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Effects of climate variability and management on shortleaf pine radial growth across a forest-savanna continuum in a 34-year experiment

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ABSTRACT

We investigated the radial growth response of shortleaf pine (*Pinus echinata*) to climatic variation and management using tree cores collected in southeastern Oklahoma at the drier, western limit of its range. Beginning in 1984, experimental units were created by various combinations of pine harvest, hardwood thinning, and fire return intervals (1, 2, 3, 4 years and none) that produced ecosystems ranging from mature, closed canopy forest to open savanna. Monthly and seasonal weather for previous- and current-year as well as growing seasons since fire were used to determine the relationship between radial growth and climate variability (1987–2018) for different management regimes. Across all treatments, growing season precipitation (~5% decrease per 100 mm decrease in precipitation), average summer temperature maximum (~7% decrease with 1 °C increase), and previous year's average October minimum temperature (~6% increase per 1 °C increase) were the variables most frequently correlated with variation in ring width. Annual wood and latewood growth increments were correlated (R^2 = 0.60) and generally responded similarly to climate variability, with latewood more sensitive to late growing season conditions. Management with frequent fire that resulted in savanna ecosystems reduced growth sensitivity to annual variation in precipitation relative to trees in a closed-canopy forest condition. Suppressed trees were also less responsive to climate variability than intermediate or co-dominant trees. Both annual wood and latewood growth were reduced by 21–33% the first year after prescribed fire for treatments with a 2- and 3-year fire return interval. Multiple regression combing temperature and precipitation variables as well as time since fire accounted for 55% of the variability in annual ring growth. Our findings indicate that a drier climate with hotter summers will likely reduce the growth of shortleaf pine growing at the western margin of its range while warmer temperatures in October, by extending the growing season, may help ameliorate the effects of warmer summers. Management to reduce stand density, either through thinning or by prescribed fire, may dampen some of the variation of growth in response to climate variability.

1. Introduction

Globally, forest-grassland transition zones occur where precipitation is marginal for tree growth such that droughts and climate change may influence the relative dominance and distribution of trees and tree canopy cover as well as productivity (Oliveras and Malhi, 2016). In the southcentral USA, temperatures have generally been increasing, and both the annual and seasonal precipitation have become more variable, resulting in more extreme dry and wet episodes (Collins et al., 2013). Climate change models predict a 2.5–4.0 °C increase in average temperature throughout this region by the latter half of this century (Collins et al., 2013). These changes are expected to increase drought frequency and intensity, which could reduce tree growth, increase tree mortality, and potentially alter associated species composition across the transition zone.

The forest-grassland transition zone in the southcentral USA encompasses 407,000 km^2 and spans northcentral Texas, central Oklahoma, eastern Kansas, northern Missouri, and much of Illinois. For most

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tree species of eastern forests, this zone represents the edge of their range as precipitation becomes limiting further west. Within the southcentral USA, management activities can modify forest structure to increase resistance and resilience to climate change. For instance, thinning typically increases resistance and recovery of tree growth to drought, presumably by increasing water availability to residual trees (Sohn et al., 2016). Management using prescribed fire shapes forest structure by suppressing juvenile woody plant recruitment and development, reducing tree growth rate, and by killing fire insensitive trees which can maintain savanna and woodland structure (Peterson and Reich, 2001; Moore et al., 2016). Prescribed fire can reduce tree diameter growth in the short-term due to crown scorch (Miller and Seidel, 1990), but can have a long-term positive effect on tree diameter growth due to density reduction (Huebschmann, 2000) or maintenance of lower density stands. Given the impact of management and potential climate change on forest structure and growth, understanding the interactive effects of management and climate variability on tree growth is necessary to understand the productivity and resilience of forest and savanna ecosystems in the future and to inform prescriptions for establishment or maintenance of desired ecosystem conditions.

Tree-ring chronologies represent a reliable archive that can be used to assess previous climate variability and predict future climate change impacts on tree growth (Cullen et al., 2001; Buechling et al., 2017; Tiwari et al., 2017; Schwab et al., 2018). They also can be used to understand the relationship between tree growth and environmental variation (Briffa et al., 1983; Cook et al., 1990; Martín-Benito et al., 2008; Fang et al., 2014), especially for trees growing in moisture-limited environments (McGuire et al., 2010). Climate variables, particularly precipitation and temperature, are the most influential factors associated with radial growth of the trees and forest ecosystem dynamics (Carrer and Urbinati, 2004; Goldblum and Rigg, 2005; Black et al., 2016). However, management activities such as thinning and prescribed fire influence tree-ring growth (Nyland, 2016) and may interact with climate variability to either amplify or dampen climate-related signals.

An annual growth ring contains earlywood and latewood, with the majority typically composed of earlywood (Stokke and Groom, 2008). Though earlywood and latewood development is often highly correlated (Meko and Baisan, 2001), the relationship between latewood and climate can be important to separate as latewood is often highly sensitive to late growing season weather (Meko and Baisan, 2001; Griffin et al., 2011). In addition to current-year impacts of weather on radial increment, previous years' weather can also have an influence. For instance, Ogle et al. (2015) reported that radial growth can be influenced by precipitation up to 4 years prior. While current-year weather usually predicts 20–40% of variation in annual radial growth, the addition of past year's weather can improve the ability to predict up to 50–70% of variation in tree ring growth (Anderegg et al., 2015; Ogle et al., 2015; Zweifel and Sterck, 2018).

Most tree-ring studies within forest-grassland transition zones focused on individual ecosystems and primarily assessed biomass, tree diameter, and canopy growth measurements on permanent plots (Szeicz and MacDonald, 1994; Briggs and Knapp, 1995; Reich et al., 2001; Peterson and Reich, 2007; Kanniah et al., 2013; Astudillo-Sánchez et al., 2017; Vitali et al., 2017). In contrast, the climate-growth interactions among differing community structures, i.e., forest, woodland, and savanna, using dendrochronology, have not been explored. In this study, we compared tree-ring chronologies to evaluate the effects of climatic variability and management on the radial growth of shortleaf pine (*Pinus echinata* Mill.) by analyzing climate signals and growth trends in closed-canopy, mature forests, and actively managed woodlands and savanna ecosystems in southeastern Oklahoma, USA.

Shortleaf pine has the largest range of any pine species in the southeastern USA and is an important economic and ecological component to the region's forests (Burns, 1990). The broad range of this species is attributed to its adaptability to a great variety of soils ranging from deep, well-drained sandy loams to shallow, rocky upland soils (Lawson and Kitchens, 1983). Among southern pines, it is considered the most drought tolerant (Klockow et al., 2020) and it is found furthest west along the gradient of decreasing precipitation. Shortleaf pine is sensitive to elevated temperature and changing precipitation (Schulman, 1942; Estes, 1970; Stambaugh and Guyette, 2004), which could affect its future growth and distribution. In southeastern Oklahoma, shortleaf pine reaches the western, drier edge of its range and should exhibit heightened sensitivity to drought and climatic variability. Shortleaf pine is a fire-adapted species that possesses thick bark that insulates mature trees, and its seedlings and saplings have a basal crook, which facilitates resprouting following topkill (Bradley et al., 2016) by the placing dormant buds at or just underneath the soil surface where they are protected. Fire exclusion leads to replacement of shortleaf pine by faster growing pine species where their ranges overlap (Stewart et al., 2015) or by fire-intolerant hardwood trees (Guldin, 1986).

We conducted our research within a long-term research area that was initiated in 1983 to develop different ecosystem structures ranging from mature forest to grassland using a combination of commercial pine harvesting, thinning of hardwoods (via herbicide injection), and subsequent fire frequency (fire exclusion and annual to four-year fire return intervals) (Masters and Waymire, 2012). During the study, two distinct periods of drought occurred, which increased the range of conditions sampled. While effects of climate on shortleaf pine tree-ring growth have been previously studied (e.g. Byram and Doolittle, 1950; Friend and Hafley, 1989; Grissino-Mayer and Butler, 1993; Guyette et al., 2007), the design of our study allowed exploration of the interactions between climate variability, stand condition, and management. Our overall goal was to determine how climate variation, different prescribed fire intervals, stand density, and tree canopy position (i.e., co-dominant, intermediate, and suppressed) affect radial growth of shortleaf pine to determine the interaction between management and climate variability, predict potential future climate change effects, and inform management.

