

Radial growth responses of post oak (*Quercus stellata*) to climate variability and management in southeastern Oklahoma, USA

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Abstract We investigated radial growth of post oak (*Quercus stellata* Wangenh.) growing in a range of stand structures (forest to savanna) created in 1984 by different harvesting, thinning, and prescribed fire intervals. We related ring width index (RWI) to monthly and seasonal climate variables and time since fire to assess impacts of climate variability and interactions with management on radial growth. The RWI of all treatments was positively correlated to minimum daily temperature the previous September and precipitation late spring and early summer the current year, and negatively correlated to maximum daily temperatures and drought index late spring - early summer. June weather was most strongly correlated in four of five treatments. While stand structure affected absolute diameter growth, the RWI of savanna and forest stands responded similarly to climate variability, and low intensity prescribed fire did not influence RWI. On average, a 100 mm reduction in June precipitation decreased RWI by 7%, a 1 °C increase in previous-year September daily minimum temperature increased RWI by 3.5%, and a 1 °C increase in June maximum daily temperature decreased RWI by 3.7%. Therefore, negative effects of drought and warmer spring and summer temperatures may be reduced by a longer growing season under warmer climate scenarios. However, management did not appear to influence RWI.

Key mrds: dendrochronology, climate, drought, radial growth, fire frequency.

Resume: Nous avons étudié la croissance radiale du chêne étoile (*Quercus stellata* Wangenh.) croissant dans une variété de structures de peuplement (forêts à savanes) créées en 1984 après avoir appliqués différents traitements d'éclaircie et de récolte suivis de différents intervalles entre des brûlages dirigés. Nous avons relié l'indice de largeur des cernes (ILC) aux variables climatiques mensuelles et saisonnières ainsi qu'au temps écoulé depuis le feu pour évaluer les impacts de la variation du climat et des interactions avec l'aménagement sur la croissance radiale. Dans tous les traitements l'ILC était positivement corrélé à la température minimale quotidienne au mois de septembre de l'année précédente ainsi qu'à la précipitation à la fin du printemps et au début de l'été de l'année en cours, et négativement corrélé à la température maximale quotidienne et à l'indice de sécheresse à la fin du printemps et au début de l'été. Les variables météorologiques du mois de juin étaient le plus étroitement corrélées dans quatre des cinq traitements. Tandis que la structure du peuplement influençait la croissance absolue en diamètre, l'ILC des peuplements de forêts et de savanes réagissait de façon similaire à la variation du climat et le brillage dirigé de faible intensité n'influencait pas l'ILC. En moyenne, une diminution de la précipitation de 100 mm entraîne une réduction de l'ILC de 8%; une augmentation de la température minimale quotidienne de 1 °C en septembre de l'année précédente entraîne une augmentation de l'ILC de 3,5%; et une augmentation de la température maximale quotidienne de 1 °C entraîne une réduction de l'ILC de 3,7%. Par conséquent, les effets négatifs de la sécheresse et des températures plus chaudes au printemps et à l'été pourraient être atténus par des saisons de croissance plus longues sous des scénarios climatiques plus chauds. Cependant, l'aménagement n'a pas semblé influencer l'ILC. [Traduit par la Redaction]

Mots-des: dendrochronologie, sécheresse, largeur des cernes annuels, bois annuel, fréquence des feux.

Introduction

Radial growth is an indicator of past climate variability that can be used to predict future climate change impacts on tree growth and ecosystem dynamics (Cullen et al. 2001; Buechling et al. 2017; Tiwari et al. 2017; Schwab et al. 2018). In recent decades, the southcentral USA has frequently experienced extreme dry and wet events due to increasing variation in precipitation (Collins et al. 2013; Oliveras and Malhi 2016). Climate models predict that the region will likely experience temperature increases of 2.5 to 4.0 °C by the second half of this century (Collins et al.

2013), which will increase vapor pressure deficit and water stress (Breshears et al. 2013; Will et al. 2013). Combined, these changes will likely decrease tree growth. Forest management activities, including thinning and prescribed fire, typically promote tree growth by reducing stand density and also enhance resistance to drought (Hood et al. 2016; van Mantgem et al. 2016).

Tree-ring attributes, including annual wood, earlywood, latewood, and wood density, archive valuable information regarding interactions between past climate variability and disturbance regimes. Assessment of growth and development using dendrochronological approaches can lead to a better understanding of

Received 23 March 2021. Accepted 5 August 2021.

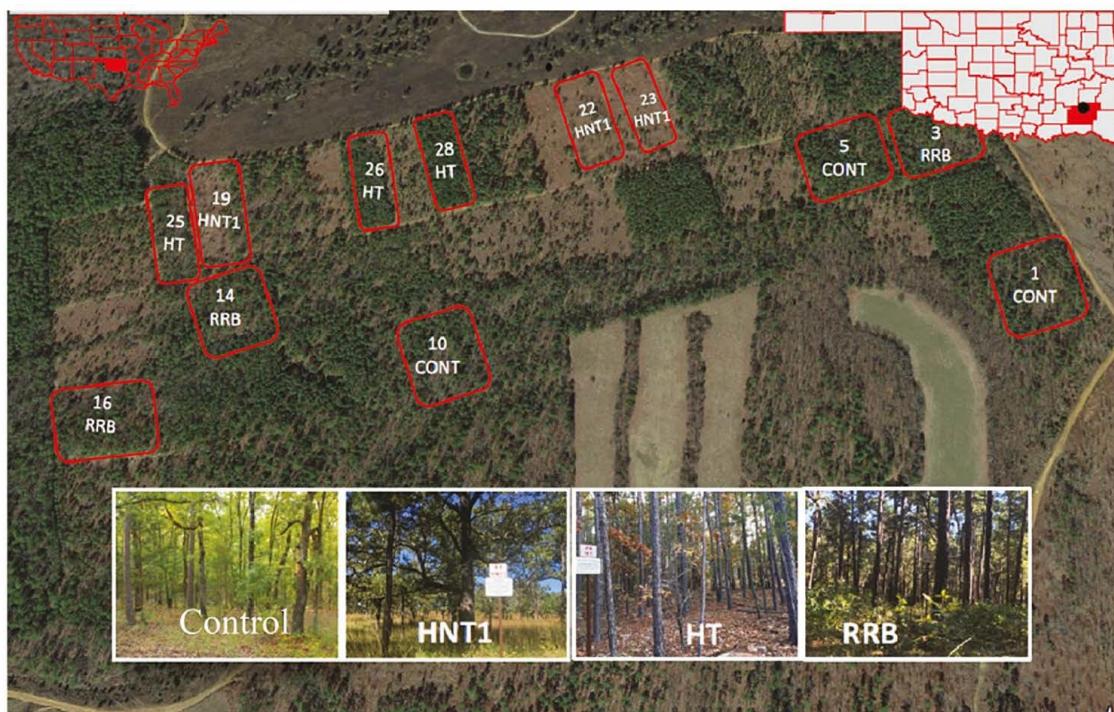
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Fig. 1. Location of study area with permanent treatment plots (red rectangles) (source: Google Earth 2019). See Table 1 for treatment definitions. [Colour online.]



the relationship between tree growth and environmental variation (see Briffa et al. 1983; Cook et al. 1990; Martin-Benito et al. 2008; Fang et al. 2014) following disturbances, especially for trees growing in water-limited environments (McGuire et al. 2010). Each annual tree ring is composed of earlywood and denser latewood, with earlywood typically composing the majority of the annual ring (Stokke and Groom 2008). Though the widths of earlywood and latewood within a given year are often correlated (Meko and Baisan 2001; Torbenson et al. 2016), late growing season weather conditions more strongly influence the formation of latewood (Meko and Baisan 2001; Griffin et al. 2011).

