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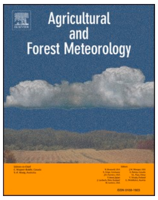

Growth response, climate sensitivity and carbon storage vary with wood porosity in a southern Appalachian mixed hardwood forest

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ABSTRACT

Disturbance regimes are often a complex suite of interacting agents that drive forest dynamics. Changes to any one or many of the agents will potentially affect future forest services such as productivity and carbon storage potential. Differences in sensitivity to disturbance events between diffuse-porous and ring-porous tree species, however, are currently unclear despite having important ecological and management implications. We used a dendroecological approach to identify whether diffuse and ring-porous species differ in their disturbance history, response to climate influence, and carbon storage potential in a mature *Quercus-Carya* stand in the Appalachian Mountains, USA. Several major abrupt growth increases indicating disturbance were identified during the history of the stand in the 1860s, 1930s, and 1960s. While both functional groups showed sensitivity to climate variables, growth reductions following drought events were more often significant for ring-porous species compared to diffuse-porous species. The decadal growth responses to drought events were similar among functional groups, and age classes, but indicated reduced growth following successive events. For the inventory year of 2015, the stand-wide aboveground live carbon content was 96.2 Mg C ha^{-1}, with 58.3 Mg C ha^{-1} captured in ring-porous species and 37.9 Mg C ha^{-1} captured in diffuse-porous species. Our results suggest that understanding how different species and functional groups respond to forest disturbance and climate variability is critical for evaluating future management scenarios and prediction of climate change feedbacks.

1. Introduction

Forests, as carbon sinks, play an important role in dampening the magnitude of global change. Climate change is expected to increase global atmospheric temperature and alter precipitation patterns in some regions, with potential to affect tree growth and species distributions (IPCC, 2014). In addition, the cumulative effects of disturbances across space and time that define disturbance regimes are projected to change, with increases in both frequency and severity that will challenge the stability of carbon stored in forests (Hurteau et al. 2019).

As climate change is predicted to increase water stress across nearly all forest types, this will have significant negative impacts on individual trees as well as whole forest dynamics (Allen et al., 2010; Anderegg et al., 2013; Brzostek et al., 2014b, 2020). Both individual and sequential drought events may have very different consequences on forest health across a global scale (Anderegg et al., 2020). Hence, understanding how both disturbance events and climate affect localized tree growth becomes more critical. Not only for quantifying ecological implications such as carbon storage and sequestration, but also for predicting economic values of commercially viable timber species that may respond differently to recent environmental changes.

Numerous interacting factors influence how trees resist and recover from natural disturbances and changing climate. At the stand-level, historical forest management may predispose forests to climatic stressors (Camarero et al., 2011). Abiotic factors such as elevation, topography and soil properties can also influence tree growth response to climate (Altman et al., 2017). Tree-level factors that may often be highly correlated such as size and age, as well as species or functional traits effect the short- and long-term responses of trees and their strategies to cope with changing conditions. For example, forest types, including broadleaf-dominated forests, appear vulnerable to increasing drought frequency, with the potential for future climate change to cause

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large-scale forest change (Choat et al., 2012; Pederson et al., 2014). To assess forest response to drought, one approach is to separate species into functional groups based on xylem anatomy, stomatal behavior and water-use: isohydric, diffuse-porous species and anisohydric, ring-porous species (Elliott et al., 2015; Hoffmann et al., 2011; Klein, 2014; Meinzer et al., 2013; Oren et al., 1999). These functional groups are defined by the physiological traits of the trees, where water use strategies may be influenced by the xylem anatomy (Meinzer et al., 2013; Sperry et al., 1994). More specifically, the groups are based on stomatal response to soilwater stress: 1) species that maintain xylem water potentials above their critical water potential level and show a high stomatal sensitivity to the vapor pressure deficit are classified as isohydric and 2) species that allow leaf and xylem water potentials to fall throughout the day and approach critical water potential levels, and that have a lower stomatal conductance sensitivity to the vapor pressure deficit are classified as anisohydric (Choat et al., 2012; Ford et al., 2011; Klein, 2014; Meinzer et al., 2013; Oren et al., 1999; Sade et al., 2012). Diffuse-porous species tend to exhibit isohydric characteristics, whereas ring-porous species correlate with anisohydric responses.

Long-term and large-scale perspectives are needed to understand the implications of changes in composition and structure of the forest and ecosystem services provided. One approach to this challenge is the use of tree rings to detect the historic assembly of the tree populations and the growth responses to disturbances of varied magnitude occurring through time. Forest reconstruction or age structure analysis, provide insight into patterns of stand development, document the timing and effects of past disturbances, and combine to define the forest's historic range of variability. Developing this context is critical for understanding the consequences of changes to contemporary vegetation patterns, such as the widespread decline in the ecological and economically important *Quercus* forests in the eastern deciduous forests of the United States (Dey 2002, 2014).

The southern Appalachian region is forecasted to experience drier summer and fall months relative to present conditions, and higher streamflow in winter with climate change (Wu et al., 2014). The vulnerability of southern Appalachian forests has likely increased with the shifting dominance from large mature and longer-lived ring-porous species (*Quercus* and *Carya*) to younger diffuse-porous species (*Acer rubrum* and *Liriodendron tulipifera)* (Vose and Elliott, 2016). As a result, carbon sequestration rates could decline and the ability of forests to serve as carbon sinks and mitigate climate change could decrease (Brzostek et al., 2014). Several studies have found that diffuse-porous species common in the southern Appalachians are more sensitive to drought compared to ring-porous species (Elliott and Swank, 1994; Elliott et al., 2015; Roman et al., 2015). On the contrary, von Allmen et al. (2015) suggest the actual radial growth rates between the two functional groups may be similar during drought. At an even finer taxonomic scale, differences in drought sensitivity have been shown among ring-porous species within the same genus where *Quercus montana* and *Q. alba* were found to be more drought resistant compared to *Q. rubra* and *Q. velutina* (Keyser and Brown, 2016). To best characterize the southern Appalachian forest response to disturbances and climate variability, examining ring- and diffuse-porous functional groups as well as species within these groups may prove the most effective approach.

Hence, we used tree-ring analysis to understand the complex disturbance history and contextualize growth rates and carbon storage of individual hardwood tree species from a mature *Quercus-Carya* stand in the southern Appalachians Specifically, our objectives were to 1) reconstruct the age distribution and disturbance history, 2) identify the climate response of physiological contrasting functional groups of trees and 3) quantify the carbon storage contributions of these functional groups. The disturbance regime of mixed-oak forests historically included frequent, small-scale disturbances punctuated by intermediate disturbances of moderate extent and frequency (Lorimer 1989). We sought to use tree growth patterns to identify how changes in land ownership, invasive species, and climate that comprised the disturbance history of the site has shaped the forest composition and structure. We hypothesize that diffuse-porous species are more sensitive to disturbance, including climate variability and non-climate related events (i.e., grow less during disturbance event years) and thus have a smaller carbon storage potential compared to ring-porous species and these differences have important implications for the ecosystem service provided by these widespread forests (Elliott and Swank, 1994; Elliott et al., 2015; Roman et al., 2015).