Specific questions we addressed were: (1) how does variation in precipitation and temperature at monthly, seasonal, and annual timescales affect radial growth of shortleaf pine, (2) how does prescribed fire affect radial tree growth, (3) how do stand density and climate variability interact to affect radial growth, and (4) how do tree canopy position and climate variability interact to affect radial growth. These questions are critical to understand resilience of forests along the forest-grassland continuum to management and disturbances and to predict future forest productivity.

2. Methods

2.1. Study sites

The study was conducted on a 53-ha research area located within the 7690 ha Pushmataha Wildlife Management Area (WMA) (Fig. 1). The Pushmataha WMA is located in the Kiamichi Mountains along the western edge of the Ouachita Mountain in southeastern Oklahoma (34°31′40″ N, 95°21′10″ W). The study area is within the mixed pine-hardwood vegetation type and juxtaposed in close proximity to relict tallgrass prairie patches (35 km), oak-hickory, and cross timbers vegetation types (Masters and Waymire, 2012). Soils are derived from sandstones and shales and belong to the Carnasaw (fine, mixed, semi-active, thermic Typic Hapludults) and Stapp (fine, mixed, active, thermic Aquic Hapludults) series (NRCS, 2019).

The climate of Pushmataha WMA is characterized as semi-humid with hot summers and moderate winters. The study area before treatment application was initially dominated by post oak (*Quercus stellata*), shortleaf pine, blackjack oak (*Q. marilandica*), and hickory (*Carya* spp.). Understory nonwoody vegetation was mainly composed of sparse herbaceous plants represented by little bluestem (*Schizachyrium scoparium),* panicums (*Panicum* spp., *Dichanthelium* spp.), sedge (*Carex* spp.), and various forb species. Whereas the understory woody vegetation was dominated by sparkleberry (*Vaccinium arboreum*), poison ivy

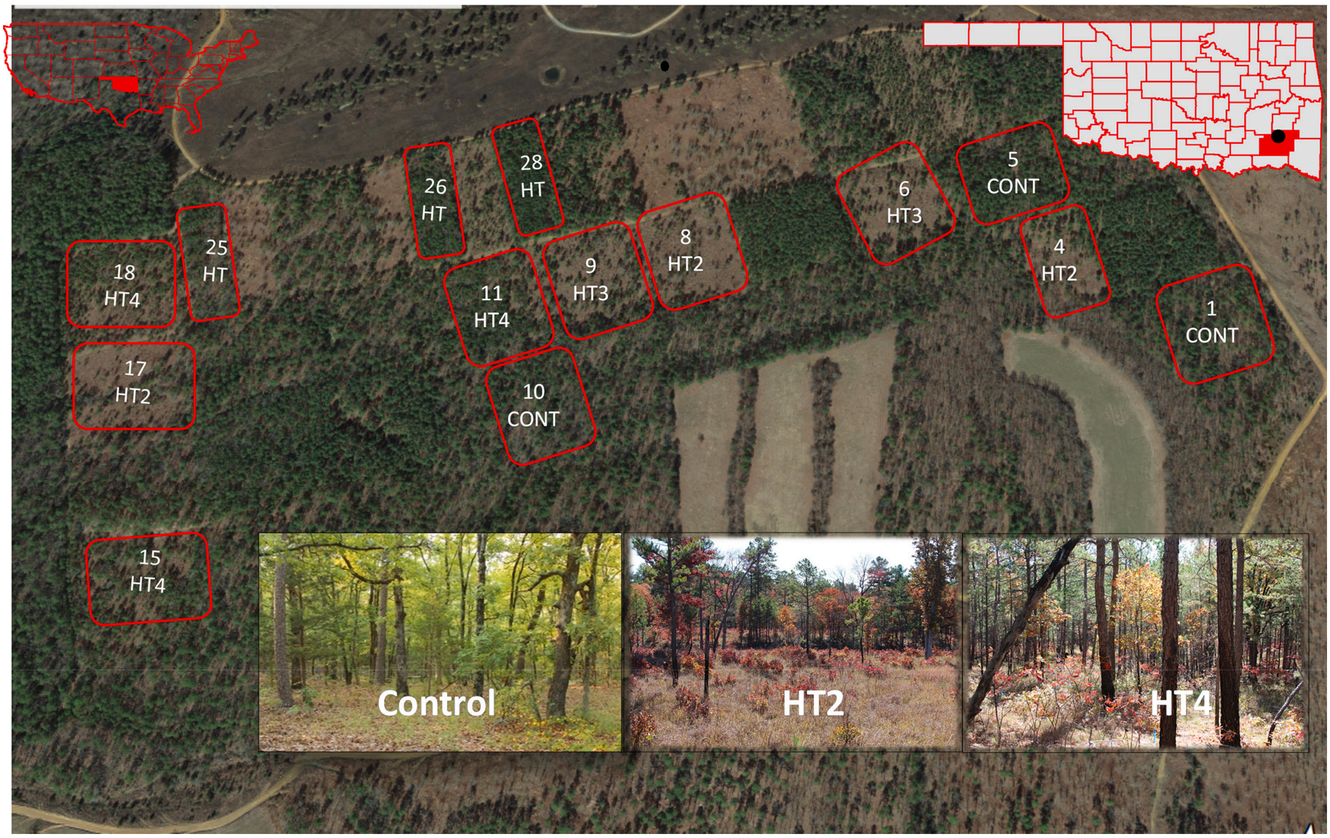

Fig. 1. Location of study area with treatment units (red rectangle) (source: Google earth 2019). See Table 1 for treatment definitions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(*Toxicodendron radicans*), grape (*Vitis* spp.), and greenbriers (*Smilax* spp.) as well as seedlings of the overstory tree species. Post-treatment experimental units were dominated by little bluestem, big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), panic grasses, and various legume and forb species. For the woody species, grape (*Vitis* spp.), winged sumac (*Rhus copallinum*), and seedlings and sprouts from the overstory species were most common post-treatment.

2.2. Treatments

Twenty-eight management units ranging from 0.8 to 1.6 ha were established with a randomized experimental design within relatively homogenous closed-canopy forest in the summer of 1983 (Fig. 1) (Masters and Waymire, 2012). During the summer of 1984, treatments were applied to each unit so that 23 units represented eight cultural treatments with three replications of each, except one treatment (HT3) which had only two replicates (Fig. 1). All treatment units (except Control) were subjected to harvest of shortleaf pine and thinning of hardwoods, and then with different time intervals of prescribed fire. Within the treated units, shortleaf pine trees with diameter at breast height 11.4 cm or larger were harvested (H), hardwoods (primarily hickory and post oak) were thinned to approximately 9 m^2 ha^{-1} basal area using single-stem injection of herbicide (T), and fire return intervals (1–4 years as well as fire exclusion) were established (Table 1).

Table 1
Description of post-treatment (1985) and current conditions (2018) of treatments. Hardwood thinning and shortleaf pine (*P. echinata*) harvesting were completed during the establishment of experimental site at the Pushmataha Wildlife Management Area, Oklahoma USA during 1984. For age and basal area, means and standard errors are presented.