Post oak (*Quercus stellata* Wangenb.) is a medium-sized tree that occurs throughout much of the central and southern portions of the eastern USA. Post oak is extremely drought- and fire-tolerant, but also shade-intolerant (Stransky 1990), such that it is outcompeted on infrequently burned, mesic sites. However, on xeric sites, oaks more often replace themselves, as mature trees tend to be shorter in stature allowing greater light availability to the understory. Additionally, seedlings exhibit prolific sprouting and deep rooting habits (Clark et al. 2007). Therefore, post oak reaches its ecological zenith in central Oklahoma and Texas along the forest-grassland ecotone (Risser and Rice 1971; Stahle and Hehr 1984; Stransky 1990), where surface fires were historically common, with reported average fire-return intervals ranging from 20 to 6.7 years (DeSantis and Hallgren 2011; dark et al. 2007).

Understanding how tree growth responds to interacting effects of climate variability and management is important to the resilience of productivity and ecosystem function to drought and climate change. This is especially important within the forest-grassland transition zone, where ecosystems can shift from woody- to herbaceous-dominated due to drought or disturbance (Policelli et al. 2019). We investigated the drivers of radial growth for post oak that were growing in a range of stand structures created by different forest management regimes near the forest-grassland ecotone of southeastern Oklahoma. Specifically, we examined

variability in annual wood and latewood of post oak to stand conditions ranging from closed-canopy forest to savanna as well as variable fire frequency (fire exclusion, 1-year and 4-year fire-return intervals) (Masters and Waymire 2012). Specifically, we addressed how annual tree-ring index (RWI), a dimensionless, relative index of annual tree diameter growth accounting for tree size, responds to the combined effects of management, i.e., reduced stand density and prescribed fire, and climatic variation. We hypothesized that (i) post oak RWI would increase in years with above average precipitation and decrease with in years with above average summer temperatures, (ii) RWI of trees growing in savannas would be less sensitive to precipitation than those growing in forest conditions, and (iii) prescribed fire would have a 1-year negative effect on RWI.

Methods

Study sites

The study was conducted on twelve experimental units ranging from 0.8 to 1.6 ha within a 53 ha forest habitat research area located within the 7690 ha Pushmataha Wildlife Management Area (WMA). The study area was located along the western edge of Ouachita Mountain in southeastern Oklahoma (34°31'40"N, 95°21'10"W) (Fig. 1). Soils of the study area were thin, rocky, derived from sandstones and shales, and belonged to the Carnesaw-Stapp association (Bain and Watterson 1979; NRCS 2019).

The climate of the study area is semi-humid with hot summers and mild winters. Pre-treatment vegetation of the study area and that of Control treatment units was characterized by mixed pine-hardwood forest dominated by post oak, shortleaf pine (*Pinus echinata* Mill.), blackjack oak (*Quercus marilandica* Münchh.), and hickory (*Carya* spp.). Understory non-woody vegetation was mainly composed of sparse herbaceous plants represented by little bluestem (*Schizachyrium scoparium* (Michx.) Nash), panicums (*Panicum* spp., *Dichanthelium* spp.), sedge (*Carex* spp.), and various forb species. Understory woody vegetation was dominated by

Table 1. Description of treatments.

Treatment	Harvest pine	Thin hardwoods	Fire-return interval (years)	Post-treatment structure 1985 ^a	Structure 2018 ^a	Basal area (m ² ·ha ⁻¹)		Average age of tree ^b
						1985	2018	
C.Ontrol	No	No	No fire	Forest	Forest	26.6::1.3	28.0::1.3	102.0::12.0
HT	Yes	Yes	No fire	Savanna	Forest	3.8::0.4	32.5::2.0	81.0::9.4
HNTI	Yes	No	1	Woodland	Savanna	9.0::1.0	6.5::1.0	89.0::5.8
RRB	No	No	4	Forest	Forest	25.4::1.2	27.0::1.1	89.0::18.7

Note: Basal area and average age of trees presented with mean :: standard error. Hardwood thinning and shortleaf pine (*Pinus edulis*) harvesting was completed during the establishment of experimental site at Pushmataha, Oklahoma, USA, in 1984. The prescribed burning was conducted in winter 1985 and succeeding years at defined intervals.

^aClassification 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 m²·ha⁻¹; Savanna: basal area=2.3 to 6.9 m²·ha⁻¹; Woodland: basal area=6.9 to 18.4 m²·ha⁻¹; Forest: basal area>18.4 m²·ha⁻¹.

^bPost oak (*Quercus stellata*) trees sampled

sparkleberry (*Vaccinium arboreum* Marshall), poison ivy (*Toxicodendron radicans* (L.) Kuntze), grape (*Vitis* spp.), and greenbriers (*Smilax* spp.) as well as seedlings of the overstory tree species, primarily oaks (*Quercus* spp.). Post treatment (see below) experimental units that were thinned and burned were dominated by little bluestem, big bluestem (*Andropogon gerardii* Vitman), Indian grass (*Sorghastrum nutans* (L.) Nash), panic grasses, and various legume and forb species. Units that were just thinned or just burned had a similar herbaceous species complements but with much less abundance. Woody species most prevalent on thinned and burned units were oak sprouts and blackberry (*Rubus* spp.). On just thinned or just burned units, sparkleberry and seedlings and sprouts from oaks were prevalent understory species. Winged sumac (*Rhus copallina* L.) was important on the burned units only.

Treatments

Experimental units were established in summer of 1983 in a randomized experimental design, with three replications per treatment, across homogeneous closed-canopy mixed pine-hardwood forest (Fig. 1) (Masters and Waymire 2012). During the summer of 1984, pine harvesting and hardwood thinning were applied to units representing the HT and HNTI treatments, but not the Control or Rough Reduction Burn (RRB) (Fig. 1). The Control was untreated closed-canopy, mature forest with the basal area of 15.5 :: 2.2 m²·ha⁻¹ (mean :: standard error) for shortleaf pine, 0.4 :: 0.2 1112·ha⁻¹ for eastern redcedar (*Juniperus virginiana* L.), and 12.5 :: 2.0 m²·ha⁻¹ for hardwoods in 2018. The average diameter at breast height (DBH), height, and age of post oak we sampled were 36 cm, 17 m, and 102 years. The RRB treatment was similar to the Control with the exception that prescribed fire was introduced beginning in 1985 and thereafter applied every 4 years. In 2018, the basal area was 15.1 :: 1.1112·ha⁻¹ for shortleaf pine and 11.9 :: 1.8 1112·ha⁻¹ for hardwoods with the average DBH, height, and age of post oak sampled 33 cm, 17 m, and 89 years, respectively. In 1984, the HT treatment plots were created by harvesting shortleaf pine trees with a DBH of 11.4 cm or larger (H) and thinning hardwoods to approximately 91112·ha⁻¹ basal area using single-stem injection of the herbicide 2,4-dichlorophenoxyacetic acid (T). Afterwards, fire was excluded from the HT treatment and the plot was allowed to regenerate naturally. In 2018, the basal area was 231 :: 6.5 1112·ha⁻¹ for shortleaf pine, 0.6 :: 0.3 1112·ha⁻¹ for eastern redcedar, and 9.5 :: 2.4 m²·ha⁻¹ for hardwoods with the average DBH, height, and age of sampled post oak 43 cm, 16 m, and 81 years, respectively. The HNTI treatment was similarly harvested (H) in 1984, but hardwoods were not thinned (NT) and prescribed fire was subsequently applied annually (1; 1-year fire-return interval). In 2018, the basal area was 1.1 :: 0.21112·ha⁻¹ for shortleaf pine and 5.4 :: 0.5 1112·ha⁻¹ for hardwoods. The average DBH, height, and age of sampled post oak were 38 cm, 13 m, and

89 years, respectively. More complete information on stand conditions in 1985 and 2018 are provided in Table 1. Fireline intensity of prescribed fire during the experiment averaged 919 and 921 kW·111⁻² for HNTI and RRB, respectively.

