

Additionally, research has found that RCWs may select trees that have low ratios of sapwood to heartwood. This tree selection basis may occur because trees with suppressed growth have less sapwood, which enables cavities to be excavated faster and have a lower risk of sap flooding the cavity (Conner and O'Halloran, 1987). However, RCWs can affect tree growth by stimulating high rates of resin production by damaging the bark surrounding cavity entrances (Ligon, 1970; Dennis, 1971; Rudolph et al., 1990). In this study, we further investigate the relationship between RCW cavities and tree physiologic characteristics through analysis of differences in climate sensitivity, ecological disturbances, and tree physiologic characteristics between cavity (RCWC) and non-cavity (control: RCWCo) longleaf pines. We also explore general effects of climate on longleaf pine growth. We hypothesize that RCWC trees, in comparison to RCWCo trees will: 1) have a greater variance in radial growth, 2) be more sensitive to climatic fluctuations, 3) will have more suppression events due to the presence of cavities and residual impacts from cavity excavation, and 4) will be older and have more resin ducts.

2. Materials and methods

2.1. Study area

We collected all tree cores from Sandhills Gameland (SGL), a protected nature reserve maintained by the North Carolina Wildlife Resources Commission (NCWRC) (Fig. 1).
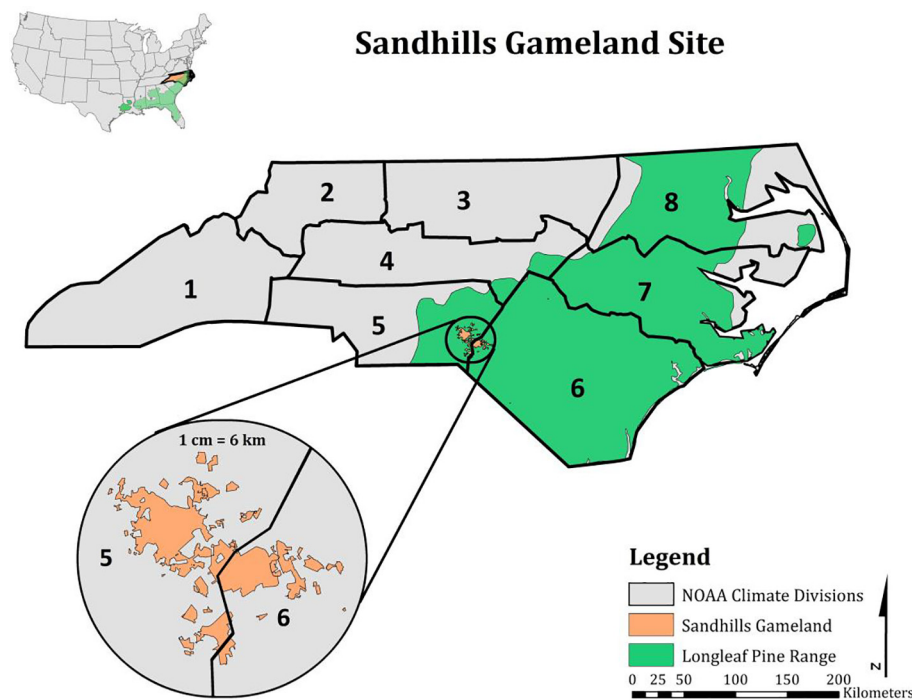
Sandhills Gameland Site

The North Carolina Sandhills region has a temperate climate with an average annual precipitation of 116.8 cm and annual mean temperature averaging 16.8 °C (North Carolina Wildlife Resources Commission, 2015). SGL spans across both the National Oceanic and Atmospheric Administration (NOAA) climate divisions 5 and 6 (Fig. 2). Initially owned by private investors and named the Broad Acres Plantation in the early 1900s, SGL was acquired by the Department of Defense (DoD) in 1942. The DoD installed Camp Mackall, an airborne training facility for World War II operations, and managed the area until the 1950s. Historically, the economy of the Sandhills region consisted of agriculture, forestry, and textile industries. Agricultural lands were mostly abandoned in the 1970s and 80s and bought by timber companies. Textile industries declined over the last 50 years, and today the area consists of primarily forestry management corporations (North Carolina Wildlife Resources Commission, 2015), as well as horse farms and developed areas. Additionally, SGL is near Fort Bragg, a major DoD installment, and popular golf courses.

These changes facilitated the formation of the North Carolina Sandhills Conservation Partnership (NCSCP) in 2000, which established successful cooperation between conservation groups and land managers interested in the region's federally endangered longleaf pine (North Carolina Sandhills Conservation Partnership, 2018). The collaboration also aides those species among the 29 federally listed endangered species associated with longleaf pine savanna habitat, such as RCW and Venus flytrap (*Dionaea muscipula*), that occur in the region (North Carolina Sandhills Conservation Partnership, 2018). NCSCP's efforts towards the conservation and recovery of RCW have been highly successful in conserving high quality longleaf pine habitat and increasing the RCW population beyond the size required for recovery (USFWS, 2003;, North Carolina Wildlife Resources Commission, 2015). Specifically, management maintains a frequent low-intensity fire regime through implementing prescribed burns every 1–3 years (personal communication, Brady Beck). Obtaining samples from trees with active RCW cavities is typically not permitted within managed RCW populations due to land management concerns and the species' conservation status. However, the strong recovery of the RCW population in SGL provided us with a unique opportunity, through NCWRC approval, to sample cores from RCW cavity trees.

2.2. Data collection

We obtained 80 historically sampled RCW tree cores collected in 1980 and 1981. The RCWC chronology retained 11 out of the 80 historical cores as the trees were either no longer alive or had substantial heart rot when resampled in 2019. We collected core samples at the diameter at breast height (DBH) from 27 complete (as opposed to partially excavated cavity starts) and naturally excavated (as opposed to artificial cavities constructed for RCWs to aid population growth) RCW longleaf pine cavity trees from our study site. These new samples included cores collected from any historical trees that were still alive. RCWC trees were in defined clusters throughout SGL, with each cluster designating an RCW social group. A numbered tree identification tag marked each RCWC tree, and the NCWRC maintains detailed records for each tree. We also collected samples from 33 RCWCo longleaf pines. For the RCWCo trees, we used a selective sampling strategy whereby we sampled at least one tree that had similar physiological characteristics that was within proximity (defined as within 200 m radius) of the RCWC tree. Thus, all RCWCo trees were mature trees with similar heights and DBH to RCWC trees. For all trees, we used increment borers to obtain a minimum of two core samples at DBH. Additionally, we recorded DBH, GPS coordinates, and observable tree characteristics for all trees sampled.