Treatments	Harvest pine	Thin hardwoods	Fire return interval (years)	[1]Post-treatment condition (1985)	[1]Condition (2018)	Basal area (m^2 ha^{-1}) (1985)	(2018)	[2]Sampledtree age
Control	No	No	No fire	Forest	Forest	26.6 ± 1.3	28.6 ± 1.3	62.4 ± 2.3
HT	Yes	Yes	No fire	Savanna	Forest	3.8 ± 0.4	33.2 ± 2.0	–
Codominant	–	–	–	–	–	–	–	31.6 ± 1.7
Intermediate	–	–	–	–	–	–	–	30.3 ± 1.3
Suppressed	–	–	–	–	–	–	–	23.8 ± 0.9
HT4	Yes	Yes	4	Savanna	Forest	3.6 ± 0.7	19.7 ± 1.9	28.7 ± 1.7
HT3	Yes	Yes	3	Savanna	Savanna	3.2 ± 0.6	5.9 ± 1.0	27.2 ± 2.9
HT2	Yes	Yes	2	Savanna	Woodland	4.9 ± 0.7	7.2 ± 0.9	40.9 ± 2.8

[1] Note classification of post-treatment and 2018 conditions of study sites was based on basal area of trees (Dey et al., 2017). Grassland: basal area <2.3 m^2 ha^{-1}; Savanna: basal area = 2.3–6.9 m^2 ha^{-1}, Woodland: basal area = 6.9–18.4 m^2 ha^{-1}, Forest: basal area >18.4 m^2 ha^{-1}.
[2] Age of trees measured at 1.37 m. Add approximately 4–7 years to estimate age of germination.

Beginning in 1985, prescribed fires were applied mostly during the dormant season (January to early April) and maintained with 1, 2, 3, and 4-year intervals as appropriate from 1985 through 2018. The only exception was 1995 when the 1- and 2-year fire return interval units were not burned. The 2-year fire return units were burned in both 1996 and 1997 to compensate. Fireline intensity of prescribed fires during the experiment ranged from 44 to 5150 kW m^{-2}. The thinned and burned units were initially characterized as grassland and savanna in 1987. The previous major disturbance at the study site was from logging was in 1930s.

2.3. Dendroecological analysis

Cores were collected from shortleaf pine trees following the 2018 growing season from Control, HT, HT4, HT3, and HT2 treatments. The HT1 treatment was excluded as it had almost no pines available for sampling. At time of core collection, the Control was a mature, closed-canopy forest; the HT treatment had succeeded to an even-aged forest, mostly regenerated after harvest in 1984; the HT4 treatment had developed as an uneven-aged forest that experienced several cohorts of regeneration since 1984; the HT3 and HT2 treatment units were savannas or woodlands maintained by the frequent fire return interval, with scattered shortleaf pine that had regenerated since treatment and a few trees that were preexisting at the time of initial treatment, but too small to harvest (Table 1). Where available, one tree was cored near each of 10 permanent plots that had previously been established in two parallel transects with plots spaced 20 m apart. The exception was for the HT treatment where a core was collected from a codominant (16.3 ± 0.4 m tall), intermediate (14.3 ± 0.3 m tall), and suppressed (9.9 ± 0.6 m tall) tree determined near each plot. The other treatments lacked sufficient canopy stratification to test canopy position. Altogether 159 cores were collected, averaging 32 trees per treatment.

Trees were cored at the breast height, i.e., 1.3 m, using an increment borer (5.15 mm diameter). The collected trees cores were dried in an oven at 60 °C for 72 h. Dried cores were mounted in grooved wooden holders with water-soluble glue, and core surfaces were sanded with progressively finer sandpaper down to a 400-grit size. The samples were first visually cross-dated under a sliding microscope (AmScope Inc., California) and then digitized using a scanner (Epson America, Inc.). Annual rings of each digitized sample were measured with the WINDENDRO image analysis system (Regents Instruments, Quebec). We used the computer program COFECHA to detect and correct the potential errors related to crossdating in the ring series (Holmes, 1983; Grissino-Mayer, 2001). COFECHA statistically assessed the quality of crossdating and measurement accuracy of the tree-ring series by standardizing the raw data of ring width and providing correlations between each segment and the whole series (Speer, 2010).

All analyses were performed on a single tree mean chronology for the common period 1987–2018. The dplR function (Bunn, 2008) was used to estimate tree-ring width indices for annual wood (RWI), earlywood (EWI), and latewood (LWI) of individual treatments and for all treatments combined by detrending the chronology (1987–2018) of each tree using the ModNegExp method by fitting the classical nonlinear model. The advantage of detrending tree-ring series was to minimize the ring width variation associated with age trends for better resolution of interannual frequency variation (Cook and Kairiukstis, 1990).

We estimated various statistical parameters to compare standardized tree-ring chronologies of annual wood, earlywood, and latewood across different treatments (Table 2). For each chronology, we calculated inter-series correlation (Rbar), average mean sensitivity (MS), standard deviation (SD), and autocorrelation (AC). While Rbar is a measure of stand-level correlation over time among samples, mean sensitivity measured year-to-year variation of ring width (Speer, 2010). Autocorrelation estimated the similarity between the given time series of tree-ring chronology and the lagged version of itself over successive time intervals (Parr and Phillips, 1999).

Table 2
Summary statistics; average tree-ring series length (years), inter-series correlation (Rbar) of chronology with master chronology, mean sensitivity (MS), autocorrelation (AC), mean tree-ring width index and standard deviation (SD) for annual wood (RWI) and latewood (LWI), value for all treatments combined (overall) and each treatment separately for annual wood and latewood. See Table 1 for treatment definitions.

Annual wood							
Site	Series length	# cores	Rbar	MS	AC	RWI	RWI SD
Overall	32	159	0.43	0.48	0.28	1.03	0.15
Control	32	27	0.63	0.48	0.32	1.00	0.27
HT codominant	32	25	0.55	0.28	0.45	1.04	0.20
HT intermediate	32	24	0.50	0.40	0.52	1.01	0.18
HT suppressed	29	21	0.10	0.43	0.59	1.06	0.21
HT4	32	23	0.27	0.30	0.11	1.00	0.17
HT3	32	15	0.34	0.82	0.03	1.04	0.28
HT2	32	24	0.28	0.53	0.07	1.16	0.25
Latewood							
Site	Series Length	# cores	Rbar	MS	AC	LWI	LWI SD
Overall	32	159	0.47	0.53	0.15	1.06	0.25
Control	32	27	0.65	0.7	0.17	1.01	0.40
HT codominant	32	25	0.62	0.53	0.28	1.04	0.31
HT intermediate	32	24	0.58	0.43	0.23	1.00	0.29
HT suppressed	29	21	0.07	0.63	0.28	0.98	0.17
HT4	32	23	0.15	0.45	0.13	1.01	0.23
HT3	32	15	0.37	0.95	0.02	1.05	0.31
HT2	32	24	0.26	0.67	0.06	1.17	0.27

2.4. Predictors of tree growth

Cores of individual trees within a given treatment unit were averaged for mean tree-ring width indices to reduce the noise and because the unit served as the experimental unit for the management treatments. We related tree-ring width indices to (1) climate variables, which included various measures of temperature and precipitation, and (2) fire management (i.e., growing years since fire, GYSF). Climate variables were computed from daily data obtained from Daymet (Thornton et al., 2018) for each year between 1987 and 2018 (32 years). Average seasonal variables including growing season (March to September), winter (January to March), spring (April to June), summer (July to September), and fall (October to December) were computed for precipitation and maximum, average, and minimum temperature for the current and previous year. We also estimated the Keetch-Byram Drought Index (KBDI) to provide a measure of drought using the equation described in Keetch and Byram (1968) and Dolling et al. (2005). KBDI is an index which measures soil drought condition under a wide range of temperature, precipitation, and meteorological factors in forested areas (Keetch and Byram, 1968). KBDI is expressed as a range from 0 to 800; a value of 0 represents complete saturation of soil while a value of 800 represents absolutely dry soils.

We explored a total of 69 variables as potential predictors of tree-ring width index. However, to minimize model over-parameterization when predicting each of the three types of RWI (annual wood, earlywood, and latewood), we first performed a correlation analysis between each predictor and the RWI. This was performed separately for each treatment as well as by aggregating data across treatments. Based on this initial analysis, we dropped predictors that were not significantly correlated ($p > 0.05$) to the ring width indices. As a result, we narrowed the focus down to only 14 predictors including three climatic variables of the previous year (annual and growing season precipitation, and October average minimum temperature), and the rest of the variables characterizing the current year (annual, spring, summer, fall maximum temperature and precipitation, and October average minimum temperature). These 14 potential predictors were used in a stepwise regression framework where backward elimination of variables simplified the model until it created the most parsimonious model with lowest error. Specifically, this process began with all supplied predictors in the model and tested how impactful the elimination of each predictor was. The model dropped a variable whose elimination resulted into the most insignificant deterioration of the model fit, repeating the process as long as the elimination resulted in a statistically insignificant loss of model fit. Competing models were compared based on their Akaike Information Criterion adjusted for small sample size (AIC). Multiple regression was used with the variables selected by a model with the lowest AIC value from stepwise regression. Coefficients of determination of each variable were estimated by dividing the sum of square of each variable by the total sum of squares of all variables and residuals.