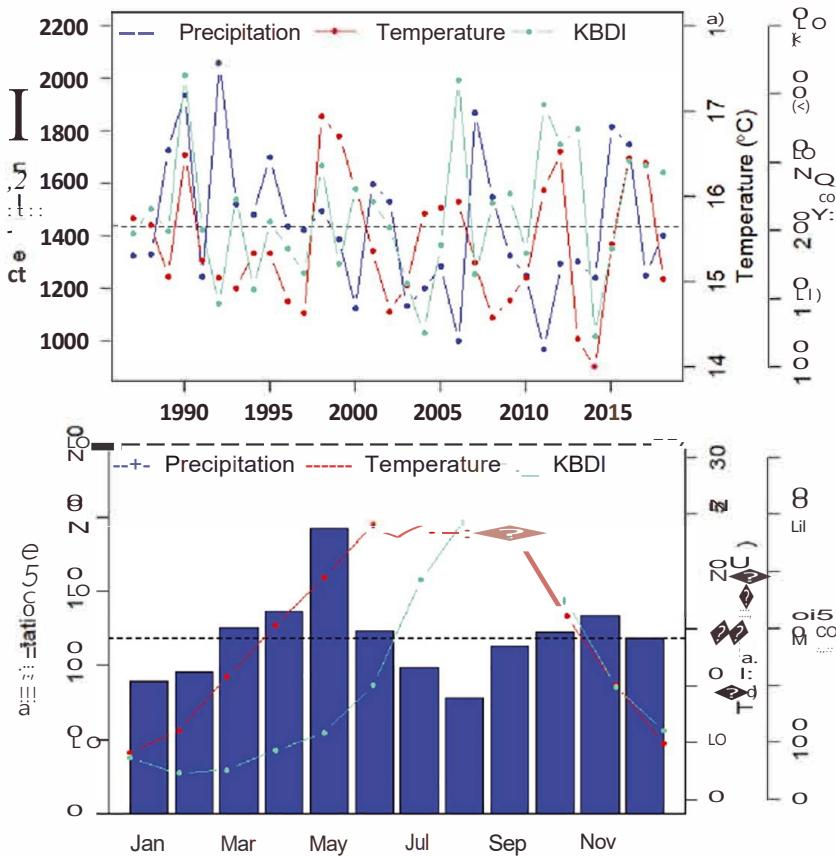
Dendroecological analysis

Following the 2018 growing season, cores were collected from post oak at the breast height, i.e., 1.3 m, using an increment borer (515 mm diameter) from the Control, HT, HNTI, and RRB treatments. Trees were sampled along two randomly located parallel transects perpendicular to the contour of the unit. In some units, 10 post oak were not available. The collected cores were air dried at 60 °C for 72 h and each core was mounted in grooved wooden holders with water-soluble glue. Each mounted core was sanded with progressively finer sandpaper down to a grit size of 400. The mounted and sanded cores were first visually cross-dated under a sliding microscope (AmScope, CA) and then digitized using a scanner. Widths of annual, earlywood, and latewood rings of each digitized sample were measured using the WINDENDRO image analysis system (Regents Instruments, Quebec). COFECHA was used to check the cross-dating and overall quality of tree-ring chronologies by standardizing the raw data of ring width and providing correlations between each series and all series combined (Holmes 1983; Grissino-Mayer 2001; Speer 2010).

Tree-ring width indices for each tree's annual wood (RWI) and latewood (LWI) were calculated on a single tree mean chronology for the post-treatment period 1987-2017. Within individual treatments and for all treatments combined the chronology of each tree was detrended using the ModNegExp method by fitting the classical nonlinear model using the dpR function (Bunn 2008). RWI and LWI are relative indices of radial tree growth that have a mean of 1.0, whereby years with below average relative growth are negative and years with above average relative growth are positive. The indices account for and eliminate effects of increasing tree size on annual growth increment (Cook and Peters 1981) for better interannual frequency variation (Cook and Kairiukstis 1990). Unlike the spline method of standardization, the ModNegExp detrending method does not remove the effects of stand density (Cook and Peters 1981), which was a factor of interest in our study.

Using all trees within a given treatment and for all treatments combined, we estimated dendrochronological attributes of RWI and LWI including series intercorrelation (Rbar), average mean sensitivity (MS), standard deviation (SD), and autocorrelation (AC) for each chronology. Rbar is a measure of stand-level climate signals, mean sensitivity measures year-to-year variation of ring width (Speer 2010), and autocorrelation estimates the similarity between given time series of tree-ring chronology over a successive time interval (Phillips and Parr 1999).

Fig. 2. (Top) Annual precipitation, temperature, and KBDI (Keetch-Byram drought index), and (bottom) average monthly precipitation, temperature, and KBDI over 32 years of the study period (1987-2017). The dashed horizontal line in each figure indicates average precipitation over the study period. Temperature and precipitation were computed from daily data obtained from Daymet (Thornton et al. 2016). [Colour online.]



Predictors of tree growth

Because management regimes were applied to the unit-level, we averaged ring width indices of trees within each unit for analyses related to climate variability and the interaction between climate variability and management. Therefore, sample size was three for these analyses with between 6 and 10 subsamples composing the unit mean.

The RWI and LWI of each treatment and all treatments combined were related to climate variability using various measures of intra-annual and inter-annual temperature and precipitation. For the RRB treatment, growing years since fire was also included. We computed climate variables from daily data obtained from Daymet (Thornton et al. 2016) for each year between 1987 and 2017 (31 years). In addition to monthly values, 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 average daily maximum, average daily minimum, and average daily temperature. We also estimated the Keetch-Byram drought Index (KBDI) (Keetch and Byram 1968) following the equation described in Dolling et al. (2005). KBDI expresses soil moisture conditions under a wide range of temperature, precipitation, and meteorological factors in and ranges from 0 to 800; a value of 0 is complete saturation of soil while a value of 800 represents absolutely dry soils (Keetch and Byram 1968).