2. Methods

2.1. Site description

The study site (referred to as the Southern Appalachian Femelschlag Study, SAFE; 35°28′N, 82°40′W) borders the Bent Creek Experimental Forest covering 60 hectares and located within the Pisgah National Forest, North Carolina (Fig. 1). The term “Femelschlag” refers to an expanding-gap silvicultural treatment implemented at this site with an initial harvest entry in 2019. The area is within the Blue Ridge Physiographic Province of the Southern Appalachian Mountains. Geology is predominantly felsic to mafic high-grade metamorphic biotite and granitic gneisses (Hadley and Nelson, 1971). Soils are Inceptisols and Ultisols that are shallow to very deep, well drained, moderately to extremely acidic, and range in texture from coarse-loam to clay; stones are scattered on the surface of some sites (Allison and Hale, 1997). Winters are cool and relatively short, while summers are generally long and warm with average monthly minimum and maximum temperatures ranging from −3.8 to 8.8 °C in January and 16.8 to 28.5 °C in July (based on Candler 1 W, NC Station Climate Normals from 1991 to 2020; NCEI, NOAA).

2.2. Data collection and processing

A forest inventory of the site was conducted in fall 2015, to characterize the vegetation prior to implementing silvicultural treatments and to calculate carbon storage potential (described in Carbon Storage Potential section). At 72 plots, the species and diameter at breast height (DBH; cm) of all trees $>=12.7$ cm DBH were recorded in 12.6 m radius fixed area plots. Midstory trees (stems $>=1.5$ <12.7 cm DBH) were recorded in nested subplots with a 5.6 m radius. Heights were recorded for the first tree encountered in each canopy crown class.

A subset of 21 inventory plots were selected to provide a range of slope, aspect, elevation, and location across the site for the dendroecological study. Within each of these 21 plots, trees were selected to provide a representative sample of both species and size classes for the site. Ring-porous species include oaks (*Quercus alba, Q. rubra, Q. montana, Q. coccinea,* and *Q. velutina*), and hickories (*Carya cordiformis, C. glabra, C. ovalis* and *C. tomentosa*). Diffuse-porous species include yellow poplar (*Liriodendron tulipifera*) and red maple (*Acer rubrum*). For consistency, approximately 10 trees per plot (236 trees in total) were remeasured, marked, and mapped for future relocation (Fig. 1). The azimuth, distance from plot center, species and DBH were recorded.

Immediately following a planned harvest in spring 2019, 236 cross-sections were cut and collected from freshly cut stumps. Generally, if we were not able to obtain a complete cross-section from the stump due to logistical harvesting constraints, wedges were cut from the downhill side of the stump. The downhill side was used due to safety and stump accessibility limits. When pre-selected stumps contained decay or were otherwise unusable, the stump was disregarded and a new sample of the same species and similar size within the gap was selected. New measurements (azimuth, distance from plot center, species and DBH) were recorded for the new sample before harvesting. Cross-sections were air dried on site for further processing.

Each cross-section was cleaned and sanded with sandpaper increasing in fineness until ring boundaries were easily discernible. Lines were drawn onto the sample to simulate the width of a standard

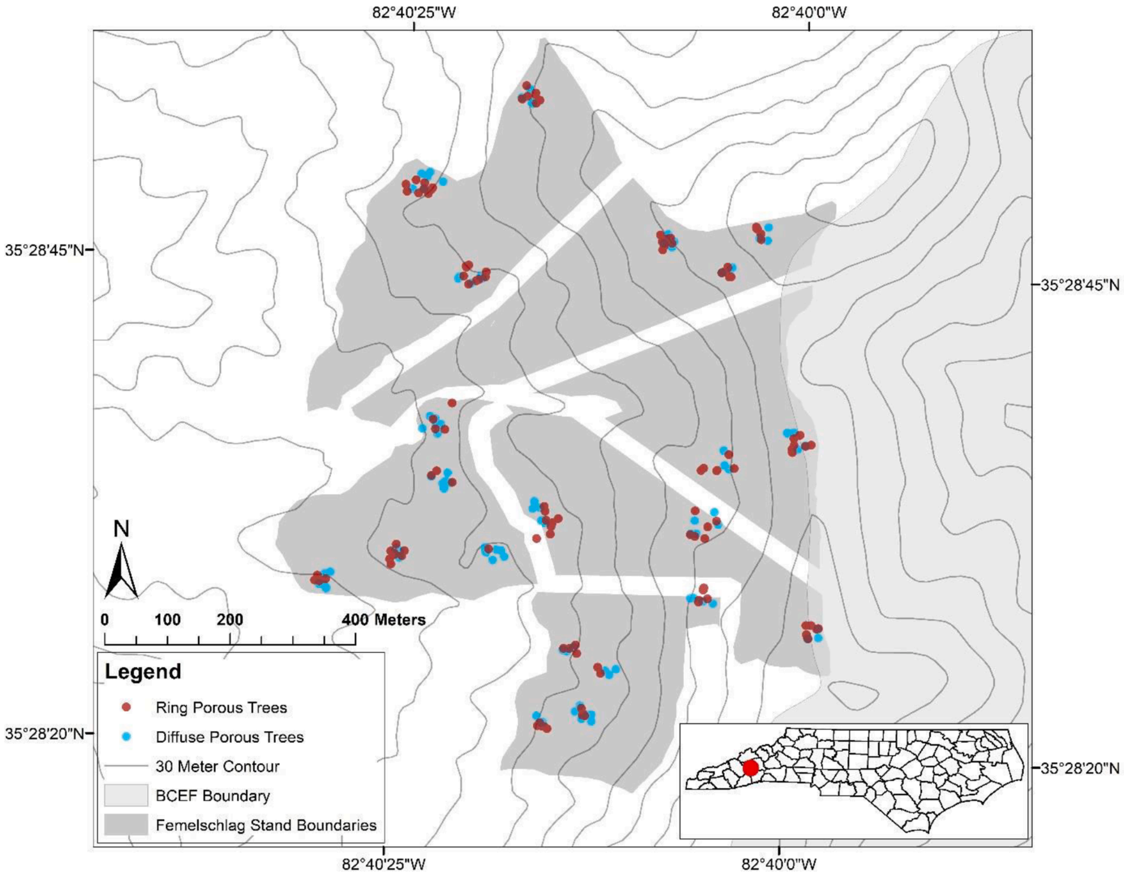

Fig. 1. Field site (the Southern Appalachian Femelschlag Experiment) is located within Pisgah National Forest, bordered by Bent Creek Experimental Forest (BCEF), within southwestern Buncombe County (red circle within inset map), NC, USA. Tree cross-sections were cut from 236 trees of two physiological groups (DP $n = 91$, RP $n = 118$) at locations across an elevational gradient.

tree core and guide measurement. Annual ring widths for each sample were measured from bark to pith using a Velmex linear encoder, stereomicroscope (Olympus), and Measure J2X software (http://www.voortech.com/projectj2x/). Annual ring widths were measured to the nearest 0.001 mm. Using stem cross-sections allowed complete measurements from outermost ring to the pith on each sample. This was followed by visual and statistical cross-dating using the software program COFECHA (Holmes, 1983). We did not use cross-sections from 27 trees due to high proportion of rot in the samples. Consequently, a total of 209 tree cross-sections were measured and cross-dated (Table 1). Ninety-one (44%) of the aged disks were from diffuse-porous (*Acer* and *Liriodendron*) and 118 (56%) were from ring-porous (*Quercus* and *Carya*) species.