As appropriate, we tested for the effect of number of growing seasons since the most recent prescribed fire. We used the term 'Growing Years Since Fire' (GYSF) where '1' represents the end of the first growing season after burning, '2' the end of the second growing season, '3' the end of the third growing season, and '4' the end of the fourth growing season. Analysis of Variance (ANOVA) was used to estimate the difference in RWI, EWI, and LWI among the treatments with Tukey's Post-hoc for multiple comparisons ($n = 3$). We used the correlation coefficient (R) to determine the relationship between RWI, climate variables, and GYSF. Multiple regression (R^2) was used to determine the coefficient of determination to determine the relationship between ring width and many climatic variables. RWI, EWI, and LWI were analyzed separately. Data processing, analysis, and plotting were done in R version 3.5.0 (R Core Team, 2020).

3. Results

3.1. Climate

Annual temperature and precipitation varied greatly over the course of the study, however no trends of increasing or decreasing temperature or precipitation or changes in variability over time were observed ($p > 0.05$; Fig. 2a). The annual maximum and minimum precipitation were 971 and 1935 mm with a mean of 1436 mm. Annual average maximum and minimum temperatures were 9.1 °C and 22.2 °C. The study site received below average precipitation for 17 of the 32 years during the experiment and experienced two periods of extended drought from 2003 through 2006 and 2009 through 2013. Based on average monthly values, precipitation reached its maximum in May (194 mm) and minimum in August (77 mm) and was bimodal in seasonal distribution (Fig. 2b). The minimum precipitation in August coincided with the hottest monthly mean temperature (26.7 °C) and typically resulted in late summer water stress (August KBDI = 507). Cooler temperatures and greater precipitation during winter and early spring typically resulted in soil moisture recharge by February before resumption of the next growing season.

3.2. Summary statistics of chronology

A total of 159 tree cores were cross-dated, measured, and estimated for ring width study. Diameter at breast height (DBH) of shortleaf pine trees across different treatments ranged from 95 mm (HT suppressed) to 419 mm (Control) in 2018 (Supplement 1). Earlywood was the dominant component and composed 66% of annual ring width when all trees were averaged. The proportion of earlywood in forested treatments (Control and HT: 70%; HT4: 67%) and savanna treatments (HT2: 62%; HT3: 61%) was not significantly different ($p > 0.05$). When annual wood RWI was considered, model results largely reflect those of the dominant earlywood component. Therefore, we focus results on RWI, which represents total radial growth for the year and LWI, which is the period of growth most sensitive to late summer drought.

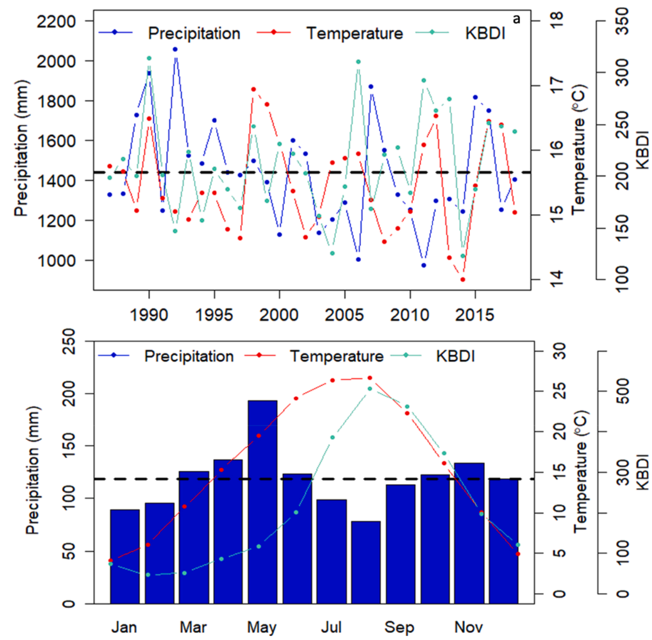

Fig. 2. (a) Annual precipitation, temperature, and KBDI and (b) average monthly precipitation, temperature, and KBDI over 32 years of the study period (1987–2018). The dashed line in each figure indicates average precipitation over the study period. Year to year variation of both precipitation and temperature was not statistically significant ($p > 0.05$) (Levene 1960). Temperature and precipitation were computed from daily data obtained from Daymet (Thornton et al. 2018).

Figures of RWI and LWI chronologies of all treatments are presented in online supplement (Supplement 2). Overall, the chronology (1987–2018) for the entire study site had a Rbar for annual wood of 0.43 (Table 2). Among treatments, the Control had the greatest Rbar for annual wood (0.63) and the HT-suppressed had the lowest (0.10), while mean sensitivity ranged from 0.28 to 0.83 for Control and HT3, respectively. The latewood Rbar was 0.47 for all treatments combined and ranged from 0.65 (Control) to 0.07 (HT-suppressed).

3.3. Growth response to climate variability and differences in response related to treatments

After examining the correlations for RWI and LWI with monthly, seasonal, and annual temperature and precipitation values (Supplement 3), we emphasized seasonal and annual intervals as they were more consistent in their relationship with tree-ring growth among treatments. The exception was October average minimum temperature, which likely was related to the timing of first frost and end of the growing season. Other than October minimum temperature, no other minimum temperature values were correlated to the ring width indices for any treatment.

Because latewood is a component of the annual growth ring, RWI and LWI were correlated. The average R^2 between annual wood and latewood was 0.60 and ranged from 0.78 for the Control treatment trees to 0.19 for the HT-suppressed treatment trees. Besides the HT-suppressed trees, the only other treatment with R^2 below 0.60 was the HT4 treatment (0.31).

When all treatments were combined, RWI was positively correlated ($p < 0.05$) with growing season, spring, and summer precipitation of the current year, and negatively correlated to average summer maximum temperature (Fig. 3). The RWI of the older, codominant trees in the Control treatment was correlated to growing season precipitation and average October minimum temperature of the previous year, growing season and summer precipitation of the current year, and negatively