2.3. Climate data

For the climate/growth relationship analyses, we used monthly Palmer Drought Severity Index (PDSI; Palmer, 1965) data, total precipitation, and average temperature data spanning the period from 1910 to 2018 sourced from the National Oceanic and Atmospheric Association (NOAA) Physical Sciences Division data portal (www.esrl.noaa.gov/psd/data/timeseries/; NOAA, 2019). PDSI is a water balance-based measure of drought severity (Palmer, 1965). Thus, it incorporates both supplies of moisture (i.e., precipitation) and potential demand through evapotranspiration (i.e., temperature). We determined climate division data were best suited as regional climatic averages may have a stronger relationship with tree-ring data than single station data because divisional data has less microenvironmental noise (Blasing et al., 1981; Tejedor et al., 2017). Additionally, longleaf pine has consistently

shown highest climate/growth relationships with divisional data (Patterson and Knapp, 2018; Mitchell et al., 2019). As SGL straddles the boundary between two climate divisions, we conducted a preliminary correlation analysis and found stronger relationships between radial growth and Climate Division 6 data, and therefore proceeded with Climate Division 6 data.

2.4. Chronologies

We created separate chronologies for the RCWC and RCWCo trees. We used standard dendrochronological procedures to process the tree-ring cores (Stokes and Smiley, 1996). We glued each core sample to a wooden mount with cells vertically aligned, then sanded the sample until the cellular structure was clear under magnification. We cross-dated the core samples using the list method (Yamaguchi, 1991) in association with a previously developed tree-ring chronology from Uwharrie National Forest, NC (Mitchell et al., 2019). We scanned the core samples at 1,200 dots per inch (DPI) resolution and digitally measured each sample to 0.001 mm precision using WinDENDRO (Regent Instruments, 2011). We verified crossdating accuracy using COFECHA (Holmes, 1983) with 50-year segments lagged successively by 25 years. When COFECHA identified problems, we re-dated the core samples to correct those errors.

A maximum of two cores per tree were insured using the RCWC tree identification number. We used latewood widths to build the chronologies because latewood is more closely related to climatic conditions than totalwood widths for longleaf pine (Henderson and Grissino-Mayer, 2009; Patterson et al., 2016). The RCWC tree chronology had a mean interseries correlation of 0.552 and a mean sensitivity of 0.455; the RCWCo chronology had a mean interseries correlation of 0.539 and a mean sensitivity of 0.457. COFECHA takes the composite chronology and calculates and removes individual tree-ring series Pearson correlation coefficients, and then takes an overall average to reach a mean interseries correlation value (Holmes, 1983). Mean sensitivity is a climate sensitivity indicator determined by the relative differences among individual tree-ring sizes (Fritts, 1976).

We standardized radial growth using the computer program ARSTAN and Friedman's Super Smoother method with a tweeter sensitivity set to five (Cook and Holmes, 1984; Friedman, 1984). Standardization is needed to remove individual tree age-related growth trends (Cook and Holmes, 1984). Friedman's Super Smoother is an adaptive, non-parametric, smoothing regression technique used to preserve low-frequency variance (Friedman, 1984). We ensured the chronologies attained an expressed population signal (EPS) of ≥0.85. EPS indicates solidity of sample depth (Wigley et al., 1984; Duchesne et al., 2017). An EPS of ≥0.85 was reached in 1910 for both RCWC and RCWCo using a 10-year overlap with a 5-year running window.

For both RCWC and RCWCO, we created a new ring-width parameter, adjusted latewood, that corrects latewood growth width for the influence of earlywood on tree growth (Meko and Baisan, 2001). Using adjusted latewood as opposed to latewood has become standard for climate-based tree-ring studies (Stahle et al., 2009; Griffin et al., 2011; Griffin et al., 2013; Crawford et al., 2015; Dannenberg and Wise, 2016; Torbenson et al., 2016; Zhao et al., 2017). Additionally, removal of latewood's dependence on earlywood improves the summer-rainfall signal (Meko and Baisan, 2001; Stahle et al., 2009; Griffin et al., 2011; Zhao et al., 2017). As longleaf pine growth is commonly driven by precipitation, this new ring-width parameter is best suited for our study (Foster and Brooks, 2001; Sayer and Haywood, 2006; Henderson and Grissino-Mayer, 2009; van de Gevel et al., 2009; Patterson et al., 2016; Goode et al., 2019; Mitchell et al., 2019).

2.5. Statistical analysis

We performed normality tests on our adjusted latewood chronologies using a Shapiro-Wilks test (Shapiro and Wilk, 1965) and a Kolmogorov-Smirnov test for Goodness of Fit (Massey, 1951) using the 'stats' package in R and the 'shapiro.test' and 'ks.test' functions, respectively (R Core Team, 2017). Although Shapiro-Wilks is one of the most powerful normality tests, it was initially developed for small sample sizes (Shapiro and Wilk, 1965; Razali and Wah, 2011; Maes et al., 2017; R Core Team, 2017). Therefore, we supplemented with a Kolmogorov-Smirnoff test to ensure the correctness of distribution type. We also performed a Bland-Altman analysis using the 'BlandAltmanLeh' R package function (Lehnert, 2014) to determine differences between adjusted latewood chronologies and if related bias occurred (Bland and Altman, 1986; Bland and Altman, 1999). Additionally, we conducted a Spearman's Ranked Correlation test to determine the strength of covariance between chronologies.

We analyzed climate/growth relationships for both the RCWC and RCWCo chronologies using the R package 'treeclim' (Zang and Biondi, 2015). We determined classical bootstrapped correlations between both chronologies and monthly average PDSI, monthly total precipitation, and monthly average temperature climate variables from previous May through current December from 1910 to 2018. We used the Fisher r-to-z transformation test to determine if significant differences existed in the strength of the primary climate/growth relationships between RCWC and RCWCo trees (Zimmerman et al., 2003).