A total of 69 variables, that included current-year and previous-year weather, were correlated to RWI and LWI. We first performed a correlation analysis between each predictor and the response

variables (i.e., RWI and LWI) to minimize the burden of an over-parameterized model for predicting both RWI and LWI. This was performed separately within each treatment as well as by combining all treatments. Next, we dropped all the predictors that were not significantly correlated with RWI or LWI for at least one treatment ($p > 0.05$). As a result, only 16 variables were retained for the multiple regression analyses. With the remaining variables, we built a series of multiple regression models with bidirectional elimination of parameters (stepwise regression). Competing models were selected based on Akaike Information Criterion (AIC) adjusted for small sample size. We also tested the impact of the number of years since the most recent prescribed fire on RWI and LWI of oak in the RRB treatment. The term "Growing Years Since Fire" was used, where 1, 2, 3, and 4 represent the annual ring for the first, second, third, and fourth growing season after burning, respectively. We also compared slopes between RWI and the three most commonly correlated climate variables among treatments. Data processing, analysis, and plotting was done in R version 3.5.0 (R Core Team 2020).

Results

Climate

Over the study period, annual precipitation varied between 971 and 2056 mm and annual minimum and maximum average temperatures were 9.1 °C and 22.2 °C (Fig. 2). Average monthly maximum precipitation was 194 mm in May and minimum was 77 mm in August (Fig. 2). Though average annual KBDI was 212, monthly KBDI reached a maximum in August (507) due to

Fig. 3. Correlations of 31-year annual **wood** (RWI, ring width index) chronologies of post oak with climate variables for different treatments and all treatments combined (Study site). Horizontal dotted lines at $r = 0.35$ and $r = -0.35$ form a 95% confidence interval; significant correlations ($p < 0.05$). Orange, blue, and red colours indicate KBD I (Keetch-Byram drought index), precipitation, and temperature, respectively. Abbreviations: Grow, growing season; Pr, previous; PPT, precipitation; T_{\max} , maximum temperature; T_{\min} , minimum temperature. All variables with one or more significant correlations are presented. See [Appendix Table A1](#) for coefficients. See [Table 1](#) for treatment definitions. [Colour online.]

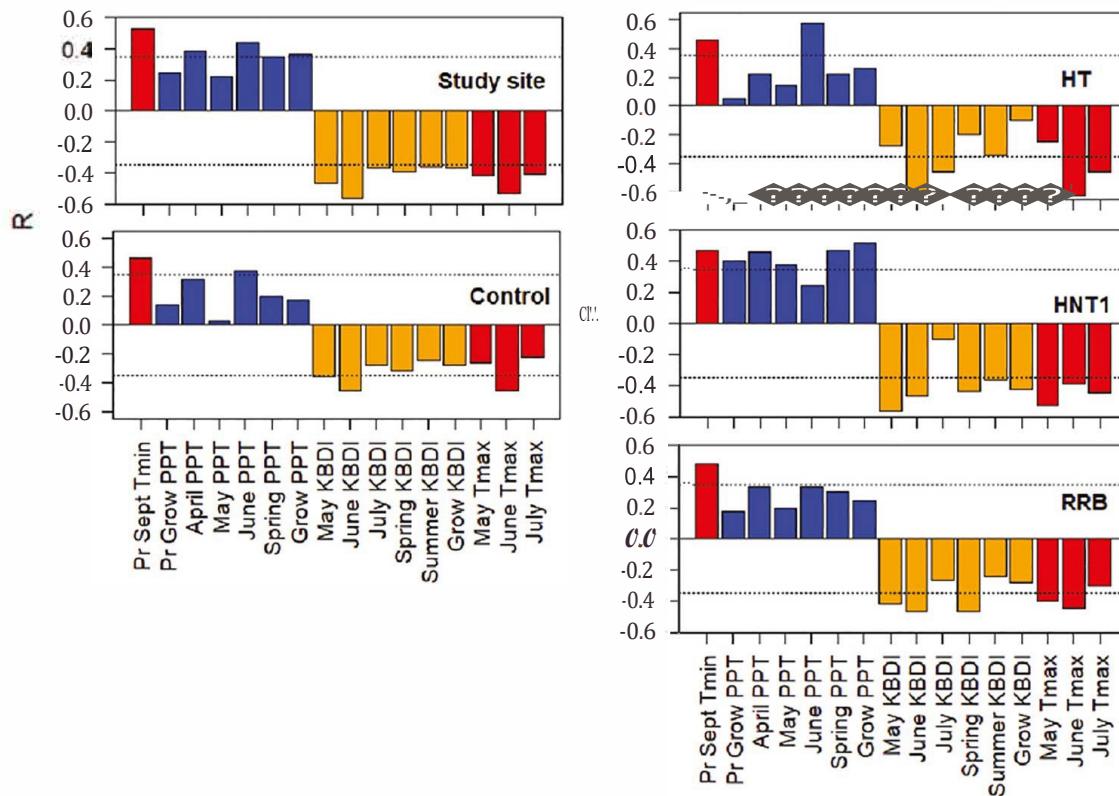


Table 2. Summary statistics including average tree-ring series length, interseries correlation (R_{bar}) of chronology with master chronology, Series interseries correlation (R_{bar}), standard deviation (SD), autocorrelation (AC), and of post oak chronology for all treatments combined and each treatment for 1987–2017.

Site	No. of cores	Series length	R_{bar}	SD	AC
All site	96	31	0.43	0.11	0.63
Control	26	31	0.42	0.10	0.62
HT	17	31	0.49	0.15	0.67
HNT1	28	31	0.38	0.13	0.58
RRB	25	31	0.37	0.10	0.65

Note: Mean ring width index for all treatments combined and individual treatments was 1.

decreasing precipitation in summer (June, July, and August) accompanied with increasing temperatures (Fig. 2). As a result, June to September typically experienced dry soil. However, soil moisture recharged before the next growing season as result of greater precipitation and cooler temperatures during winter and early spring. Over the time period of the study, we observed no significant trend in either higher or lower average temperatures or average precipitation. We found considerable variation from year to year in these parameters (Fig. 2).

Summary statistics

A total of 96 post oak tree cores were cross-dated and measured (Table 2). The resulting chronologies across the study site varied in length from 51 to 226 years; however, we considered tree chronologies from the year of 1987, which was 3 years after the

thinning treatments were employed in 1984 (Appendix Fig. A1). The average DBH growth for the HNT1, HT, RRB, and Control treatments were 2.29, 2.80, 1.89, and 1.74 mm·year⁻¹ (Fig. A2). Mean interseries correlation for all chronologies ranged from 0.37 (RRB) to 0.49 (HT) for RWI, while the mean sensitivity of RWI ranged between 24 and 25. The standard deviation, and first-order autocorrelation are presented in Table 2. The average proportion of early-wood and latewood composing the annual ring was similar (49.9:50.1). Average RWI was 1.0 for all treatments.

Growth response to climate variability

Both previous-year and current-year climate variability influenced RWI, but generally there were not differences among treatments. Previous-year September average daily minimum temperature was positively correlated with RWI in all treatments combined as well as all individual treatments, and previous-year growing season precipitation was positively correlated with RWI for HNT1 (Fig. 3). Current-year conditions during April to July were positively correlated with RWI. For precipitation, the period April through June, and therefore Spring and Growing Season averages also, was most important with June having the highest correlation for monthly precipitation in all treatments combined as well as for Control, HT, and RRB. April precipitation had the highest correlation for HNT1. RWI was negatively correlated with maximum temperatures for the period May to July. The highest correlation for temperature was with June mean daily maximum temperature for all treatments combined, Control, HT, and RRB. The HNT1 treatment was best correlated with May maximum temperature. Similarly, RWI was negatively correlated with **KBDI** during the period May to July, and therefore also Spring, Summer, and Growing Season. The correlation was strongest with June **KBDI**.