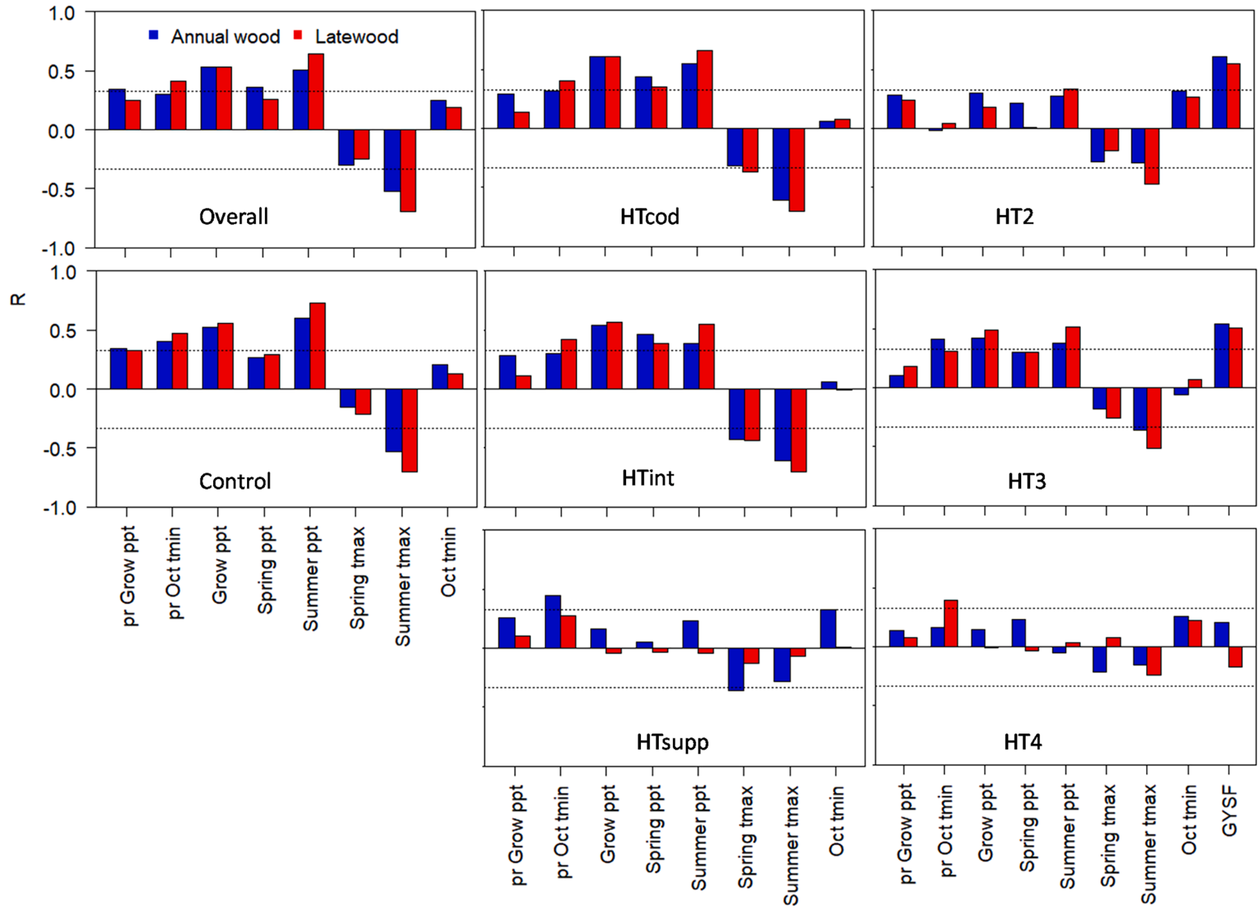

Fig. 3. Correlations of 32-year annual wood (RWI) and latewood (LWI) chronologies of shortleaf pine with different climate variables from different treatments. Horizontal dotted lines at r = 0.33 and r = -0.33 form a 95% CI; significant correlations ($p < 0.05$). (Abbreviation cod: codominance; int: intermediate; sup: suppressed, pr: previous, ppt: precipitation, tmax: maximum temperature, tmin: minimum temperature, Grow: growing season, Oct: October). All variables with one or more significant correlations are presented.

correlated to average summer maximum temperature (Fig. 3). The RWI of codominant and intermediate trees of the HT treatment, trees approximately 30-years-old, was correlated to annual, spring, and summer precipitation of the current year and negatively correlated to average spring and summer maximum temperatures. The RWI of the codominant trees also was correlated with previous year average October minimum temperature (Fig. 3). In contrast, RWI of the suppressed trees in the HT treatment was correlated to both previous year and current year average October minimum temperature and negatively correlated to average spring maximum temperature (Fig. 3). The RWI of HT2 and HT3 trees was positively correlated with growing seasons since fire. The HT2 trees also were correlated to average October minimum temperature while the HT3 trees were correlated with growing season, spring, and summer precipitation as well as previous year's average October minimum temperature and negatively correlated to average summer maximum temperature (Fig. 3). The RWI of trees in the HT4 treatment was not significantly correlated to any environmental variable.

Correlations with LWI were similar as those for RWI with a few exceptions. In general, precipitation during summer was more important for latewood than annual wood. As opposed to RWI, spring precipitation was not significantly correlated to LWI for all treatments combined. Summer precipitation was correlated to LWI of HT2 while it was not for RWI. Additionally, the strength of relationships between LWI and summer precipitation was greater than those between RWI and summer precipitation (Fig. 4). Similarly, average spring temperature maximum was not correlated with LWI of HT-suppressed trees, but average summer maximum temperature was correlated with LWI of the HT2 whereas it was not for RWI. Compared to RWI, the correlation between average summer maximum temperature and LWI was stronger (Fig. 3). LWI of the HT4 treatment was only correlated with previous year's average October minimum temperature. No variables were significantly correlated with LWI for the HT-suppressed trees.

Fig. 4 shows the range and variability for RWI and the three most commonly correlated variables, growing season precipitation, previous October minimum temperature, and summer maximum temperature. For RWI, the slopes for growing season precipitation varied between 0.0004 and 0.0006 mm^{-1} (averaged 0.0005 mm^{-1} for the five significant correlations), the slopes for average summer maximum temperature ranged from -0.055 to -0.082 $^{\circ}C^{-1}$ (averaged -0.069 $^{\circ}C^{-1}$ for the five significant correlations), and the slopes for previous year average October minimum temperature ranged from 0.039 to 0.070 $^{\circ}C^{-1}$ (averaged 0.057 $^{\circ}C^{-1}$ for the four significant correlations) (Fig. 5). For LWI, the slopes for growing season precipitation varied between 0.0006 and 0.0011 mm^{-1} (averaged 0.0008 mm^{-1} for the five significant correlations), the slopes for summer maximum temperature ranged from -0.075 to -0.162 $^{\circ}C^{-1}$ (averaged -0.119 $^{\circ}C^{-1}$ for the six significant correlations), and the slopes for previous year October minimum temperature ranged from 0.054 to 0.112 $^{\circ}C^{-1}$ (averaged 0.083 $^{\circ}C^{-1}$ for the six significant correlations) (Fig. 6).

3.4. Growth response to prescribed fire

Both RWI and LWI were significantly smaller in the growing season immediately after prescribed fire for the HT2 ($p = 0.0007$, $p = 0.0008$) and HT3 ($p = 0.0009$, $p = 0.019$), but not for the HT4 treatment ($p =$

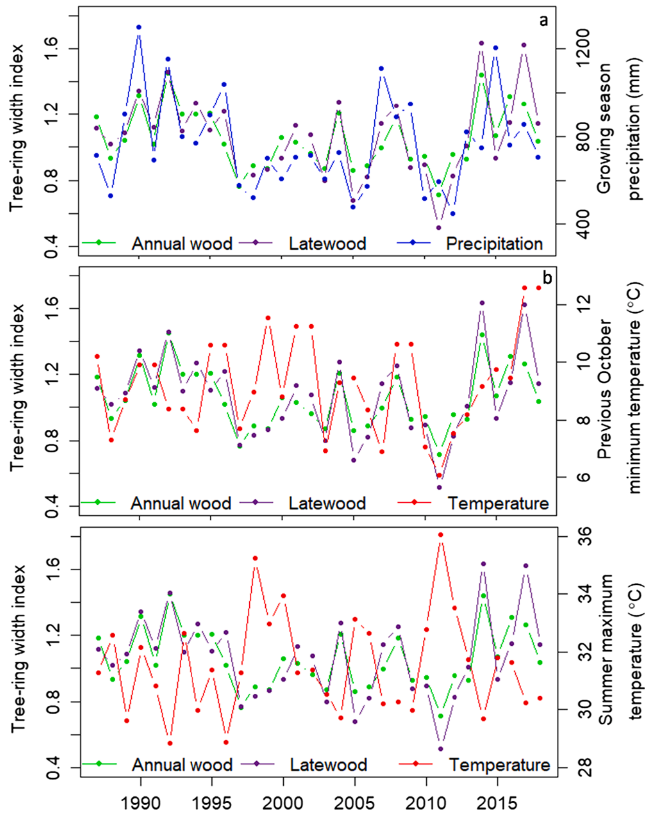

Fig. 4. Time series of standardized tree-ring width index for annual wood and latewood, and (a) current year growing season precipitation, (b) current year average summer maximum temperature, and (c) previous year average October minimum temperature for all treatments combined from 1987 to 2018.