We tested for differences between RCWC and RCWCo adjusted latewood chronologies through time using classical bootstrapped 25-year moving correlation analysis from previous May through current December from 1910 to 2018 using the same three climate variables (Biondi and Waikul, 2004; Zang and Biondi, 2015). We performed a one-tailed z-test for independent proportions between RCWC and RCWCo on significant correlation occurrence for all moving interval correlations (Röhmel and Mansmann, 1999). Additionally, we examined variability between RCWC and RCWCo moving correlation results using a time-varying parameter regression state-space model (Durbin and Koopman, 2012) with an addition of the Kalman filter (Kalman, 1960; Cook and Johnson, 1989; Visser et al., 2010; Bishop et al., 2015; Maxwell et al., 2019). We used the 'dlm' R package and ran analyses with an average of June, July, and August for PDSI, total precipitation, and average temperature for both RCWC and RCWCo (Petris, 2010). Additionally, we performed a Rodionov regime shift detection analysis using a 10-year cut-off length and a Huber's Tuning Constant of 1 conducted at a 0.05 significance level to further investigate temporal stability and associations in our PDSI, RCWC, and RCWCo data (Rodionov, 2004; Rodionov and Overland, 2005).

We used the R package 'TRADER' to identify ecological disturbances on individual trees (Altman et al., 2014). We used annual non-standardized totalwood measurements (mm; 1910–2018) for each sample (n = 30) for both RCRW and RCRCo chronologies (total n = 60). We used a radial-growth averaging method, the 'growthAveragingALL' function in 'TRADER', which decreases the likelihood of Type I and Type II errors and requires less *a priori* data (Nowacki and Abrams, 1997; Hart et al., 2012; Trotsiuk et al., 2018). We identified moderate suppressions if there was a 25–50% growth change and major suppressions if there was a > 50% growth change. We used a seven-year length minimum to identify a suppression event, and suppression events were required to be at least 10 years apart to filter out fire events (Nowacki and Abrams, 1997).

We detected moderate and major suppression events during 1910–2018. Then, we created a composite figure of all suppressions and visually compared the temporal pattern to the pattern of the climate/growth relationship derived from both moving interval correlations. We determined small-scale spatial groupings of suppression events in RCWC and RCWCo trees based on three criteria. First, three or more trees needed to be involved in the group. Second, trees involved in suppression groups were required to be < 1,000 m apart. Third, we chose a minimum of four synchronous suppressions. For our ecological disturbance statistical difference analysis, we performed one-tailed and two-tailed Wilcoxon Rank Sum Tests on the number of suppressions

detected per tree (total n = 60) to determine if a significant difference (p < 0.1) was present between tree types. We plotted NOAA's Climate Division 6 annual average PDSI from 1910 to 2018 (www.esrl.noaa. gov/psd/data/timeseries/) to determine if suppression events coincided with drought in RCWC and RCWCo trees (NOAA, 2019).

We explored the physical characteristics of both RCWC and RCWCo longleaf pines to determine if any significant differences were present. We determined tree age using only complete tree record cores that included bark to near pith (13 RCWC; 27 RCWCo), excluding cores with heart rot. We estimated missing rings to pith with a comparison of ring-width patterns and the aid of pith locator diagrams (Duncan, 1989). We counted the number of resin ducts in the latewood bands (where they primarily occur) during 1950–2018 for 30 RCWCo cores and 19 RCWC to compare total count differences between RCWC and RCWCo trees (Koch, 1972; Lorio, 1986). We did not include 11 RCWC trees that were from the historically archived data due to the bark date being 1980 or 1981. We tested for significant differences between RCWC and RCWCo trees in the total number of resin ducts per core (1950–2018; n = 49) and non-standardized latewood widths (n = 60) using one-tailed and two-tailed Wilcoxon Rank Sum Tests as data were non-normal. We conducted one-tailed and two-tailed independent samples *t*-tests for the normally distributed tree age data (n = 40).

3. Results

3.1. Chronologies

Our Shapiro-Wilks tests determined the RCWC chronology was non-normally distributed with a bimodal curve (p < 0.05) and the RCWCo chronology was normally distributed with a unimodal curve (p > 0.05). We found no long-term growth trends in either standardized chronology (Fig. 3). Our Bland-Altman analysis at a 95% confidence interval found a mean difference of 0.00036, with the greatest standardized width difference in 1911 (0.44). Our spearman correlation test found a strong correlation coefficient of 0.859 (p < 0.001; Fig. 3).

3.2. Climate/growth analysis

We found that RCWC and RCWCo chronologies responded similarly to average monthly PDSI, total monthly precipitation, and average monthly temperature (Fig. 4). Both chronologies had significant positive relationships with PDSI from July–December (Fig. 4). RCWC had the strongest relationship with current October PDSI (r = 0.418; n = 108) and RCWCo with current September PDSI (r = 0.389; n = 108). We determined that summer and fall precipitation had significant positive relationships with growth for RCWC and RCWCo (Fig. 4). Both RCWC and RCWCo had a positive response to wet summers and falls. Average monthly temperatures were unrelated to both chronologies except for a positive relationship with May temperature for both, and a negative relationship with August temperature for RCWCo (Fig. 4). Previous months had little to no impact on current-year growth for all climate variables and were mostly not significant (Fig. 4). Comparatively, monthly climate variables of the current year had the most impacts. We found no significant differences in R-values based on the Fisher r-to-z transformation test.

3.3. Temporal climate/growth analysis

Moving-correlation analysis shows similar trends and relationships in both RCWC and RCWCo chronologies for all average monthly PDSI, total monthly precipitation, and average monthly temperature. PDSI had a significantly positive relationship with radial growth through time during June–December (Fig. 5). In comparison, prior months illustrate mostly negative relationships. We identified a weakened climate response period in the RCWC previous months that began in the 1957–1981 moving interval and ended in the 1977–2001 interval. The same weakened climate response was not as substantial in the RCWCo trees. RCWC also had a stronger and more significant relationship with PDSI than RCWCo (p < 0.001; Table 1).