2.3. Tree-ring width and basal area chronology development

A smaller subset of tree-ring series ($n = 95$ series) were selected and used for the climate-growth analyses. Selection was based on visual and statistical cross-dating accuracy (>0.25 species intercorrelation), geographic location (to maximize range of elevation and distribution across site), and length of timeseries (age) To remove non-climatic influences of long-term growth trends (e.g., competition, stand dynamics), we created a standardized index (Ring Width Index; RWI) by dividing the observed annual growth by the fitted total growth based on a 50-year spline using the dplR Package (Bunn, 2008) in R Studio (R Core Team, 2021). We acknowledge the shortcomings of detrending, primarily its influence on annual biological growth patterns (Bose et al., 2020; Zang et al., 2012). However, we chose to use this method to attempt to standardize tree growth data across species and age classes and provide a comparable set of data relative to other dendrochronological studies.

Table 1
Summary of growth, size, and age statistics by species. Mean BAI (cm2 yr-1) calculated for time period 1923–2019 (to include ≥10 samples per species).

Species	No. of trees	Age (years)	DBH (cm)	Mean BAI (cm^2 yr^{-1})	
Diffuse-porous			-	-	19.7
Acer rubrum	40	Mean	94	30.8	12.8
		Min/Max	47/121	14.7/54.4	
Liriodendron tulipifera	51	Mean	95	48.2	28.9
		Min/Max	48/121	18/80.6	
Ring-porous			-	-	26.5
Quercus alba	25	Mean	151	50	28.6
		Min/Max	91/215	25/80.6	
Quercus coccinea	11	Mean	107	42.3	24.5
		Min/Max	80/139	26.5/54.9	
Quercus velutina	9	Mean	143	55.3	27.1
		Min/Max	95/225	33.9/82.8	
Quercus montana	27	Mean	138	52.3	24.8
		Min/Max	83/202	20.2/84	
Quercus rubra	21	Mean	117	63.9	41.1
		Min/Max	79/199	28/107.7	
Carya spp.	25	Mean	125	34	12.9
		Min/Max	48/213	16.7/68.3	

Series were divided into 2 composite chronologies by functional group: diffuse-porous ($n = 30$) or ring-porous ($n = 65$). The subsample signal strength (SSS) was calculated to estimate the period with a suggested strong climate signal in site chronologies with SSS above 0.85 (Fig. S1). This metric is used to support how well a reduced number of series or trees represents the full chronology or tree sample (Wigley et al., 1984). Consequently, chronologies for both diffuse and ring-porous functional groups were developed.

Basal area increment (BAI) chronologies were calculated for each functional group to quantify the amount of biomass accumulated per year to relate growth and carbon flux at the site. We converted tree-ring width series to tree-ring area series (i.e. basal area increment) based on the diameter of the tree and width of each measured ring with the "dplR" package (Bunn, 2008). This estimated constant basal area for each tree is calculated as the median constant basal area for each biological age following methods of Biondi (1999) and Biondi and Qeadan (2008). BAI was calculated for 95 raw tree ring width series, using the same smaller subset of tree ring series used for the RWI (see previous paragraph). A Levene's test was used to evaluate interannual variation in BAI for both functional groups to test for homogeneity of variance before proceeding to a *t*-test used to compare the means between groups.

2.4. Disturbance detection

The raw tree-ring width series were used for past disturbance detection and determination of establishment periods. Establishment date was calculated by subtracting the number of growth rings from year of harvest (2019). We calculated the frequency of growth release events, i.e. the abrupt radial growth increase of trees as a reaction to improved light conditions after the death of a disturbed neighboring canopy tree or trees detection of the improved light conditions (Altman, 2020 using all 209 samples with the TRADER package (Altman et al., 2014) in R (R Core Team, 2019). We used the percent growth change method (%GC), developed by Nowacki and Abrams (1997). This method computes the percentage growth change between average radial growth over the preceding 10-year period:

$$\%GC = [(M2 - M1) / M1] * 100$$

where M1 is average growth in a 10-year period (including the target year), and M2 is the average radial growth over the subsequent 10-year period (excluding the target year). This metric is particularly useful in determining a trees' resilience, or recovery from disturbance events (Lloret et al., 2011). The minimum threshold for release is 25% growth change (increase) for moderate and >50% for major release (Nowacki and Abrams, 1997). Finally, results of establishment and disturbance reconstruction were summarized to 10-year intervals, which minimized the bias caused by the lag of tree response to disturbance events and help to identify stand wide events (Altman, 2020). Stand wide disturbance was defined as an interval with more than 60% of trees showing release.

2.5. Climate-growth relationships

Composite RWI chronologies for diffuse and ring-porous functional groups were used for analysis of climate-growth relationships to understand the effect of local drought, precipitation, and temperature on annual radial growth. Total monthly precipitation and average monthly temperature data were obtained for Buncombe County, North Carolina from 1895 to 2019 (https://www.ncdc.noaa.gov/). Palmer Drought Severity Index (PDSI) data were obtained for the Southern Mountains climate division of North Carolina, including Buncombe County, from 1895 to 2019 on a monthly basis (https://www.ncdc.noaa.gov/). The PDSI quantifies drought across space and time, providing positive values for wet years and negative values for dry years (Alley, 1984; Palmer, 1965). We evaluated the association of climate and growth by calculating bootstrapped Pearson correlation coefficients between annual growth from tree-ring chronologies (RWI) and monthly averages of PDSI, precipitation, and temperature from previous year's September to current year October as well as 3-month moving averages. Analyses were conducted with the "treeclim" R package using the 'dcc' function (Zang and Biondi, 2015) for the period 1910–2019 for each functional group separately. Significance of the relationships between growth and climate was assessed through a 1000-fold bootstrapping procedure that calculates confidence intervals of Pearson's *r* for significance testing.

2.6. Drought vulnerability

The most severe drought events were identified by ranking the annual PDSI records from 1895 to 2019. The six lowest values (5%) were below −3, which has been suggested to indicate severe to extreme drought (Palmer, 1965). The years were tightly clustered in two cases, (1925–1926 and 2007–2008) and separated by one year in the last case (1986 and 1988). The years 1985 and 1987 were also among the lowest values on record, so the years combined into one drought event (1985–1988). The mean PDSI during these 3 drought periods (1925–1926, 1985–1988, and 2007–2008) were −3.67, −2.93, and −3.58, respectively compared to the mean PDSI of 0.07, for the entire time period of available data (1895–2019). These drought periods also represented time periods with precipitation levels substantially below mean annual precipitation of 123 cm; 92 cm (−26% below mean annual precipitation), 96 cm (−22%) and 92 cm (−25%), respectively. A correlation analysis was used to test for relationships between PDSI and RWI of both functional groups.