0.27, p = 0.98) (Fig. 7). Annual wood RWI for HT2 increased by 27% between the first and second year after burning. Annual wood RWI of the HT3 treatment increased by 49% and 45% comparing the second and third year after burning to the first year. Similar increases were calculated with GYSF for LWI.

3.5. *Multiple regression analysis*

The multiple regressions constructed using the significant seasonal and annual variables explained on average 55% of the variation in RWI (with exception of HT4 which was not significant) (Table 3). Previous year's conditions were included in the model for the overall combined, Control, HT-Codominant, and HT-suppressed treatments. Current year precipitation, either growing season or spring, was included in the model for all treatments except HT-suppressed. Average summer and fall temperature maximums were included in all models except for the HT-intermediate where only average summer temperature maximum was included, and HT-suppressed where average spring temperature maximum was included. Average October minimum temperature was included for the HT-suppressed treatment model. GYSF was included for both the HT2 and HT3 model.

On average, the multiple regressions explained 55% of the variation in LWI (with exception of HT-suppressed which was not significant) (Table 4). Previous year's growing season precipitation was included in the model for the Control while previous year's average October minimum temperature was included for models of the all treatments combined, Control, HT-intermediate, and HT4 treatments. Spring precipitation was not included in any of the models, but growing season precipitation was for all treatments combined, Control, HT-Codominant, and HT-intermediate treatment trees. Average summer temperature maximum was included for all significant treatments and average fall temperature maximum for the Control treatment. Average October minimum temperature was included for the HT4 treatment. As for RWI, GYSF was included for the models for LWI for the HT2 and HT3

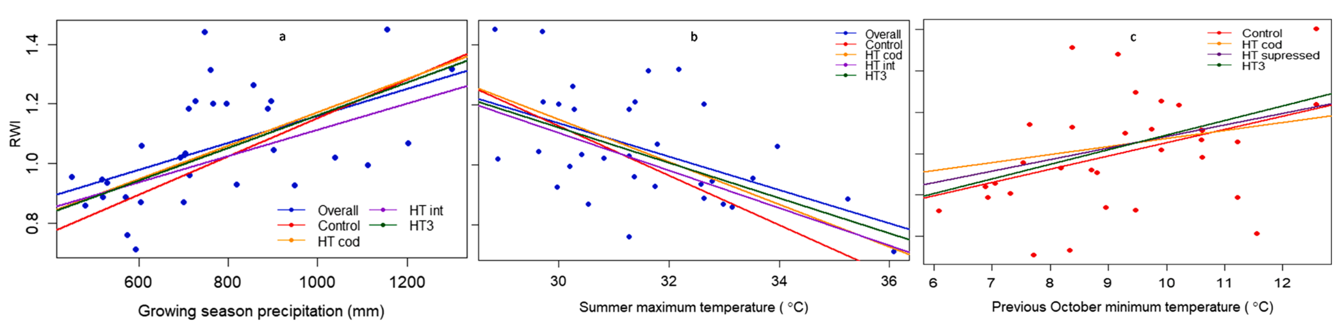

Fig. 5. Significant relationships between RWI and (a) current year growing season precipitation, (b) current year average summer maximum temperature, and (c) average October minimum temperature of previous year for the overall site (all treatment combined) and different treatments. The data points in (a) and (b) are the overall RWI calculated from trees in all treatments combined and those in (c) are from Control treatment (Abbreviations; cod: codominant, int: intermediate).

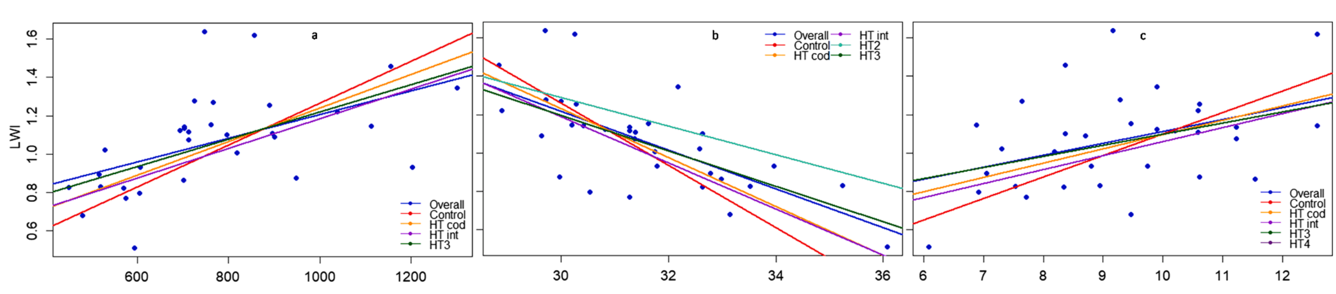

Fig. 6. Relationship between LWI and (a) current year growing season precipitation, (b) current year summer maximum temperature, and (c) October minimum temperature of previous year for overall site (all treatment combined) and different treatments. Data points are for the overall chronology of all treatments combined. (Abbreviation; cod: codominant, int: intermediate).

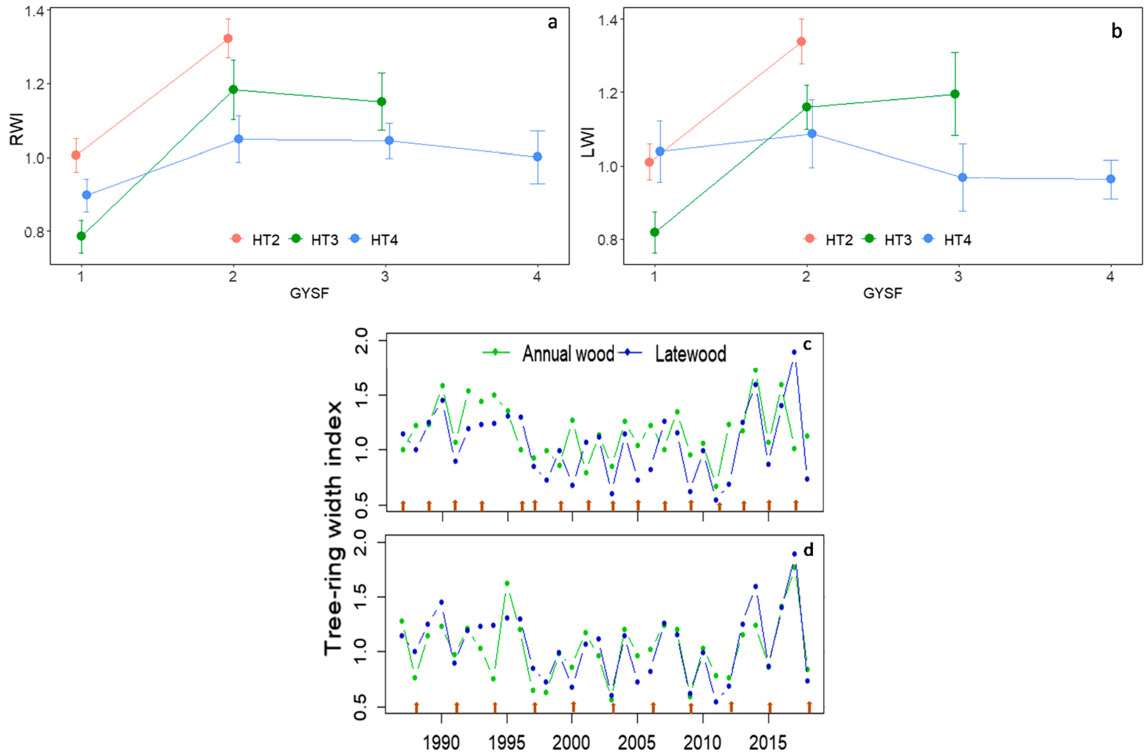

Fig. 7. Changes in standardized tree-ring width of (a) annual (RWI) and (b) latewood (LWI) for different treatments related to growing years since fire (GYSF) (1987 – 2018) and time series of annual wood and latewood for (c) HT2 and (d) HT3 treatments. Points in a and b represent mean values with standard error. The arrows in figures (c) and (d) indicate the year of burning beginning in 1987 for HT2 and 1988 for HT3 treatments.