Precipitation had similar patterns to PDSI through time for both chronologies (Fig. 5). Current months had a positive trend while those in the previous year were typically negative. Wet summers and autumns had a positive effect on growth for both RCWC and RCWCo chronologies. Additionally, previous dry summers had an overall negative effect on ring growth for both chronologies with a more negative effect for RCWC (Fig. 5). We found a similar weakened climate response period using precipitation to the one we found with PDSI in both RCWC and RCWCo. We found positive, strong, and significant (p < 0.05)
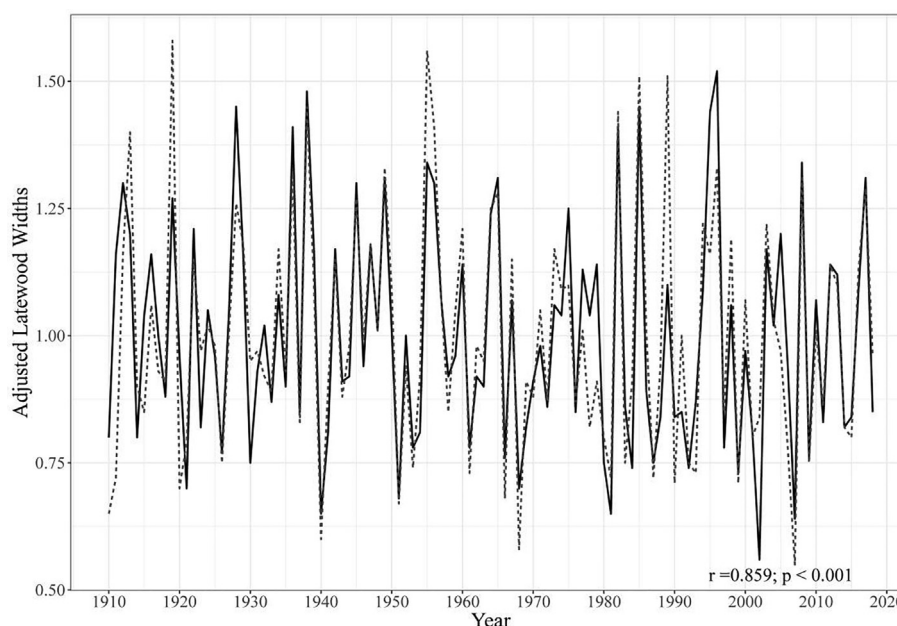

Fig. 3. Comparison between cavity (solid line) and control (dashed line) adjusted latewood chronologies. Correlation coefficient for Spearman correlation was significant (r = 0.859; p < 0.001).
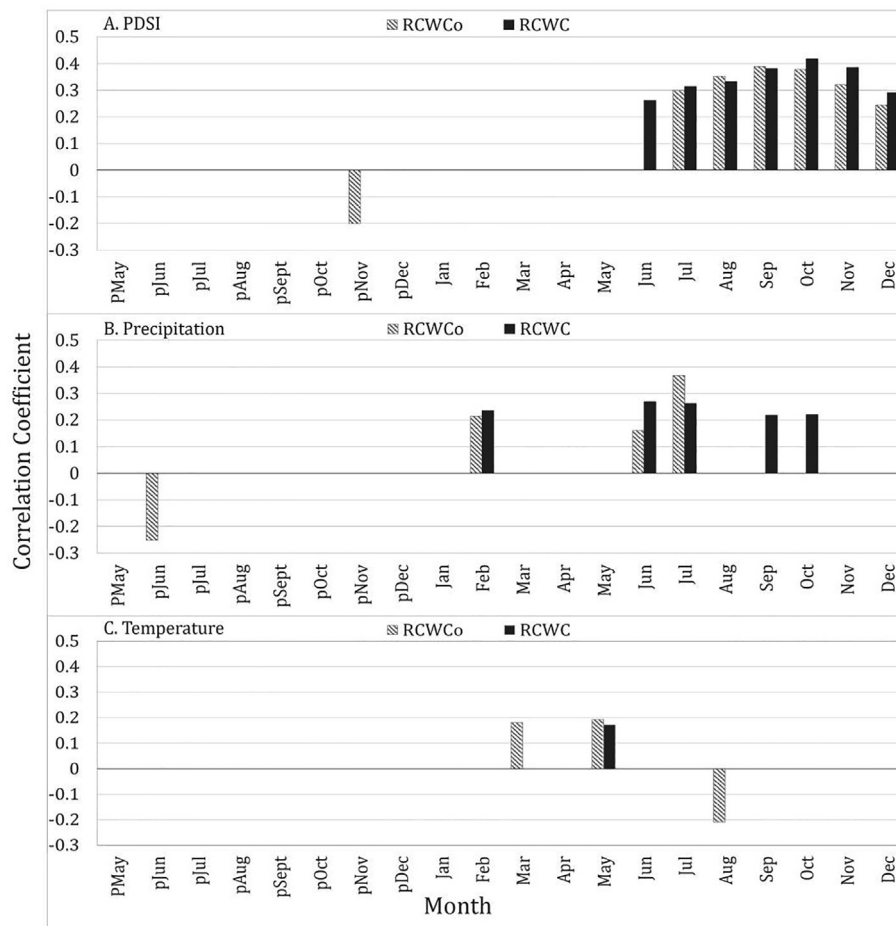
Fig. 4. Significant climate/growth relationships between 1910 and 2018 (R-value) of RCWC (black bars) and RCWCo (stripped bars) with A. average monthly PDSI, B. total monthly precipitation, and C. average monthly temperature. A month starting with 'p' denotes a previous year's month.

climate/growth relationships with precipitation in June, July, September, and October (Fig. 5). However, RCWC positively associates more with wet conditions than RCWCo and has a notable drop in climate signal around 1965. RCWC had a consistently positive relationship with February precipitation, but RCWCo's relationship with that variable was not temporally stable. We found no significant difference between RCWC and RCWCo in overall occurrence percentages for precipitation through time (Table 1).

We discovered that the overall weak relationship between adjusted latewood and average temperature is likely due to the instability of these relationships through time (Fig. 5). We found RCWCo to be more responsive to temperature than RCWC (Table 1). The Kalman filter found no difference between RCWC and RCWCo for JJA PDSI, total precipitation, or average temperature. However, this analysis did detect stable relationships for both RCWC and RCWCo for PDSI and total precipitation and did not for average temperature. The Rodionov regime shift detection analysis found regime shifts beginning in 1925, 1936, 1958, 1985, and 2013 for PDSI data (Fig. 6), but there were no regime shifts identified for either RCWC or RCWCo chronologies.