Fig. 4. Time series of previous-year September mean minimum daily temperature (Sept. T_{\min}) and current-year June KBDI (Ke etch-Byram drought index) with standardized post oak annual wood (RWI, ring width index) for all treatment combined 1987-2017. [Colour online.]

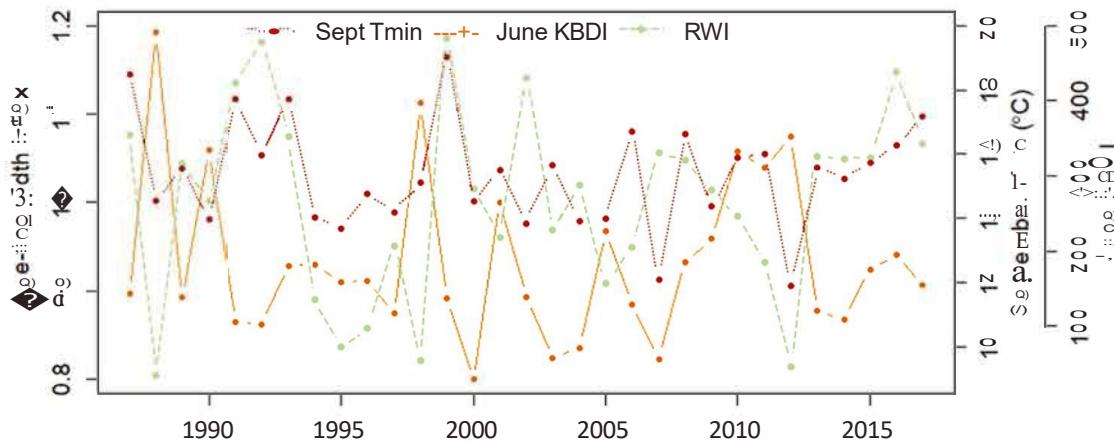


Table 3. Partial R² for each variable to explain variation of ring width index (RWI) estimated using backwards selection regression models.

	Annual wood										Total If	
	Tmin		PPT			KBDI			Tmax			
	Pr Sept.	PPT	Pr Grow	April	June	Grow	June	May	May	June	July	
All site	0.27	—	—	0.15	0.24	—	—	—	-0.05	—	—	0.71
Control	0.21	—	—	—	0.17	—	—	-0.10	—	—	—	0.48
Hf	0.20	—	—	—	0.34	—	-0.08	—	—	—	—	0.62
HNT1	0.13	0.16	—	—	—	0.23	-0.11	—	-0.07	—	-0.08	0.78
RRB	0.23	—	—	—	—	—	—	—	-0.09	-0.19	—	0.51

Note: The negative sign indicates a negative relationship between a variable and RWI. Only significant R² values are shown. Grow, growing season; Pr, previous year; PPT, precipitation; Tmax, maximum temperature; T_{\min} , minimum temperature. See Table 1 for treatment definitions.

for all treatments combined, Control, HT, and RRB, while once again, the strongest correlation for HNT1 was a month earlier in May.

Overall, the correlations between RWI and previous-year's September minimum daily temperature (R ranged from 0.46 to 0.53) and current-year June KBDI (with exception of HNT1) (R ranged from -0.46 to -0.61) were strongest, and RWI and LWI fluctuated similarly in response to these variables (Fig. 4). The slopes of RWI and previous-year September minimum temperature ranged between 0.029 and 0.044 (average 0.035) (Fig. 5a; Appendix Table A1). The slopes of RWI and current-year June precipitation ranged between 0.0005 and 0.0014 (average 0.0008) (Fig. 5b; Table A1). The slopes of RWI and current-year June KBDI ranged between -0.0004 and -0.0009 (average -0.0006) (Fig. 5d; Table A1). The slopes between RWI and current-year June maximum temperature ranged between -0.028 and -0.061 (average -0.037) (Fig. 5c; Table A1). Differences in slopes between treatments were significant, and the HT treannent had the steepest slope for previous-year's September average daily minimum temperature, current-year June precipitation, June KBDI, and June average daily maximum temperature ($p < 0.05$; Table A1). Growing years since fire was not significantly correlated with RWI for the RRB treatment that was burned every 4 years ($R = 0.01$; $p = 0.83$) such that there was no pattern in RWI and time since fire.

Stepwise multiple regression models eliminated some of correlated variables. The multiple regressions explained 71% of the variation in RWI when all treatments were combined (Table 3) and RWI was influenced by previous September minimum daily temperature (27%) and the remainder by the current-year April and June precipitation. For individual treatments, the multiple regressions explained 48%, 62%, 78%, and 51% of variability for

the Control, HT, HNT1, and RRB treannents, respectively. Previous September minimum daily temperature explained variability in RWI for all treannents, particularly in the Control and RRB treatments (Table 3). June precipitation, June KBDI, and May maximum daily temperature of the current year were each included in the model of two individual treatments (Table 3) and some measure of precipitation and temperature of the current year also were included for each treannent.

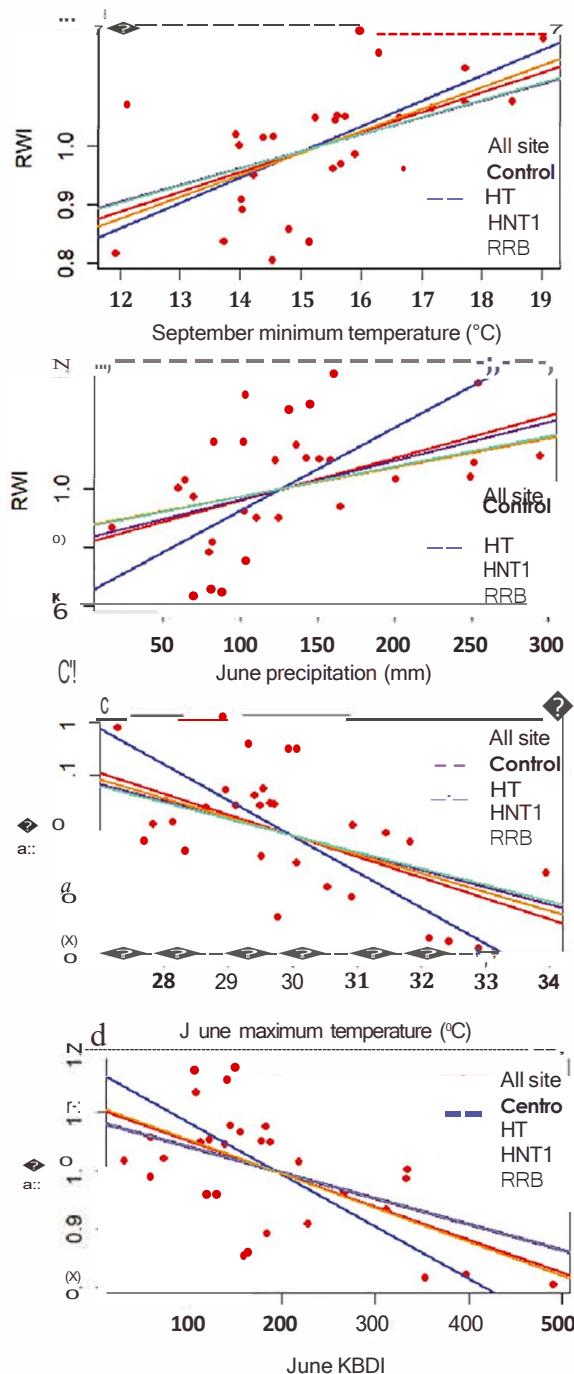
Results for LWI and RWI were highly correlated and largely tracked each other. The average R^2 for the correlation between annual wood and latewood was 0.76 and ranged from 0.47 for RRB to 0.95 for HT. Results for the correlations between weather variables and LWI were very similar to those presented for RWI (Table A2; Fig. A3).