Table 3
The results of multiple regression for annual wood RWI for all treatments combined (Overall) and for individual treatments. The coefficient of determination (R^2) for each variable was estimated using the stepwise regression model. The negative sign was added to R^2 values when the correlation it represents was negative. Abbreviations: pr: previous year, ppt: precipitation, t: temperature, max: maximum, min: minimum, grow: growing, GYSF: growing year since fire. See Table 1 for treatment definitions. See appendix 1 for coefficients and intercept of full model.

Site	pr Grow ppt	pr Oct tmin	Grow ppt	Spring ppt	Fall ppt	Spring tmax	Summer tmax	Fall tmax	Oct tmin	GYSF	Total	p-Value
Overall	0.11		0.25	–	–	–	−0.09	−0.09	–	–	0.54	0.001
Control	0.12	0.11	0.17	–	–	–	−0.06	−0.10	–	–	0.57	0.003
HT codominant	0.08	–	–	0.18	–	–	−0.30	−0.05	–	–	0.62	0.0003
HT intermediate	–	–	–	0.21	0.06	–	−0.27	–	–	–	0.54	<0.0001
HT suppressed	–	0.20	–	–	–	−0.18	–	–	0.07	–	0.45	0.003
HT4	–	–	–	–	–	–	–	–	–	–	–	–
HT3	–	–	–	0.05	–	–	−0.18	−0.07	–	0.29	0.59	0.0006
HT2	–	–	–	0.10	–	–	−0.05	−0.08	–	0.32	0.55	0.0004

Table 4
The results of multiple regression for LWI for all treatments combined (Overall) and for individual treatments. The coefficient of determination (R^2) for each variable was estimated using a stepwise regression model. The negative sign was added to R^2 values when the correlation it represents was negative. Abbreviations: Pr: previous year, ppt: precipitation, t: temperature, max: maximum, min: minimum, grow: growing, GYSF: growing year since fire. See Table 1 for treatment definitions. See appendix 1 for coefficients and intercept of full model.

Sites	Pr Grow ppt	Pr Oct tmin	Grow ppt	Summer tmax	Fall tmax	Oct tmin	GYSF	Total R^2	p-Value
Overall	–	0.17	0.19	−0.16		–	–	0.52	0.0002
Control	0.11	0.17	0.23	−0.12	−0.06	–	–	0.69	<0.0001
HT codominant	–	–	0.37	−0.20	–	–	–	0.57	<0.0001
HT intermediate	–	0.17	0.24	−0.18	–	–	–	0.59	<0.0001
HT suppressed	–	–	–	–	–	–	–	–	–
HT4	–	0.14	–	−0.09	–	0.17	–	0.40	0.03
HT3	–	–	–	−0.27	–	–	0.26	0.53	<0.0001
HT2	–	–	–	−0.23	–	–	0.32	0.55	<0.0001

treatments.

4. Discussion

Our goal was to determine how climate variation, different prescribed fire intervals, stand conditions, and tree canopy position affect radial growth of shortleaf pine. Previous dendrochronological studies in shortleaf pine mainly examined the response to climate variability (Schulman, 1942; Byram and Doolittle, 1950; Grissino-Mayer and Butler, 1993; Guyette et al., 2007). Our work expands and furthers the understanding related to the interactions between climate, management, and stand dynamics, i.e., how do management and stand condition affect sensitivity to climate variability.

Overall, we found some similarities among treatments in response of tree ring indices to climate variability, but some differences were related to management and stand conditions. Namely that prescribed fire in savannas reduced diameter growth the year after burning, suppressed trees were less responsive to climate variability than intermediate or co-dominant trees, and trees growing in savanna ecosystems appeared to be less sensitive to annual variation in precipitation than trees in a closed-canopy forest condition. Regarding the general responses to climatic variability, precipitation during the current growing season and average maximum summer temperatures were most frequently correlated to tree-ring growth regardless of management and stand condition and there was a shift towards greater importance of summer conditions for latewood development. Either previous year or current year October minimum temperature was correlated for most of the treatments. In general, correlations for RWI and LWI with temperature and precipitation were stronger than for KBDI (data not shown).

Precipitation is the most common factor influencing annual variation in growth rate of tree diameters where water is limiting (Watson and Luckman, 2001; George et al., 2008; Lopez et al., 2017; Dannenberg et al., 2019). Our study was near the western, drier edge of the shortleaf pine natural range. While the soil textures are loamy to clayey and have moderate water holding capacity, they contain between 3 and 35% coarse fragments plus abundant rocks which reduce their volume (https://soilseries.sc.egov.usda.gov/). The relatively low precipitation and rocky nature of the soil likely contributed to the strong correlation between reduced radial growth and periods of below average precipitation. The negative correlations between tree-ring width indices and average maximum summer temperature also were likely a function of water stress and drought. Higher temperatures increase vapor pressure deficits (VPD), which cause increased transpiration and tree water stress. This process in turn decreases stomatal conductance and carbon gain (Breshears et al., 2013; Will et al., 2013). Likewise, high summertime temperatures are often correlated with periods of drought in part because atmospheric moisture, that tends to moderate temperatures, is usually lower during drought (Martin et al., 2020). At our study site, average maximum summer time temperature was positively correlated to KBDI ($r = 0.77$) and negatively correlated to summer precipitation ($r = -0.67$) (Adhikari et al., 2021).

The correlations we found between ring width indices and precipitation and summer temperature are in general agreement with other studies relating shortleaf pine tree ring growth to climate variability (Byram and Doolittle, 1950; Friend and Hafley, 1989; Grissino-Mayer and Butler, 1993; Guyette et al., 2007). Previous dendrochronological studies in shortleaf pine found latewood most strongly correlated to July-September precipitation in western Arkansas (Schulman, 1942), annual growth correlated with late summer soil moisture in North Carolina (Friend and Hafley, 1989), annual ring growth correlated with spring and summer precipitation and temperatures and summer PDSI in Georgia (Grissino-Mayer and Butler, 1993), and annual ring growth most strongly correlated to current-year PDSI in Missouri (Stambaugh and Guyette, 2004). Precipitation and temperautre also were correlated to ring growth of the closely related loblolly pine (*P. taeda*) (e.g., Friend and Hafley, 1989; Jordan and Lockaby, 1990; Grissino-Mayer and Butler, 1993).

We separated latewood from annual wood because latewood is particularly sensitive to summertime environmental conditions in shortleaf pine (Schulman, 1942) and because shortleaf pine typically shows a relatively poor correlation between earlywood and latewood formation (Torbenson et al., 2016). In our study, the R^2 for the correlation between earlywood and latewood averaged 0.41 and ranged between 0.17 and 0.46 for individual treatments, which is generally greater than the average for shortleaf pine ($R^2 = 0.30$) reported by Torbenson et al. (2016). Overall, we found fairly similar results between annual wood and latewood with some shift to greater importance of summer conditions for latewood which is consistent with findings by Schulman (1942). This is because the latewood is often influenced by late summer or late growing season weather (Meko and Baisan, 2001; Griffin et al., 2011) as its formation usually begins mid-July for southern pines in the upper Gulf region (Jayawickrama et al., 1997). We also examined earlywood separately and found similarities with annual wood (Supplement 4) but with little importance of summer conditions for earlywood formation.

The correlation with average October minimum temperature (both previous year and current year) were the only minimum temperatures related to tree-ring growth. At our study site, first frost is typically mid to late October. The positive influence of current year October temperature on radial growth might be related to cessation of diameter growth. Byram and Doolittle (1950) found that ring growth of shortleaf pine near Asheville, NC, USA was mostly complete by late August but did not reach its fullest extent until October. Relationships with previous year October minimum temperatures likely are related to prior year's carbon storage (Kozlowski and Pallardy, 1996). While shortleaf pine has the capacity to photosynthesize year-round when temperatures are above freezing, it is possible that freezing temperatures induce physiological changes which lessen the efficiency of carbon gain. Similar to our study, Grissino-Mayer and Butler (1993) found that previous year's November temperatures were correlated to tree-ring growth. The potential impact of stored carbohydrate is further indicated by the correlation with previous year's precipitation for the Control and HT treatments.