Growth sensitivity analysis, in terms of short-term percent change in BAI, was performed on each functional group in response to the three defined drought periods. This was done by comparing the mean BAI during the drought event to the mean BAI of the same number of years prior to the drought event (i.e., if the drought was 2 years, the 2 previous years of BAI were used). Paired t-tests were used to test if the pre-drought BAI differed from BAI values during each event. To evaluate longer-term growth responses (10 year response) to the drought events, we compared BAI 10-years before and after the individual extreme droughts using the treeclim R package (Zang and Biondi, 2015). An analysis of covariance was used to evaluate whether the means in BAI 10 years post drought differed across levels of specific drought event, age class and functional group or species group while controlling for the covariate of pre-drought BAI. Both growth sensitivity analysis and long-term growth response analysis are key in understanding tree resilience after disturbance, as well as resistance to current disturbance events (Lloret et al., 2011).

2.7. Carbon storage potential

Species and stand level carbon biomass pools were calculated using the site inventory data ($n = 72$ plots) and the Southern Variant of the Forest Vegetation Simulator (FVS; Keyser, 2008). The Forest Vegetation Simulator is an individual-tree, distance-independent, forest growth and yield model used to predict changes in forest vegetation based on specified disturbance or management regimes (Dixon, 2002). Model inputs included variables measured during the forest inventory (Section 2.1). Biomass, expressed as dry weight, was assumed to be 50 percent carbon for the total aboveground live pool modelled in FVS (Hoover and Rebain, 2010). Aboveground live tree carbon (ATC) values (Mg C ha^{-1}) were summarized by species and represent stand wide carbon storage values.

Annual carbon storage (Mg C ha^{-1} year^{-1}) was estimated for each functional group using the 2015 inventory. The carbon accumulated in each species was estimated by applying the proportion of BAI (modelled in Section 2.3) to basal area, to the carbon stored in each species in 2015. These rates were summed by functional group.

3. Results

3.1. Tree-ring chronologies

Quercus alba had the oldest mean age (151 years) with ages ranging from 91 to 215 (Table 1). Several other *Quercus* sampled provided series spanning over 200 years. *Acer* and *Liriodendron* were younger than the ring-porous species, with average ages of 94–95 years and maximum ages of 121 years. The subset selected for further analysis had an average series intercorrelation of 0.39, with individual species ranging from 0.25 to 0.46 (for *Carya* spp. and L. *tulipifera*, respectively) reflecting the level of difficulty of cross-dating the different species (Table S1).

The mean chronologies of BAI from all cored trees (Fig. 2a) illustrates the year-to-year variability in biomass accumulation for the functional groups with both groups, including a mix of ages, exhibiting overall positive growth trends through time (1920–2019). Biomass increment peaked in 1969 for ring porous species and three decades later (2000) for diffuse porous species. The Levene test confirmed the interannual variation in BAI series from 1923 to 2019 was similar for functional groups ($p = 0.42$). However, the mean BAI was significantly different between groups ($t = 4.9$, $p < 0.001$), with the mean BAI of ring-porous species (26.5 ± 0.99 cm^2 yr−1) greater than that of diffuse porous species (19.7 ± 1.1 cm^2 yr^{-1}). BAI of ring porous species ranged from 12.9 to 41.1 cm^2 yr^{-1}, with *Quercus rubra* having the highest mean BAI of this group (41.1 ± 1.79 cm^2 yr^{-1}). Diffuse-porous species ranged from 12.8 cm^2 yr^{-1} for *A. rubrum* to 28.9 cm^2 yr^{-1} for L. *tulipifera*. Functional group tree ring width chronologies were similar to one another and displayed declines during the 3 drought periods (Fig. 2b).

3.2. Disturbance detection and establishment

We identified 932 individual growth release events across the history of the stand, with 654 fitting the criteria for major releases and 278 for minor releases. Several stand wide release events (>60% of trees showing a release event) were detected (Fig. 3a). The first event occurred during the 1860s, where 77% of sampled trees showed either a major (58%) or moderate (19%) release event. The next stand wide event was detected during the 1930s (with relatively large increases from 1932 to 1935), when 80% of sampled trees showed either a major (66%) or moderate (14%) release event (Fig. 3a). The last stand wide release occurred during the 1960s (with increases from 1965 to 1968), where 76% of sampled trees showed either a major (62%) or moderate (14%) release event (Fig. S2).

The establishment timelines of both functional groups exhibit similar patterns, with the ring-porous species ranging in establishment dates from 1795 to 1971 and diffuse-porous species establishment dates ranging from 1898 to 1972 (Fig. 3b). Establishment peaked early in the 20th century, with 49.5% ($n = 45$) of the diffuse-porous trees and 36.7% ($n = 44$) of the ring-porous trees establishing during this period from 1910 to 1930. An establishment pulse ($n = 9$, 10%) of diffuse-porous trees occurred simultaneously with a release event occurring in the 1960s.

3.3. Climate-growth analysis

Radial growth (represented by RWI) of both ring and diffuse-porous species was most strongly related to the PDSI as opposed to temperature or precipitation individually (Fig. 4; Table S2). Growth of both functional groups exhibited a strong positive relationship with the PDSI during the previous fall and early winter (September–January). Ring-porous species also showed significant positive correlations with PDSI values throughout the growing season (Fig. 4). Diffuse-porous species had weaker, but still positive correlations with PDSI and temperature during the growing season. Growth of ring-porous species showed a significant positive relationship with June-August and October temperature. A negative relationship between growth of diffuse-porous species and April precipitation was the only significant relationship detected with precipitation for both functional groups.

3.4. Drought vulnerability

Both functional groups exhibited a trend for declining growth in response to drought, however only ring-porous species showed a significant growth reduction (Table 2). Drought induced significant growth declines in 1985–1988 and 2007–2008 for the ring-porous species ($p<0.001$ for both events). By the last drought event (2007–2008) investigated, the diffuse-porous species sensitivity was nearly significant ($p = 0.09$). The magnitude of the growth reductions was greater for the ring-porous species relative to the diffuse-porous, with ring-porous species decreasing 4, 19 and 18% for each event and diffuse-porous species decreasing 1, 6 and 11% (Table 2). Drought had a stronger effect on radial growth with each subsequent drought period.