3.4. Ecological disturbance

Our running-mean suppression analysis detected a total of 43 moderate suppressions in the RCWC trees and 36 in the RCWCo trees. Additionally, we found 29 major suppressions in RCWC trees and 24 in RCWCo trees. RCWC trees had more suppressions overall and more major suppressions than RCWCo trees ($p < 0.1$ for both; $n = 30$; Fig. 7). However, there was no difference in moderate suppression totals for RCWC and RCWCo trees. There were no stand-wide major,

moderate, or combined suppression events, with the three highest amounts of overall suppression events occurring in 1964, 1961, and 2001 with 18.3%, 16.7%, and 15% of trees affected, respectively (Fig. 6; $n = 60$). We did find that a severe drought occurred in 2002, which was only one year after a large suppression event (Fig. 6).

We found four small-scale grouping of suppression events for RCWC trees and two for RCWCo trees (Fig. 7). From 1937 to 1940, group A had seven major or moderate suppression events. Two trees were from the same cluster, while the other four were from an adjacent cluster about 70 m away. Group B had eight suppression events in a 5-year period from 1961 to 1966, including a historical core denoted as group b (Fig. 7). Three trees were in the same cluster about 16 m apart while the other three were in another cluster ≤800 m away. In 1982, group C had five events that involved four trees and were all located in the same cluster. Seven suppression events occurred in group D from 1997 to 2001 and all but one tree was in the same cluster. Group E represents suppression of four RCWCo trees, all in the same cluster, during 1974 and 1975. Group F suppressions occurred in 2000 and 2001 and involved suppressions of four trees, with three in the same cluster (Fig. 7). We did not find any groups to occur before, during or after drought. However, we did find three groups (A, D, F) that preceded drought by one year.

3.5. Tree characteristics

We found no significant differences between RCWC and RCWCo for age or latewood width. However, RCWC had significantly more resin ducts (1950–2018) than RCWCo ($p < 0.05$; Table 2).
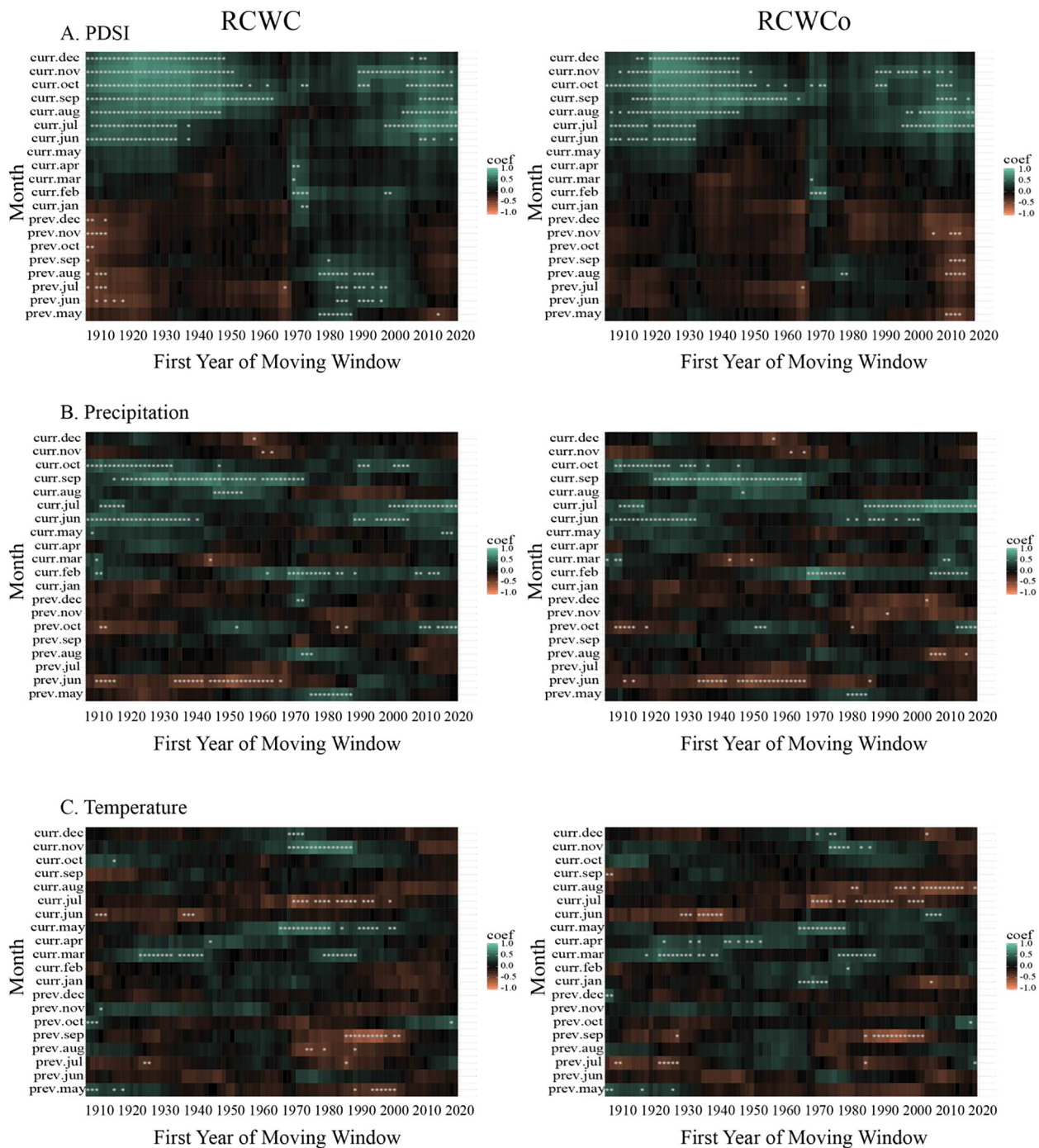
Fig. 5. Moving interval correlations (1910–2018) for RCWC (left column) and RCWCo (right column) with A. PDSI, B. precipitation, and C. temperature. Green indicates positive correlation coefficients (coef; r) while orange indicates negative correlation coefficients (coef; r), asterisks indicate a significant interval (p < 0.05). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

4.1. Climate/growth analysis

We found PDSI to be the most significant climate variable that impacts longleaf pine adjusted latewood width at our SGL site. Mean monthly temperature is not closely aligned with adjusted latewood for longleaf pine, with only three months in the current year producing significant relationships (Fig. 4). Longleaf pine typically has a strong positive association with precipitation and PDSI (Foster and Brooks, 2001; Bhuta et al., 2009; Patterson et al., 2016; Mitchell et al., 2019).