Separating the effects of wildfire from those of drought on tree-ring development is often difficult because wildfires are most common in drought years (Guyette et al., 2007). By imposing regular prescribed fire regimes since 1985, we conclusively separated the effects of climate variability from fire. Shortleaf pine is very fire-tolerant and can recover from complete crown scorch caused by dormant season fires (see Carey, 1992). The effect on growth depends on severity of scorch (Byram and Doolittle, 1950) and can range from no effect (Langdon, 1971) to a 75% decline in diameter growth the year after fire (Garren, 1943). In our study, a prescribed fire every two or three years reduced tree-ring growth by 21–33% on average. While complete crown scorch did not typically occur, most burns in the HT2 and HT3 treatments caused moderate amounts of delayed heat-induced needle browning in the year-old foliage cohort. Fire every four years caused little reduction in growth, likely related to reduce fireline intensity due to a change in fuel architecture and composition with the shift from savanna to woodland to forest. In the savanna, grasses, grass likes and forbs (1-hr time-lag fuels) were the primary carrier of a given fire. Whereas, live woody fuels (10-hr-size-class) and dead leaf litter (1-hr size class) increased proportionally as grassy fine fuels (1-hr time lag) declined following transition to woodland and forest structure, thus creating a less combustible fuel bed. Fireline intensity for the HT2, HT3, and HT4 treatments averaged 1941, 1381, and 802 kW m^{-2}, respectively.

The reduction in growth due to prescribed fire is likely associated with lower leaf area available for current-year photosynthesis and allocation of previously stored carbohydrate to needle growth rather than stem growth. Both RWI and LWI decreased in response to prescribed fire indicating persistent effects throughout the growing season. Shortleaf pine keeps its needles for one-and-a-half years such that needle area should be fully recovered one growing season after fire. Despite the detrimental effects on needle area, prescribed fire likely has positive effects by releasing nutrients which could benefit tree growth in the second or third year after fire (Kauffman et al., 1994).

Within the HT treatment, we had the opportunity to determine how tree canopy position affected the response of growth to climate variability. While co-dominant trees were faster growing (2.8 rings cm^{-1}) (Supplement 1) and had more light availability than the slower growing intermediate trees (3.3 rings cm^{-1}), ring growth of both responded similarly to temperature, precipitation, and were both correlated to average October minimum temperatures. In contrast, suppressed trees were generally non-responsive to temperature and precipitation with annual wood related only to growing season length, i.e., average October minimum temperature. The extremely slow growth of suppressed trees (5.7 rings cm^{-1}) may have made it harder to measure relative differences among years, but likely their subordinate canopy position and competitive disadvantage made it difficult for them to make use of resources when periodically abundant.

While we had several droughts during our study, we did not have enough discrete drought events to specifically test for resistance and recovery of radial growth to drought. Rather we developed regression relationships that incorporated 30 + years of climatic variability. In the context of resistance to drought, response to current year conditions is most relevant, while recovery is best reflected by the relationship with previous year's conditions (Huang et al., 2018). Related to resistance, the slopes of the relationships between ring width indices and current year precipitation and temperatures tended to be steeper and correlations stronger for trees in closed-canopy forests (Control and HT) than savannas (HT2 and HT3), which likely indicates greater resistance to drought for trees in the savanna treatments. Alternatively, trees growing in the savanna ecosystems in our study compete with abundant herbaceous vegetation (~265 kg $ha^{-1}y^{-1}$; Adhikari et al., 2021; Feltrin et al., 2016) and suffer regular crown damage associated with prescribed fire, which may mute their responsiveness to periods with abundant rainfall. In a meta-analysis of thinning effects on drought resistance and recovery, Sohn et al. (2016) found that resistance was greater in thinned stands when considering all species, but that differences for studies involving conifers were less pronounced. However, recovery from drought was more pronounced in thinned conifer stands than non-thinned conifer stands (Manrique-Alba et al., 2020), which matches our findings that the Control and HT trees were more affected by previous year's precipitation.

The general lack of correlation between environmental conditions and ring growth of the HT4 treatment likely has due to the transition of this treatment from savanna to forest during the study period and associated changes in competition, community composition, stand density, and fire intensity, which likely confounded climate signals. Between 1985 and 2018, the HT4 treatment experienced the greatest increase in both basal area (3.6–20.7 m^2 ha^{-1}) and canopy cover (7.3–52.4%) due to the growth of residual trees and periodic recruitment of new trees (Adhikari et al., 2021).

One of our major goals was to determine how climate change might affect future growth of shortleaf pine at the margin of its western range. Our findings clearly indicate that reduced precipitation in the current year, particularly spring and summer, will decrease radial growth. On average, a 100 mm reduction in growing season precipitation will reduce RWI by 5%. Based on the steepness of slope between precipitation and RWI, the Control, HT-codominant, and HT-intermediate were more sensitive to precipitation, likely due to greater tree-to-tree competition for soil water within denser stands. Previous year precipitation was mainly correlated to trees in the Control treatment, but the slope of this relationship was less than half as steep than for current-year growing season precipitation.

Based on our findings, increasing mean daily summer maximum temperature will reduce growth. A 1 °C increase in temperature is expected to decrease RWI by 7%. As discussed above, this is likely a function of plant water stress mediated through VPD (Dannenberg et al., 2019) or due to the correlation between drought and higher summer temperatures (Way and Oren, 2010). Average maximum daily spring temperature was correlated in a few instances, but fall temperatures were not correlated to growth. Potentially counterbalancing the negative effects of increased summer temperature are the positive effects of warmer October temperatures, which might extend the growing season. The slopes of the relationship between previous year's average October minimum temperature and RWI were similar among treatments and indicated a 6% increase in growth per 1 °C increase. Therefore, the seasonality of temperature increase resulting from potential climate change will be important regarding future growth responses.

Our multiple regressions generally predicted greater than 50% of the variation in radial growth. This is more than previous efforts in shortleaf pine such as 20–40% (Friend and Hafley, 1989), 43% (Stambaugh and Guyette, 2004), and 46% (Grissino-Mayer and Butler, 1993). Perhaps the geographical position of our study area on the margin of the range increased sensitivity to climate variability or inclusion of a greater number of variables increased the strength of our models (Sala et al., 1988). Like our models, previous multiple regressions all included some measure of precipitation or drought, temperature, and previous year conditions. However, the models differ on specific factors included, which may relate to regional differences in climate, differences in soils and site conditions, or differences in stand condition and stand age. In the context of number of trees sampled and the broad range of stand condition incorporated, our study was robust. An interesting outcome of our multiple regressions was that average fall temperature maximum was included for a number of models even when it was not significantly correlated by itself. This seems to indicate that fall temperatures may contribute to growth, but the response is masked by other variables until separated in the multiple regression process.

5. Conclusions

Variation in temperature and precipitation affected radial growth of shortleaf pine regardless of management and stand conditions along the forest-savanna continuum in the southcentral USA. Prescribed fire reduced radial growth the growing season after fire except for the four-year fire interval. Stand density and tree canopy position interacted with climate variability in that radial growth of suppressed trees was less sensitive to climate variability, and radial growth of trees from savanna systems appeared more resistant to periods of below-average precipitation. The impact of future climate change on growth of shortleaf pine may be mixed. Reduced precipitation and higher summer temperatures may reduce growth, but warmer October temperatures may increase growth. Management to reduce stand density, either through thinning or by prescribed fire, may dampen some of the variation of growth in response to climate variability and increase resistance and resilience of the tree component of woodlands and savannas along the forest-grassland ecotone.

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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Author's contribution

Each author has made significant contribution. AA and REW designed study, developed methods, conducted field study, and wrote the manuscript. AA also analyzed the data. REM established the research site and is responsible for spearheading the long-term maintenance of the site. He also contributed to writing the manuscript and historical data. HA provided guidance for the dendrochronological work and helped write the manuscript. KP assisted with data analysis and contributed to writing the manuscript. CBZ and OJ contributed to the development of the research question and helped write the manuscript.

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