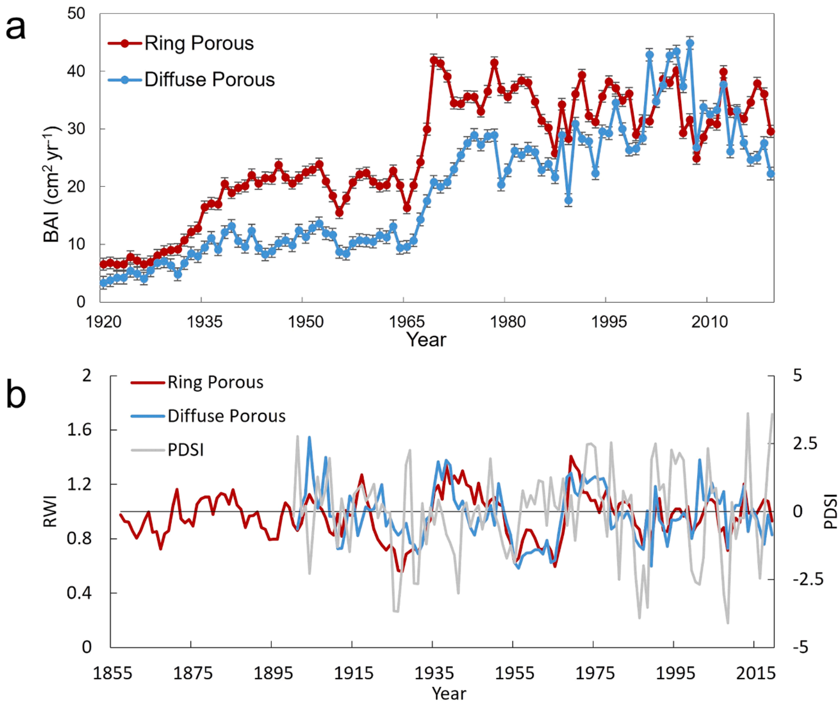

Fig. 2. (a) Mean chronologies of BAI (left y axis) for diffuse and ring-porous species (sample sizes appear in Table 1). (b) Standardized and detrended ring width index chronologies for diffuse and ring-porous species are compared with the Palmer Drought Severity Index (PDSI) for 1855 – 2019.

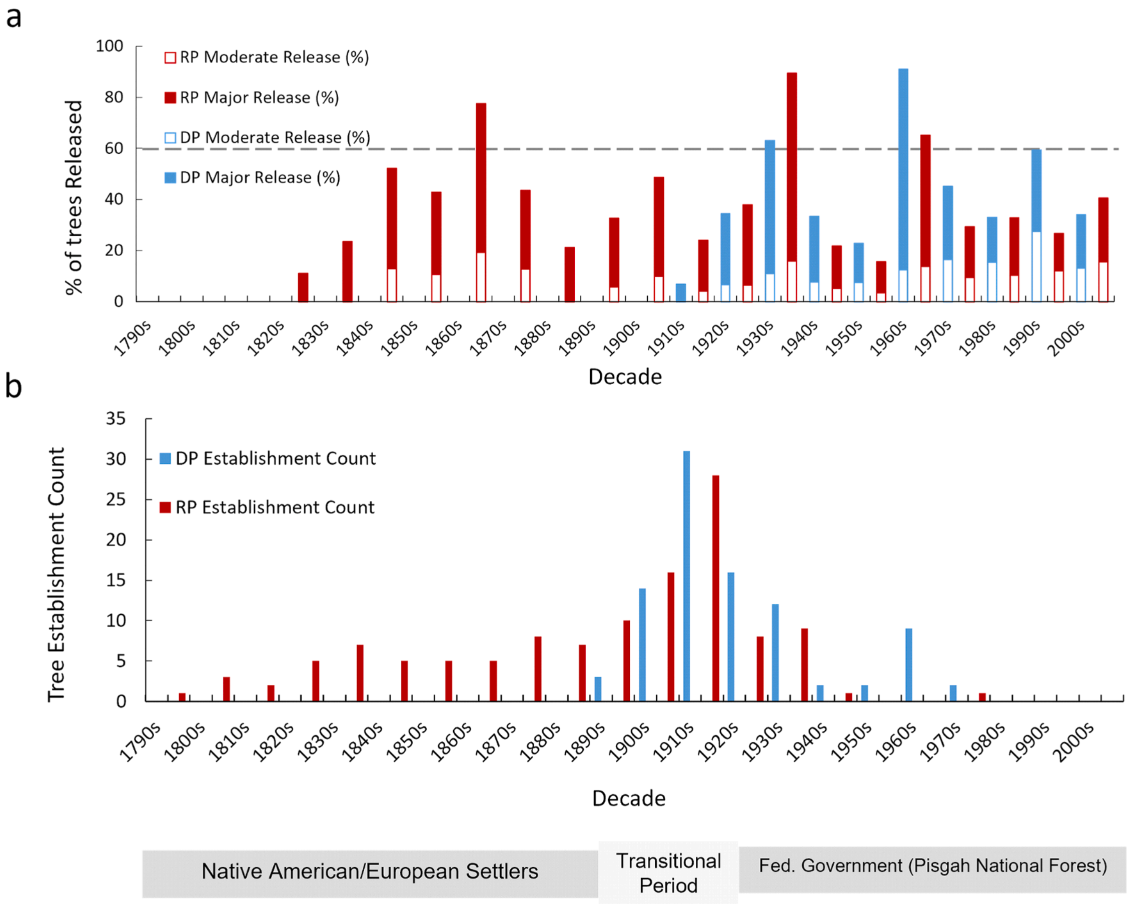

Fig. 3. (a) Stand release analysis showing both moderate and major release events from 1820 to 2010 by decade for ring-porous (RP) and diffuse-porous (DP) species. We used a 60% threshold to indicate that an event was standwide. (b) Stand establishment timeline, showing establishment year for each sample tree. Also displayed is site ownership over time; from Native American and European settlers to ownership by the federal government. As the stand transitioned ownership, a large portion of sampled trees were able to establish.

The mean decadal growth following drought events differed by functional group, even after taking prior growth rates into account (disturbance event P value = 0.05, pre-drought growth $P < 0.0001$) (Table S3). Growth following the third drought event in 2007–2008 was significantly lower than growth following the second drought event, with mean 10 yr growth of 22.7 + 1.5 and 26.5 + 1.5 cm^2 yr^{-1}, respectively (P value for difference = 0.01). For all three drought periods, ring-porous species showed a pattern for greater growth following the drought compared to diffuse-porous species, though statistically borderline (ring-porous = 26.1 + 1.6 versus diffuse-porous = 23.2 + 1.5 cm^2 yr^{-1}, P value = 0.1). Growth patterns were not different among age classes (P value= 0.8) (Fig. 5).

3.5. *Carbon storage potential*

At the species level, L. *tulipifera* represented the largest ATC value at 24.75 Mg C ha^{-1} followed by *Q. rubra* at 20.14 Mg C ha^{-1} and *Q. montana* at 19.18 Mg C ha^{-1}. Diffuse-porous species represented approximately 40% (37.9 Mg C ha^{-1}) of the ATC across the stand while ring-porous species represented approximately 60% (58.3 Mg C ha^{-1}) of the ATC across the stand for the sampled species (Table 3). Based on the 2015 inventory, the mean annual ATC storage rate was 1.5 Mg C ha^{-1} year^{-1} for ring-porous species and 2.3 Mg C ha^{-1} year^{-1} for diffuse-porous species.