Our results show that the combination of temperature, precipitation, and soil moisture recorded in the PDSI created a stronger relationship with radial growth than precipitation (Palmer, 1965). Overall, our climate/growth results suggest that our hypothesis of RCWC being more climate-sensitive on a long-term time scale (i.e., 1910–2018) is not supported.

Precipitation is often one of the most influential climate factors for longleaf pine growth (Foster and Brooks, 2001; Sayer and Haywood, 2006; Henderson and Grissino-Mayer, 2009; van de Gevel et al., 2009; Patterson et al., 2016; Goode et al., 2019; Mitchell et al., 2019). This sensitivity has allowed for longleaf pine to be used for climate

Table 1

Moving interval correlation analysis percentages of significant relationships between RCWC and RCWCo average monthly PDSI, average monthly temperature, and total monthly precipitation variables between years 1910 and 2018 for previous May-current December. P-values (n = 1700) are from a one-tailed z-test for independent proportions between RCWC and RCWCo chronologies. Significant p-values are in bold font.

Climate Variable	Type	Significant Percentage	p-value
PDSI	RCWC	22.1%	**p < 0.001**
	RCWCo	16.3%	
Precipitation	RCWC	13.0%	p = 0.105
	RCWCo	11.6%	
Temperature	RCWC	7.2%	**p = 0.098**
	RCWCo	8.5%	

reconstructions such as tropical cyclone precipitation (Knapp et al., 2016). Current June and July precipitation (r > 0.2) had the highest impact on RCWC tree growth similar to the relationships we found with PDSI during summer. While February precipitation can be an essential driver of longleaf pine radial growth, our results reveal only a weak, positive relationship with February precipitation using adjusted latewood (Fig. 4; Henderson and Grissino-Mayer, 2009). While there are fewer significant monthly relationships for precipitation compared to PDSI, we found no significant differences between the RCWC and RCWCo trees for all months using the Fisher r-to-z transformation test.

4.2. Temporal climate/growth analysis

Temporal stability of climate/growth relationships is critical for dendroclimatology studies (Wilson and Elling, 2004) as this consistency facilitates predictability of global carbon cycle changes (Briffa et al., 1998a; Briffa et al., 1998b). Our long-term climate/growth correlation results suggest that both RCWC and RCWCo trees respond similarly to climate. However, when using the shorter 25-year intervals in our moving-interval analyses, we found that RCWC had more significant relationships than RCWCo for PDSI and less for average temperature (Fig. 5). While our analyses do not reveal why this occurs, we postulate there may be some physiological differences (e.g., resin ducts) between RCWC and RCWCo trees that cause RCWC to be more susceptible to evapotranspiration and better suited for cavity construction, or that

some aspect of the cavity excavation process and presence makes them more sensitive to drought. RCW are also known to select trees that have higher resin flows to aid in predator deterrence through maintenance of resin wells around cavity entrances (Rudolph et al., 1990). Additionally, RCW resin well maintenance induces high resin flow, which may contribute to tree stress (Jackson, 1974; Rudolph et al., 1990; Ross et al., 1997). We postulate that this increase in RCWC tree stress increases climate sensitivity.

Our study site history could also aid in understanding RCWC associations with climate sensitivity. SGL management maintains a frequent fire regime, which has a direct impact on longleaf pine growth and stand dynamics (Binkley et al., 1992; Brockway and Lewis, 1997; Van Lear et al., 2005; Lavoie et al., 2010). Disturbance events such as RCW cavity excavation impact climate sensitivity, which would likely exacerbate the switch and weakened period in climate response (Fritts, 1976). Furthermore, our Kalman filter found both RCWC and RCWCo to have an unstable relationship with JJA average temperature. We posit this result is attributable to precipitation, not temperature, being the most limited factor for longleaf pine growth. Additionally, climate response instability is likely due to the species temporarily switching its most limiting factor due to its environmental conditions (Maxwell et al., 2019).

Overall patterns for PDSI show a mostly positive relationship with adjusted latewood through time for current year growth, except for a period from around 1970–1995. During this period, growth in the previous year clearly shows a shift in the climatic signal (Fig. 5). This weakened climate response affected both chronologies but was more pronounced in the RCWC chronology (Fig. 5; Table 1). Although we detected five regime shifts in PDSI annual averages, none occurred during the weakened climate response for either chronology (Figs. 5, 6). In the context of climate change, anomalous temperature increases could negatively impact longleaf pine through decreasing water availability in the clay and sandy soils found in the region and may have an association with impacts related to teleconnections of large-scale weather patterns (Iverson et al., 2008; Leathers et al., 1991). Additionally, these oscillations directly affect fire regimes by changing weather patterns that influence scheduling of prescribed fires (Pielke and Landsea, 1999; Yocom et al., 2010). Fire suppression allows midstory development that introduces more cavity kleptoparasites and nest predators of RCWs and otherwise degrades RCW habitat, as well as
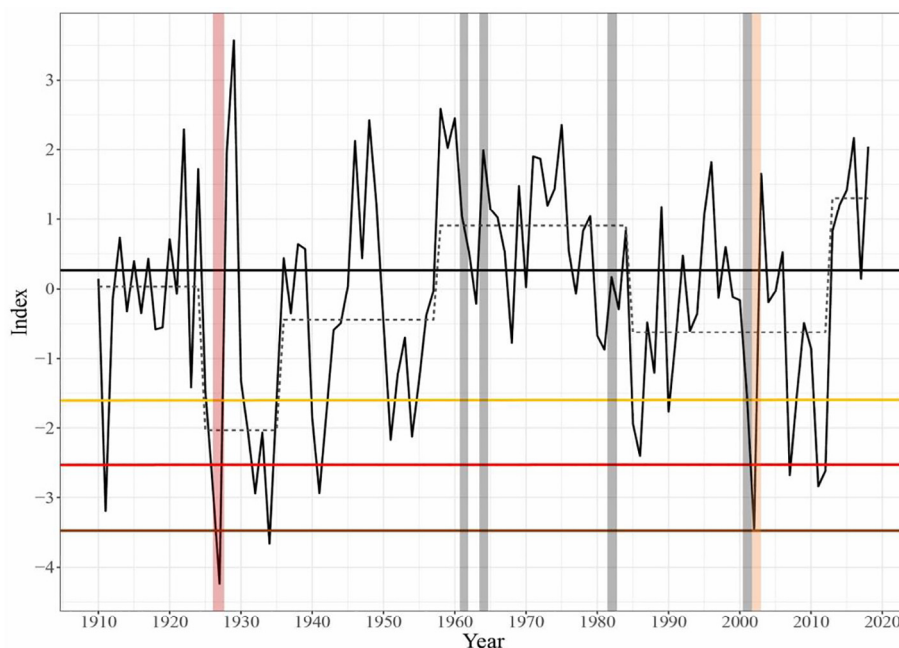