Discussion

We examined how climate variability over 31 years, prescribed fire (none, 1-year and 4-year return interval), and stand structure (savanna and forest) affected relative changes in radial growth of post oak by establishing tree-ring chronologies across a range of stand types established and maintained by different management regimes. There are previous post oak dendrochronology studies (Johnson and Risser 1973; Blasing and Duvick 1984; Stokes et al. 1995; Clark et al. 2007; LeBlanc and Terrell 2009; LeBlanc and Stahle 2015; Prolif and Goldblum 2016) that focused on climate or recreating fire history, but our work expands and furthers our knowledge regarding potential interactions between climate and management.

Somewhat surprisingly, prescribed fire every 4 years and stand structure, i.e., savanna vs. forest, had very little interaction with climate variability impacts on RWI. In other words, the relative

Fig. 5. Relationship between standardized post oak RWI (ring width index) and (a) previous-year September mean daily minimum temperature, (b) June precipitation, (c) June mean daily maximum temperature, and (d) June KBDI (Keetch-Byram drought index). Data points are for all treatments combined. Slope lines of Control and RRB almost overlap. See Table 1 for treatment definitions. [Colour online.]



ring width growth of post oak in savanna and forest stands both increased and decreased similarly in response to weather, and prescribed fire did not influence relative ring width growth at an annual timescale. These results do not support our hypotheses related to potential management effects on RWI. Our analysis of tree-ring chronologies from the forest-grassland transition zone indicated that post oak radial growth was best correlated to

growing season length the previous year (previous-year September daily minimum temperature) and precipitation, maximum temperature, and soil moisture status during late spring and early summer of the current-year (May-July). Correlation with current-year precipitation, temperature, and KBDI support our hypothesis, but the relatively strong and consistent positive correlation with previous-year September daily minimum temperature was not anticipated.

Oaks store carbon produced during the previous year to support pre-leaf-out radial growth the following year (McLaughlin et al. 1980; Zweifel et al. 2006). All treatments showed a positive relationship between previous-year September minimum temperature and RWI. This is likely related to the length of the previous growing season as post oak foliage typically undergoes senescence in September and October. Even though leaves are still photosynthetically active into October (Torquato et al. 2020a), stand-level water use, and presumably carbon gain, decrease precipitously in September (Torquato et al. 2020b). The net effect is that cooler minimum temperatures in September likely reduce carbon gain and storage potential available for the next year's growth. Similarly, shortleaf pine RWI at the same site was influenced by October minimum daily temperature of the previous- and current-years (Adhikari et al. 2021a), which likewise indicated a positive effect of longer growing seasons, but a shift to 1 month later for the evergreen pine.

Our finding that RWI was positively correlated with late spring and summer precipitation and negatively correlated to late spring and summer maximum temperatures is similar to other studies (Uohn and Risser 1973; Stockton and Meko 1983; Stahle and Hehr 1984; Leblanc and Staln 2015; Prolie and Goldblum 2016). Leblanc and Stahle (2015) reported climate effects on radial growth of four oak species, including post oak from 55 sites spanning from Florida to Texas. They found that radial growth was strongly correlated with precipitation and negatively correlated with average maximum temperatures during the current growing season. However, among the four oak species in that study (*Quercus macrocarpa* Michx., *Q. velutina* Lam., *Q. prinus* L., *Q. stellata*), post oak had the greatest number of correlations with precipitation and temperature from the previous growing seasons or prior dominant season and these correlations were most pronounced in sites from the Southern Great Plains. We did find the previously discussed correlation with previous-year September minimum daily temperature, and that RWI of the HNT1 treatment was also correlated with previous-year's growing season precipitation at our site.

Drought reduces photosynthesis of post oak (Torquato et al. 2020a), which translates into lower overall growth. KBDI is a measure of soil moisture, which is a function of input (precipitation) and losses (evapotranspiration). Higher temperatures during the growing season increases vapor pressure deficit, which accelerates evapotranspiration (Breshears et al. 2013; Will et al. 2013) so it is not surprising that precipitation (positive), maximum temperatures (negative), and KBDI (negative) were all related to RWI. In our study, June (precipitation, KBDI, maximum daily temperature) was the month with the strongest correlations with RWI for all treatments combined and three individual treatments. June precipitation was best correlated to herbaceous growth (Adhikari et al. 2021b) and shortleaf pine RWI (Adhikari et al. 2021a) at our site, indicating the general importance of late spring weather conditions in determining productivity. At our site, May is the wettest month on average and KBDI rapidly increases in June to reach a peak in August (Fig. 1). A wet and cool June likely extends conditions of high soil moisture, which increases growing season carbon gain and current-year radial growth.

We hypothesized that post oak growing in the savanna treatment (HNT1) would be less sensitive to climate variability than those growing in closed canopy conditions (Control, HT, RRB) because decreased stand density is often correlated to greater resilience and resistance to drought (Schmitt et al. 2020). Stand

structure affects tree diameter growth (e.g., *Masters and Waymire 2012*). However, we found little difference among treatments in the response of RWI to climate variability indicating trees of all treatments are changing similarly on a relative basis due to weather. There was a shift in importance of precipitation, temperature, and KBDI a month earlier (May) for the HNfl treatment. These results were consistent with earlier work at the same site that found that oak leaf $\delta^{13}\text{C}$, an indicator of stomatal closure, suggested that trees in the HNfl treatment were experiencing greater stomatal closure than trees in the HT treatment (*Freeman et al. 2019*). Part of the reason for the lack of difference in RWI between the HNfl and forest treatments could be due to abundant root competition from herbaceous vegetation in the savanna treatment (*Feltrin et al. 2016*), which likely accounts for a larger fraction of ecosystem water use than within forest treatments. Or, it could be that the more open stand conditions in the savanna increased air movement, reduced humidity, and increased temperature, which increase vapor pressure deficit and potential evapotranspiration on a per-tree basis. There were a greater number of significant correlations between RWI and environmental variables for the open-grown HNfl treatment trees than for other treatments, which does not support reduced sensitivity of trees in the savanna treatment. The HT treatment, which started with the least and ended with the greatest basal area, did have steeper slopes between RWI and important environmental variables, which may indicate some degree of greater sensitivity of RWI to climate variability, but only in very dense stands.

The RRB treatment afforded the opportunity to determine whether periodic fire, every 4 years, caused a decrease in radial growth. We found little indication that relatively low fireline intensity, dominant season fires had an impact. In contrast, shortleaf pine at our site did show a 1-year reduction in growth when fire was applied every 2 or 3 years (*Adhikari et al. 2021a*). Given that the fires were usually conducted in late dormant season, the fires did not affect oak leaves. Rather, fire may need to be of higher intensity, with long enough residence time to damage the stem or buds to affect oak radial growth (*Dey et al. 2017*).