4. Discussion

4.1. *Climate-growth relationships*

Comparison of tree growth, measured as RWI or BAI, between functional groups did not confirm our hypothesis that diffuse-porous species are more sensitive to and negatively affected by extreme drought events. Tree growth responses across both functional groups were rather uniform across age classes for each species group (Fig. 5). This suggests BAI response to drought was not a function of tree age as much as the physiology of individual species when comparing tree-level determinants of drought response (Martinez-Vilalta et al. 2011). Perhaps the water relations strategy of plants is a better predictor of their response. It would follow that ring-porous species are more sensitive to short, intense drought events while diffuse-porous species are more sensitive to moderate, long drought events (Klein, 2014). The correlations between RWI and PDSI, temperature, and precipitation across the longest available time period (1910–2019) for diffuse-porous species suggests that, although they are sensitive to climate variability, the growth-climate relationships were not significantly different from ring-porous species (Fig. 4).

Growth had the strongest relationship with PDSI, which is consistent with other literature indicating drought as one of the strongest predictors of tree growth (Anderegg et al., 2013; Anning et al., 2013; Boisvenue and Running, 2006; Chen et al., 2012; Elliott and Swank, 1994; Pederson et al., 2012). When examining functional group response to climate-driven disturbances (i.e. the three most severe droughts available on record), two of the three investigated drought

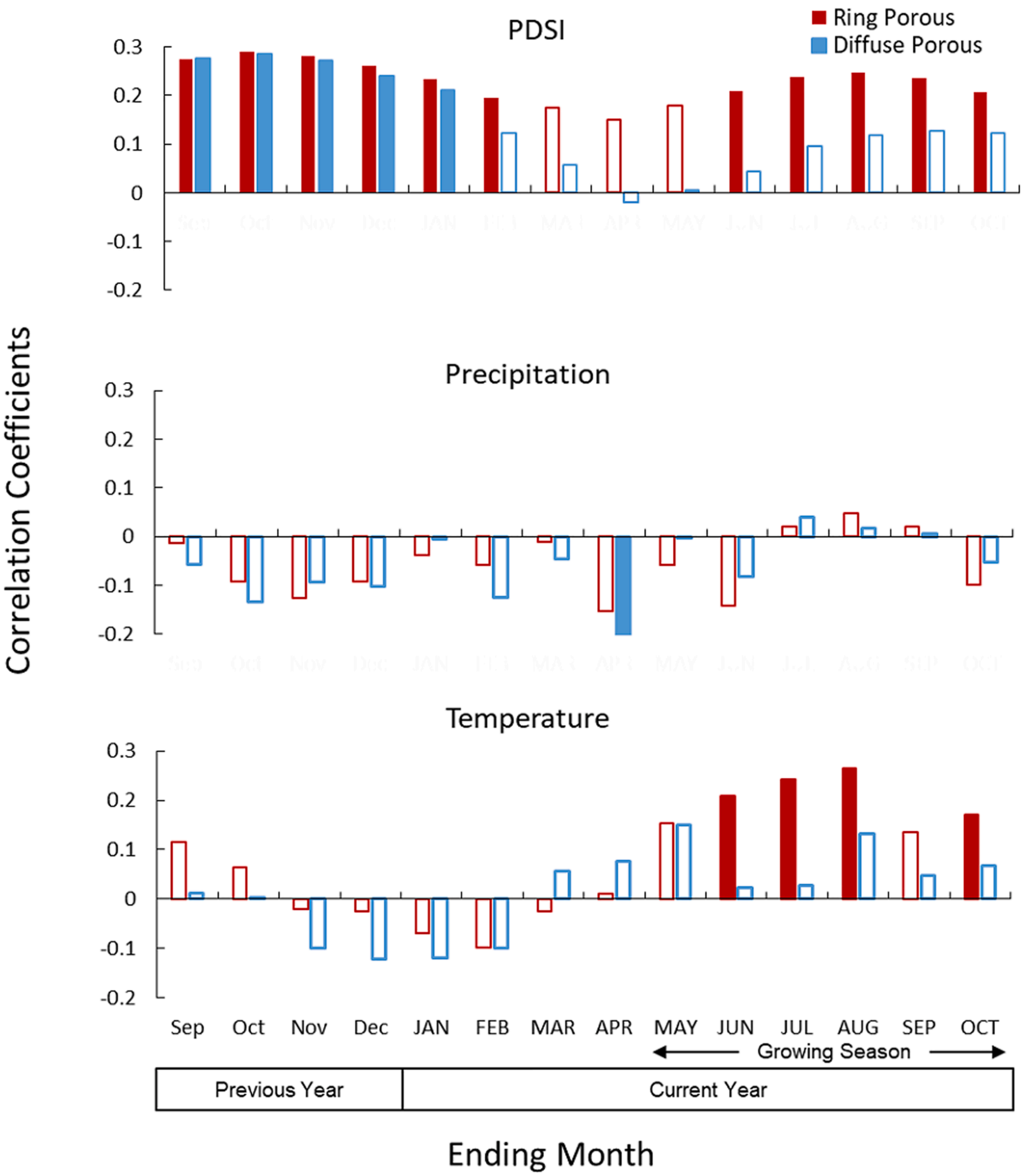

Fig. 4. Correlation coefficients (Pearson's *r*) for diffuse and ring-porous species groupings for the relation between RWI and PDSI, precipitation and temperature in the observation period 1923–2019. Correlations are between current year growth and a 3-month aggregated climate variable. Aggregates are displayed using the ending month of the 3-month period of analysis, (i.e., "JUL" represents average for May, June and July values). Significant correlations (shown as solid bars) are shown if $p<0.1$.

Table 2

Growth changes during identified drought events calculated separately for wood functional groups. Average PDSI was calculated as the mean of monthly values for the multi-year drought events and compared with the average of the same number of years prior to the period to produce the percent change in PDSI. Mean BAI pre-drought and during the drought period was calculated for each series and the growth differences were tested using a paired *t*-test. The percent change is from pre- to during drought growth.