Fig. 6. Climate Division 6 annual average PDSI from NOAA (1910–2018). Grey boxes indicate the highest percentage of trees suppressed for both suppression detection methods; years 1961, 1964, 1982, and 2001. The orange box is a severe drought with large suppression association. An extreme drought event is illustrated by a red box. Extreme drought is −4 or less (brown line), severe drought is −3 to −3.9 (red line), moderate drought is −2 to −2.9 (orange line) (Dai and National Center for Atmospheric Research Staff, 2017). Dotted line represents significant (p < 0.05) Rodionov regime shifts in the divisional PDSI data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
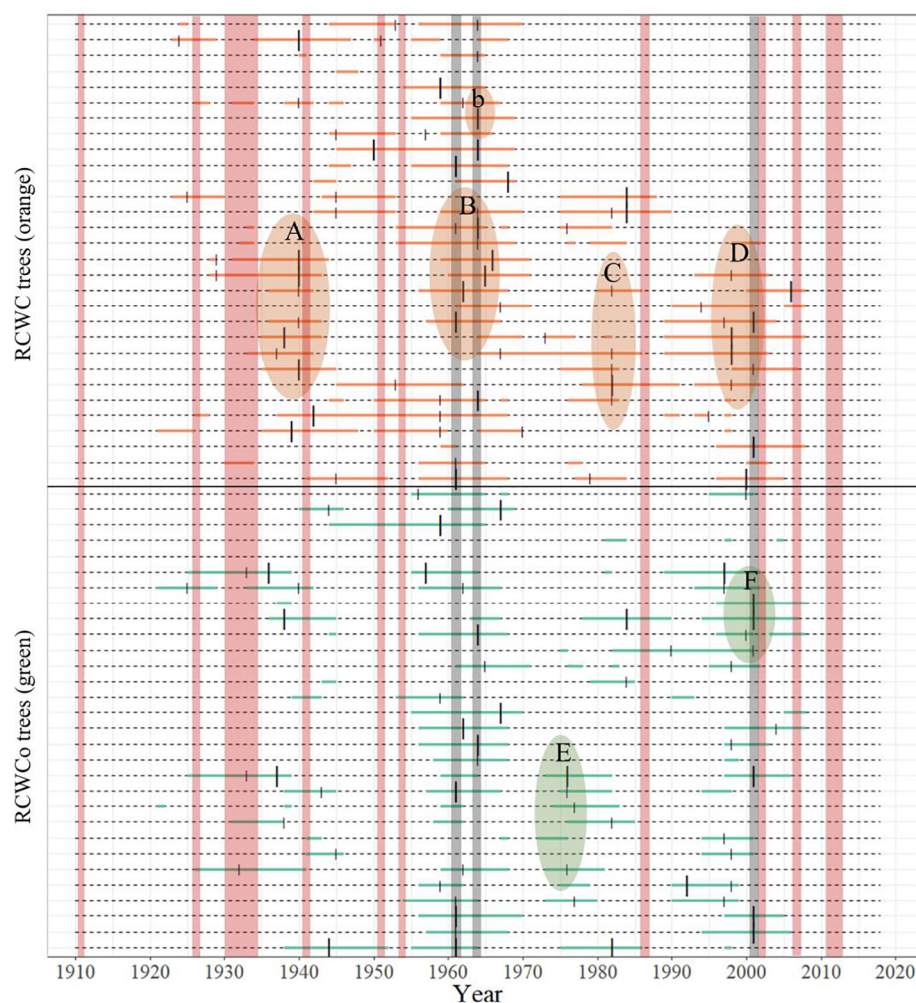
Fig. 7. Running-mean analysis with RCWC and RCWCo trees. Major suppression events are denoted by long tick marks (> 50% growth change, suppression length > 7 years, gap between suppressions > 10 years) and moderate suppression events by short tick marks (< 50% and > 25% growth change, suppression length > 7 years, gap between suppressions > 10 years). Orange horizontal lines represent suppression of RCWC trees, green lines are suppressions for RCWCo trees; A and B signifies either the first or second core sampled from the tree. Grey shading highlights the years 1961, 1964, and 2001, the three years with the highest percentage of trees impacted at 16.7%, 18.3%, and 15.0%, respectively. Red shading highlights periods of drought (Dai and National Center for Atmospheric Research Staff, 2017). Ovals and letters illustrate smaller spatial scale groupings of major or moderate suppressions for RCWC trees (orange) and RCWCo trees (green). One oval labeled for a single suppression event, b, is associated with the larger group, B. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Wilcoxon Rank Sum Test results for differences in total resin ducts (1950–2018) and non-standardized latewood width (mm); and *t*-test results for a difference in age, between RCWC and RCWCo trees. Significant p-values are in bold font.

Characteristic	Strongest Relationship	p-value	Sample Size
Resin Ducts	RCWC > RCWCo	**p = 0.02**	n = 49
Latewood Width	RCWC < RCWCo	p = 0.12	n = 60
Age	RCWC < RCWC	p = 0.22	n = 40

allowing southern pine beetle outbreaks that kill cavity trees to occur more often (Conner et al., 1991; Conner and Rudolph, 1991; Loeb et al., 1992; Waldrop et al., 1992; Conner and Rudolph, 1995; Gilliam and Platt, 1999; Conner et al., 2001; Loudermilk et al., 2011).