The purpose of separating Jatewood from annual wood was because Jatewood increment is typically related to summertime and late growing season conditions (*Lebougeois 2000; Meko and Baisan 2001; Griffin et al. 2013*) and because post oak previously exhibited poor correlation between earlywood and Jatewood (*Torbenson et al. 2016*). In our study area, annual wood and Jatewood were highly correlated among the treatments with an average $R^2 = 0.76$, which was greater than the average correlation ($R^2 = 0.28$) reported from central Texas by *Torbenson et al. (2016)*. In addition, we found almost identical influences of the climate variables on growth of both annual wood and Jatewood of post oak.

On average, a 100 mm reduction in current-year June precipitation resulted in an 7% decrease in post oak RWI. The temperature effects indicated that a 1 °C increase in previous-year September minimum daily temperature increased RWI by 3.5% while a 1 °C increase in June maximum daily temperature decreased RWI by 3.7%. Therefore, the potential effects of climate change will depend on timing of changes in precipitation (importance of late spring and early summer being) and on seasonality of temperature change, since a warmer September has the potential to compensate for a hotter late spring – early summer.

In our study, multiple regression models explained between 48% (Control) and 78% (HNfl) of the variation for RWI, which was higher than the 24% to 38% reported by *Stalile and Helu (1984)* across Arkansas, Oklahoma, and Texas, and the 15% to 54% reported by *Stockton and Meko (1983)* across Arkansas and Oklahoma. *LeBlanc and Terrell (2009)* found that climate variability explained 23% to 64% variability of radial growth of white oak (*Quercus alba L.*) of eastern North America. *Arming et al. (2013)* reported similar results to *LeBlanc and Terrell* for white oak in Ohio, USA. The generally lower total R^2 between climate variables and radial growth of post oak from other studies

could be due to confounding effects of other environmental variables, including soil properties such as coarse fragment fraction (*Iverson et al. 2008*). Previous September minimum temperature was included in models for each treatment because this did not co-vary with other variables. In contrast, some combination of late spring – early summer precipitation, KBDI, and maximum temperature was included in each model and varied depending on the covariance structure among variables.

As we hypothesized, both temperature and precipitation affected radial growth of post oak, with impacts of late spring and early summer most important. Previous-year September temperatures also had an impact, presumably due to its effect on growing season length and carbon storage for subsequent growth. We found little influence of stand structure on sensitivity of RWI to climatic variability likely due to aggressive competition from herbaceous vegetation or greater transpiration in our savanna ecosystem or possibly that trees were beyond the age where they quickly respond to growing conditions. Fire on a 4-year return interval did not affect RWI of these mature trees. While diameter growth of post oak will increase or decrease in response to management, management to reduce stand density or dormant season prescribed fire does not appear to affect the relative diameter growth of trees in response to climate variability and future droughts.

Author contributions

Each author has made significant contribution. M and RW designed study, developed methods, conducted field study, and wrote and reviewed the manuscript. M analyzed the data. RM and HA reviewed and edited the manuscript.

Funding

The study was sponsored by USDA-NIFA (grant Nos. 2018-67014-27504 and WNP00009). Additional funding was provided by Oklahoma Agricultural Experiment Station, McIntire-Stennis project No. OKLO 3151, and Oklahoma Forestry Services.

Competing interests

The authors declare that there is no conflict of interest

Acknowledgements

We thank Kaitlyn McNeil for assistance with tree-ring measurements in the laboratory. We thank the Oklahoma Department of Wildlife Conservation, in particular Jack Waymire; the numerous Oklahoma State University faculty, students, and staff; and the staff of the Kiamichi Forestry Research Station for assistance managing the study area field work.

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Appendix A

Appendix Tables A1-A2 and Figures A1-A3 appear on the following pages.

Fig. A1. Standardized oak tree-ring width index chronology for annual wood (RWI) of different treatments beginning in 1987. Note: The red smoothing line is a 5-year spline fit. Shaded area is sample size with scale on the right axis. [Colour online.]

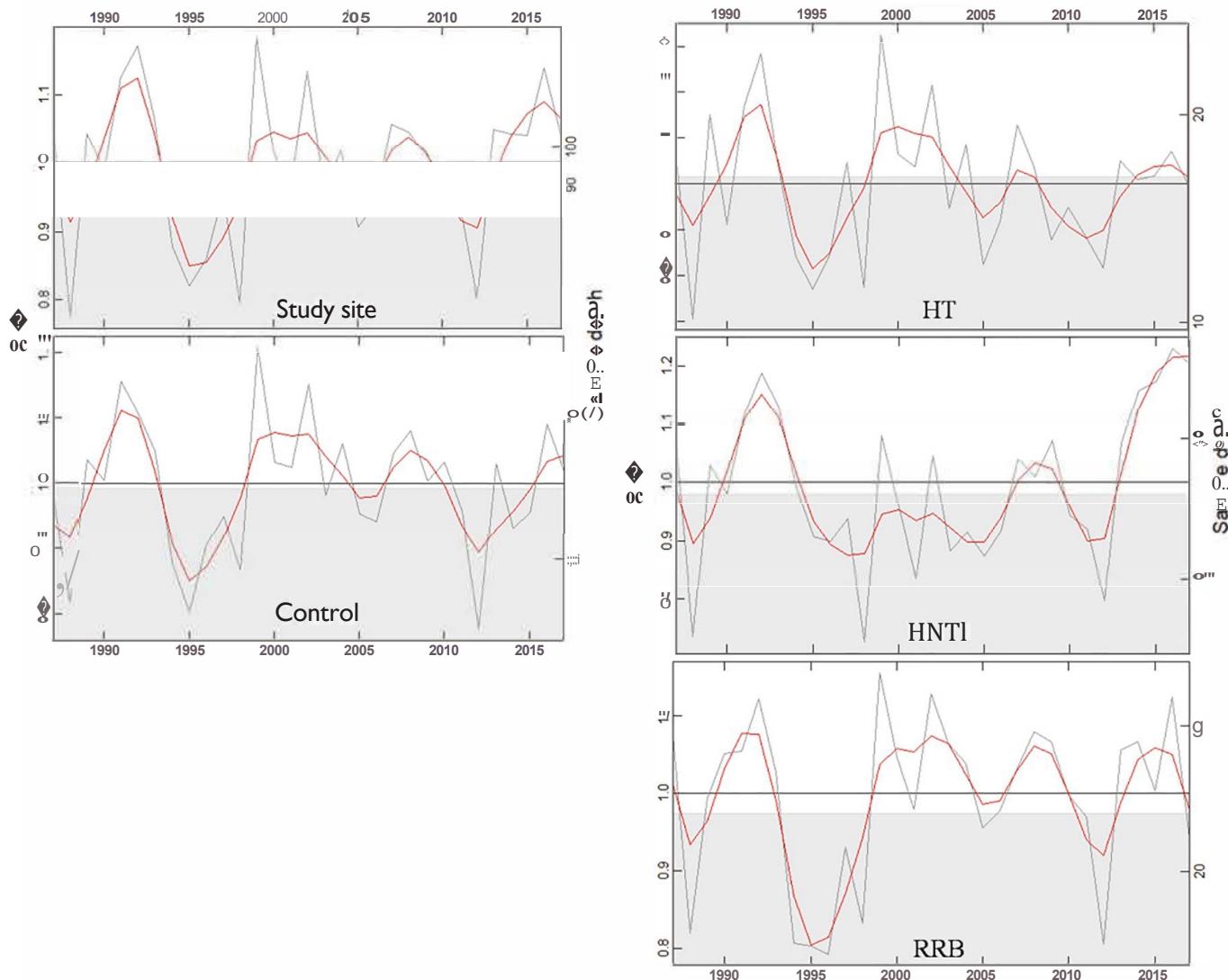


Fig. A2. Average diameter at breast height (DBH) of post oak trees for different treatments from 1987 to 2018. [Colour online.]