	PDSI			Ring-porous				Diffuse-porous				
	Average	Change	*n*	Pre	Drought	Change	*P* value	*n*	Pre	Drought	Change	*P* value
Drought years		%		BAI cm^2 yr^{-1}	%			BAI cm^2 yr^{-1}	%			
1925–1926	−3.7	16,200	62	7.0	6.7	−4	0.28	17	4.8	4.7	−1	0.42
1985–1988	−2.9	1291	65	38.1	30.9	−19	<0.001	30	26.0	24.3	−6	0.26
2007–2008	−3.6	61,624	65	35.6	29.1	−18	<0.001	30	40.4	35.8	−11	0.09

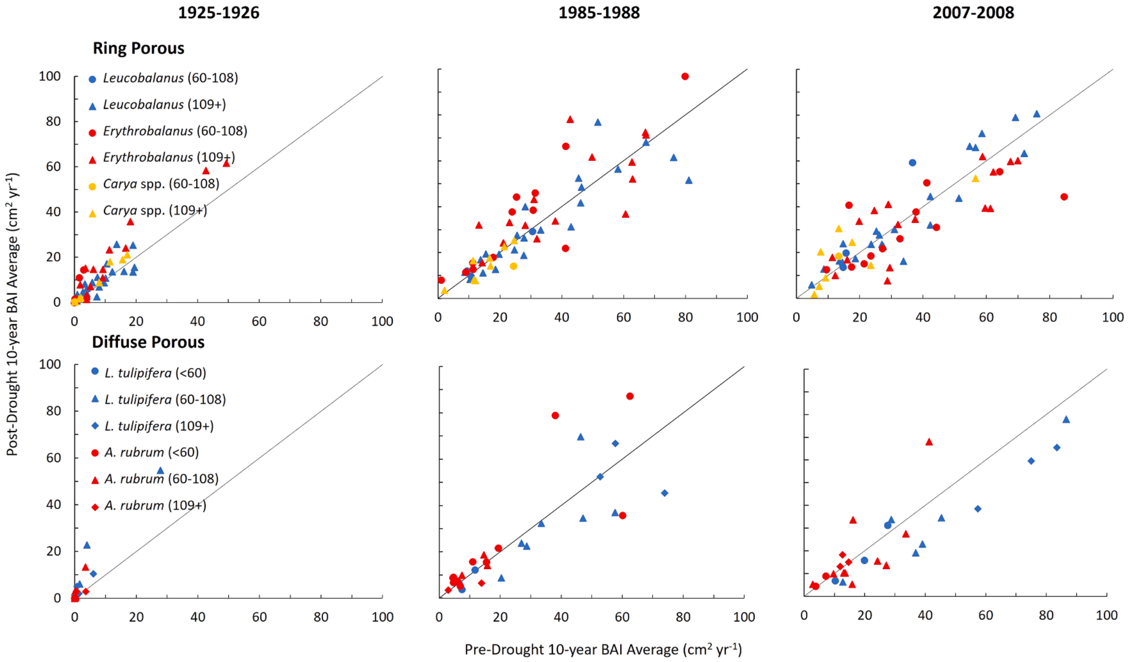

Fig. 5. BAI averages for 10-year periods before and after the 3 major droughts (1925–1926, 1985–1988, and 2007–2008). Species are sorted into the white oak group (*Leucobalanus; Q. alba* and *Q. montana*), red oak group (*Erythrobalanus; Q. rubra, Q. coccinea*, and *Q. velutina*), hickory (*Carya* spp.), tulip poplar (L. *tulipifera*), and red maple *(A. rubrum*) with ring-porous species displayed on the upper panel and diffuse-porous species displayed on the lower panel. Age classes are separated into 3 establishment clusters: after 1960 (ages <60), between 1911 and 1959 (ages 60–108), and pre-1910 (ages 109+). The line is for reference of a 1:1 relationship. An ANCOVA on these data indicated pre-disturbance growth strongly influenced post-drought growth patterns ($p<0.0001$) and mean post-drought growth was significantly lower following the 2007–2008 drought than the prior event.

Table 3

Density, basal area, and Aboveground Total Carbon values for all species across SAFE site ($n = 72$ plots). ATC values represent stand wide aboveground carbon on a per hectare basis. Trees >=12.7 cm DBH were recorded on 12.6 m radius plots, and midstory trees (stems >=1.5 <12.7 cm DBH) were recorded on nested subplots with a 5.6 m radius. Rows in bold represent species of focus in this study.

Species	Density (Stems ha^{-1})	Basal Area (m^2 ha^{-1})	ATC (Mg C ha^{-1})
Liriodendron tulipifera^{DP}	**123**	**10.41**	**24.75**
Quercus rubra^{RP}	**38**	**6.21**	**20.14**
Quercus montana^{RP}	**68**	**7.59**	**19.18**
Acer rubrum^{DP}	**428**	**5.85**	**13.18**
Quercus alba^{RP}	**17**	**3.07**	**8.14**
***Carya* spp.**^{RP}	**63**	**2.02**	**7.02**
Oxydendrum arboreum	115	2.77	6.18
Quercus coccinea^{RP}	**6**	**1.14**	**2.93**
Betula lenta	78	0.69	1.39
Fraxinus americana	36	0.55	1.28
Quercus velutina^{RP}	**13**	**0.49**	**1.11**
Nyssa sylvatica	31	0.48	1.03
Robinia pseudoacacia	3	0.26	0.79
Magnolia spp.	22	0.18	0.42
Cornus florida	33	0.13	0.17
Acer negundo	47	0.10	0.17
Magnolia acuminata	1	0.06	0.15
Tsuga spp.	12	0.11	0.13
Carpinus caroliniana	1	0.02	0.04
Ilex opaca	13	0.01	0.04
Sassafras albidum	26	0.01	0.02
Total	**1174**	**42.15**	**108.23**

RP = Ring-porous.
DP = Diffuse-porous.

events (1985–1988 and 2007–2008) showed ring-porous species with significant growth differences before and during the drought (Fig. 2a, Table 2). During the most severe drought on record (2007–2008), diffuse-porous species showed an −11% change in growth from pre-drought to drought years ($p = 0.09$) while ring-porous species showed an −18% change in growth over the same period ($p < 0.001$) (Table 2). This contrasts previous studies that show diffuse-porous species are more sensitive to climatic extremes (Elliott et al., 2015; Oren et al., 1999) than ring-porous species. Explanations for why these results differ from previous studies may be due to site-specific differences in soil, topography, and local precipitation (Anning et al., 2013; Novick et al., 2022). Another site-specific condition that may influence differences in functional group response to disturbances is groundwater availability, which is in part determined by local precipitation, soil drainage, and rooting depth levels (Fan et al., 2017; Mackay et al., 2020; McLaughlin et al., 2020). Additionally, the range of age and size of trees included in the studies may have differed which would introduce variability in the potential vulnerability of the trees to drought (Bennet et al. 2015; Serra-Maluquer et al., 2018; Zang et al., 2012). Recent broad-scale studies indicate that environmental factors are the dominant drivers explaining drought sensitivity as opposed to individual species traits such as water uptake efficiency (D'Orangeville et al., 2018; Gazol et al., 2017; Novick et al., 2022).