4.3. Ecological disturbance

From our running-mean analyses, we found RCWC trees to have significantly more suppression events than RCWCo trees overall, and significantly more major suppression events (Fig. 7). We presume that this difference is due to the stressors imposed on trees during the period of cavity excavation and cavity use. While we did not find any standwide suppressions (> 25% of trees affected; Rubino and McCarthy, 2004), we found one event that affected 18.3% of the trees, which suggests a possible stand-wide event occurred in 1964. This large-impact event could potentially be related to a high-intensity fire or a silvicultural treatment in 1964. The 7-year suppression minimum and 10-year gap between suppressions likely filtered out some fire-caused

suppression. However, longleaf pine does have extensive fire-resistant defenses that could have influenced suppression detection sensitivity (Andrews, 1917; Chapman, 1932; Heyward, 1939; Wahlenberg, 1946; Croker and Boyer, 1975; Platt et al., 1988; Platt et al., 1991; Platt, 1999). For example, eastern Texas longleaf pine cavity trees have notable suppression and release events (Conner and O'Halloran, 1987). Although this finding is dependent on methods for suppression and release detection based on a growth rings/cm measurement for more than five years, our usage of the Nowacki and Abrams (1997) method found a similar result (Rentch et al., 2002; Hart et al., 2008; Altman et al., 2016; Abiyu et al., 2018).

Suppressions we found in both RCWC and RCWCo trees had small-scale spatial patterns. We propose two possible explanations for the small spatial groupings to occur. First, the affected cluster(s) may have been suppressed by the same microenvironmental factors. Second, for RCWC trees, we suspect that the affected cluster(s) were trees suppressed by RCW cavity excavation and/or use. We found small-scale spatial groups in the late 1990s/early 2000s for both RCWC and RCWCo trees. Due to this similarity, we postulate that these two suppressions are not due to RCW cavity excavation. However, the 1982 event occurred only in RCWC trees, which could mean RCWs created cavities that suppressed growth. This event along with another exclusively RCWC tree suppression event in the late 1930s both had drier conditions (negative PDSI) that may have led to carbon starvation. A stressor such as carbon starvation potentially makes it easier for RCW to excavate a cavity. However, the extra stress on the tree also increases the likelihood of mortality (McDowell et al., 2008). Furthermore, stress caused by limited water availability can increase the viscosity of the sap

produced by the phloem. This thicker sap makes these trees preferentially selected by RCW because of the increased predator deterrence effectiveness (Wallin et al., 2003; McDowell et al., 2008; Woodruff, 2013).

4.4. Tree characteristics

We found significantly more resin ducts in RCWC trees from 1950 to 2018 (Table 2), which agrees with prior findings on RCW tree selection (Ross et al., 1997). RCWs select longleaf with more resin ducts because of their increased resistance to bark beetle outbreaks (Santoro et al., 2001; Nowak et al., 2008). Also, RCWs may choose trees that have more resin ducts due to a positive relationship with resin flow and bark beetle resistance found in similar species (Rudolph et al., 1990; Ferrenberg et al., 2014). All other physical characteristics were not significantly different between RCWC and RCWCo (Table 2). However, age may not be critical to RCW cavity tree selection for this tree stand (Field and Williams, 1985). RCW selection factors could also differ depending on management practices (James et al., 1997), and SGL has been carefully managed with frequent prescribed burns since the late 1990s (North Carolina Wildlife Resources Commission, 2015).

5. Conclusion

Our study is the first, to our knowledge, to use dendroecological methods to examine differences between trees that the endangered red-cockaded woodpecker selects for their nesting cavities, and nearby control trees with visually similar physiological characteristics that RCW did not select. RCWs require a roost cavity for each group member (Ligon, 1970; Walters et al., 1992). Creation of these cavities creates stability in an environment and sets the carrying capacity of the population (Horn, 1978; Walters, 1991). Because cavities are a critical resource for RCW, competition for trees that RCW select for their nesting cavities is critical to the evolution of cooperative breeding behavior for RCW (Horn, 1978; Hansell, 1993; Walters, 1991; Walters et al., 1992).

Using adjusted latewood widths, we found no significant differences between RCWC and RCWCo in radial growth or long-term climate/growth relationships. Physiologically, there are no differences between RCWC and RCWCo in width of adjusted latewood bands. What we did find are three key distinctions between RCWC and RCWCo trees using adjusted latewood chronologies and individual tree radial growth measurements. First, significant climate signals in RCWC and RCWCo climate/growth relationships shift through time. Second, RCWC trees experienced more frequent suppression events than RCWCo trees. Last, resin ducts were more prevalent in RCWC trees than RCWCo trees. Our results show that RCWC trees are more sensitive to climate than RCWCo trees over shorter intervals and the process of cavity construction and maintenance likely result in more frequent radial growth suppressions. If a period of suppressed growth was concurrent with a climatic event like an extreme drought, the possibility exists that RCWC trees would be more susceptible to senescence (Sayer and Haywood, 2006; Rivero et al., 2007).

We discovered that RCW cavity excavation, presence, or maintenance potentially cause more climate/growth instability and sensitivity over short periods, more radial growth suppressions, and more resin duct prevalence. However, as most of our findings are local stressors, management has a higher likelihood for successful prevention of RCWC tree mortality. Specifically, RCW management practices could emphasize extra precautions for RCWC or cavity-started trees during prescribed fires and periods of drought-like conditions. Additionally, because of RCW's dependence on longleaf pine, RCW's status should also improve as more effective management of longleaf pine throughout its range is implemented. We successfully investigated two well-studied species and found new information about both species by utilizing a new multi-scalar perspective using tree-ring science methods.

CRediT authorship contribution statement

April L. Kaiser: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization. **Peter Soulé:** Conceptualization, Methodology, Investigation, Resources, Writing - review & editing, Supervision, Project administration. **Saskia L. van de Gevel:** Conceptualization, Methodology, Investigation, Resources, Writing - review & editing, Supervision, Project administration. **Paul Knapp:** Conceptualization, Methodology, Resources, Writing - review & editing, Supervision. **Arvind Bhuta:** Resources, Writing - review & editing. **Jeffrey Walters:** Resources, Writing - review & editing. **Evan Montpellier:** Methodology, 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.

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