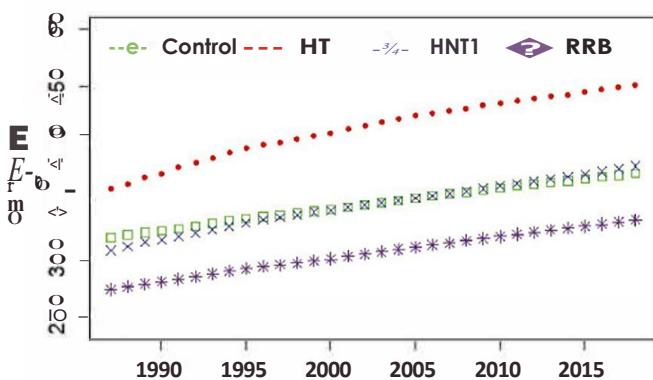


Fig. A3. Correlations of 32-year latewood (LW1) chronologies of post oak with different climate variables from different treatments. Horizontal dotted lines at $r = 0.35$ and $r = -0.35$ form a 95% confidence interval; significant correlations ($p < 0.05$). Orange, blue, and red colours in the bar graphs indicate KBDI (Keetch-Byram drought index), precipitation, and temperature, respectively. Abbreviations: Pr, previous; PPT, precipitation; T_{\min} , minimum temperature; T_{\max} , maximum temperature; Grow, growing season. All variables with one or more significant correlations are presented. [Colour online.]

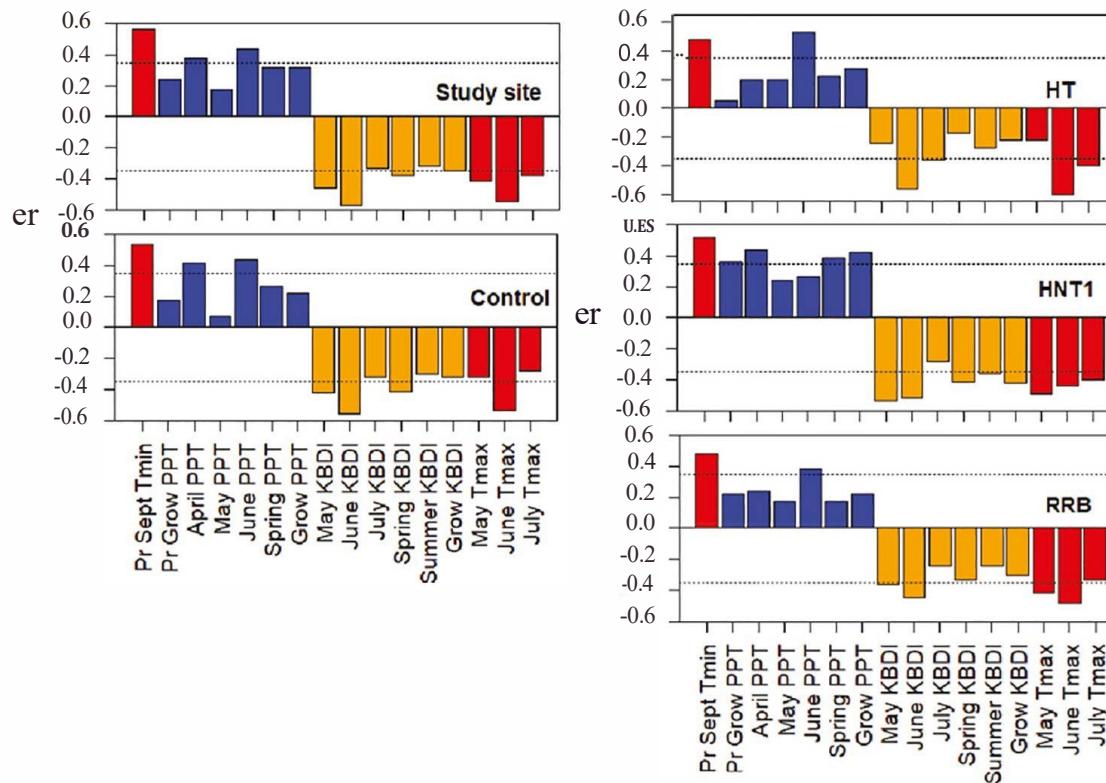


Table A1. Slope values for relationship between ring width index and climate variables for different treatment.

Site	T _{min}				PPT				T _{max}				KBDI												
	Pr Sept.	Pr Grow	April	May	June	Spring	Grow	May	June	July	Spring	Summer	Grow	May	June	July	Pr Sept	Pr Grow	April	May	June	Summer	Grow	May	June
All site	0.0340	0.0001	0.0006	0.0002	0.0007	0.0002	0.0002	-0.0007	-0.0006	-0.0003	-0.0004	-0.0004	-0.0006	-0.0339	-0.0357	-0.0207									
Control	0.0290	0.0000	0.0005	0.0000	0.0007	0.0001	0.0000	-0.0005	-0.0004	-0.0002	-0.0008	-0.0002	-0.0004	-0.0207	-0.0296	-0.0108									
HT	0.0437	0.0000	0.0014	0.0002	0.0014	0.0002	0.0002	-0.0006	-0.0009	-0.0005	-0.0008	-0.0005	-0.0007	-0.0304	-0.0613	-0.0326									
HNT1	0.0375	0.0002	0.0005	0.0005	0.0009	0.0004	0.0003	-0.0010	-0.0006	-0.0003	-0.005	-0.0004	-0.0008	-0.0284	-0.0323	-0.0284									
RRB	0.0291	0.0000	0.0006	0.0002	0.0005	0.0002	0.0001	-0.0006	-0.0004	-0.0002	-0.002	-0.0002	-0.0004	-0.0305	-0.0282	-0.0145									

Note: Grow, growing season; Pr, previous year; PPT, precipitation; T_{\min} , minimum temperature; T_{\max} , maximum temperature.

Table A2. The coefficient of determinant (R^2) for each variable to explain variation of LW1 estimated using stepwise regression model.

	Latewood								Total R^2		
	T _{min}		PPT			KBDI		T_{\max}			
	Pr Sept.	Pr Grow	April	June	Grow	Summer	May				
All site	0.32	—	0.14	0.23	—	—	—	-0.05	0.74		
Control	0.28	—	0.17	0.23	—	—	—	—	0.68		
HT	0.28	—	—	0.28	—	—	—	—	0.56		
HNT1	0.24	0.13	—	—	0.15	-0.06	-0.5	0.73			
RRB	0.27	—	—	0.15	—	—	-0.17	0.59			

Note: Negative signs were added when the relationship was negative. Pr, previous year; PPT, precipitation; Grow, growing season; T_{\min} , minimum temperature; T_{\max} , maximum temperature. See Table 1 for treatment definitions.