4.2. Disturbance and establishment analysis

The pronounced peaks in tree establishment during the ownership transition time period (1910–1930) for the stand is particularly striking and highlights the impacts of different forest managements. Early literature chronicles the frequent burning and harvesting of this area before federal protection (Ayres and Ashe, 1905; Flatley et al., 2013; Gragson and Bolstad, 2007; Nesbitt, 1941). Land management practices by the Native Americans and early European settlers are reflected in relatively even ring-porous species establishment throughout the 1800s and few long-lived diffuse-porous species. In contrast, after the area was federally protected in 1914 as the Pisgah National Forest, this forest developed with less anthropogenic interference (e.g., grazing, biomass extraction, subsistence living). This switch to less intensive management activities reduced opportunities for the establishment of the fire and disturbance adapted ring-porous species and created conditions conducive to the establishment and recruitment of primarily diffuse-porous species. These patterns are consistent across the region (Abrams and Copenheaver, 1999; Hutchinson et al., 2008)

The 1860s time period was dominated by major growth releases. Historical records of past disturbances extending back to the 1860s are limited though, complicating the confirmation of possible causes of detected releases preceding 1860. However, we suggest that selective timber harvesting (i.e., high-grading), along with land clearing and domestic livestock grazing common throughout the area during this time period may have affected tree growth on the site during this time (Ayres and Ashe, 1905; Nesbitt, 1941). The large release during the 1930s is likely the result of the sudden and widespread chestnut (*Castanea dentata*) mortality in the stand (Butler et al., 2014). American chestnut was a dominant species in the southern Appalachians through the early 20th century (Paillet, 2002). The invasive chestnut blight, caused by the fungus, *Cryphonectria parasitica*, entered the southern Appalachians and western NC in the 1920s-1930s (Elliott and Swank, 2008; Gravatt and Marshall, 1926). Chestnut mortality stretched over the next several decades until the species existed only in the understory as saplings (Elliott and Swank, 2008). Climate-growth influences are extracted through stand release analysis and knowledge of local disturbances that have affected stand growth (Camarero et al., 2011; Pederson et al., 2014). While it is difficult to attribute the specific effect the chestnut blight had on remaining trees in this stand, the temporal overlap suggests that disturbances such as this may also have influenced radial tree growth in addition to past droughts (Van de Gevel et al., 2012). Few studies have directly linked the effects of drought on tree pathogens (Kolb et al., 2016). Possibly, the major drought event in the late 1920s led to bark cracks and wounds in the stressed trees that were required for entry of the necrotrophic pathogen, *C. parasitica* (Roane et al., 1986). Alternatively, the drought may have negatively affected the pathogen due to reduced moisture availability. In addition to the chestnut blight, a severe ice storm was documented to have occurred in winter of 1932 with reported tree mortality throughout western North Carolina (Abell, 1934). These combined disturbances and subsequent tree mortality likely allowed previously inaccessible water, nutrients, and light to be accessed and utilized by the remaining trees studied here (Altman 2020).

A stand wide release event occurred during the 1960s, and coincides with a decline in radial growth in *Quercus* species throughout the southern Appalachians that has been reported elsewhere during the 1950s and 1960s (Phipps and Whiton, 1988; Tainter et al., 1984). In addition, the climate data for Buncombe County, NC indicates below average precipitation for 1950–1956 and for four years in the 1960s (1963, 1965, 1968, and 1970). Such prolonged periods of reduced precipitationeffectively stunted growth across this stand, potentially leading to drought related mortality reported in other parts of the region (Elliott and Swank, 1994; Klos et al., 2009). Hence, we suggest that drought related mortality led to a reduction in competition and together with dissipating drought conditions this resulted in a stand-wide growth release.

The releases in the 1990s are likely in response to wind events, another natural disturbance agent important to the region. Several studies have quantified and analysed the effect that historical hurricanes have had on the creation of canopy gaps in the southern Appalachians (Clinton and Baker, 2000; Greenberg and McNab, 1998; McNab et al., 2004). Thirty wind caused gaps across a 2400 ha study site in the Southern Appalachians (adjacent to the site used in this study) were identified following Hurricane Opal (category 4) in 1995 (McNab et al., 2004). Other studies in this area related to Hurricane Opal suggest that high-intensity wind events can have substantial influence on forest structure and species composition (Greenberg and McNab, 1998). We expect other growth releases may be consequences of the frequent storm and wind-related disturbances common to the region.

4.3. Carbon storage implications

Diffuse-porous species comprised 37.9 Mg C ha^{-1} while ring-porous species comprised 58.3 Mg C ha^{-1} of the carbon storage potential for this mature mixed hardwood forest. While cross-sections were not obtained for every species present in the stand, the subset used in this study represents approximately 90% of the total aboveground live carbon for the stand, with the remaining 10% stored in midstory and less dominant species including *Oxydendrum arboreum, Fraxinus americana,* and *Robinia pseudoacacia.* In total, the SAFE stand represented 108.2 Mg C ha^{-1}. The carbon storage potential of these mixed forests reflects the individualistic responses exhibited by species and will therefore continue to change with future climate and compositional shifts.

The difference in BAI between diffuse and ring-porous species have direct implications for carbon storage potential. Other studies have compared different forest types and species and their respective carbon storage potentials, noting that understanding ecological and site conditions are critical in interpreting any ATC results (Nabuurs and Mohren, 1995). Previous studies in the region have reported ATC values of 108.7 Mg C ha^{-1} across several southern Appalachian forest stands 30 years post-thinning (Keyser and Zarnoch 2012) and values ranging from 132 – 174 Mg C ha^{-1} from stands in Great Smoky Mountains National Park along an elevation gradient (Moore, et al. 2012). ATC rates of 1.5 Mg C ha^{-1} year^{-1} for ring-porous species and 2.3 Mg C ha^{-1} year^{-1} for diffuse-porous species represent the carbon accumulated in one year (2015). These very different rates reflect variability in the density, size and age of the two functional groups. Currently ring-porous species, with a mean diameter of 49.6 cm, represent a larger portion of stand biomass than the diffuse-porous species (mean diameter of 39.5 cm). The climate analysis suggests that understanding stand composition will be critical in predicting how carbon storage is impacted by future drought events.

Predicting future species composition on the site can be informed by current models and observations of compositional shifts in southern Appalachian forests (i.e., mesophication), with changes in species altering ATC storage potentials. As diffuse-porous species become more common and ring-porous species (mainly *Quercus* spp.) decline due to poor regeneration and recruitment (Fei et al., 2011), carbon storage capacity of the forest may increase in the near term since diffuse-porous species store up to double the amount of carbon that dominant ring-porous species achieve. This is supported by research showing shade-tolerant, diffuse-porous species persist in the understory and eventually out-compete the canopy-dominant, ring-porous species (Abrams, 1998).

As climate change continues to influence forests on a global scale, tree growth responses will be an important factor in understanding the future potential for carbon storage. Drier summer and fall months along with higher winter streamflow are predicted for the southern Appalachians (Wu et al., 2014). This increase in precipitation may lead to higher levels of soil erosion and deterioration of soil quality (Hoomehr et al., 2016). These changes, along with warming-induced stress, may lead to a decrease in forest tree growth and the ability to sequester carbon even with increased atmospheric CO_2 (Brzostek et al., 2014b; Silva and Anand, 2013).

5. Conclusions and management implications

In general ring porous species were older and larger, with greater mean basal area increments than the diffuse porous species that have established only in the last century following changing land ownership and disturbance regimes. These patterns equate to ring porous species having a larger biomass carbon stock and storage potential on the site. The structure and composition of this site is one that can be extended to millions of hectares of the mixed oak forest type dominant across the southern Appalachian Mountain region.

We found evidence of significantly greater short-term growth declines for ring porous species relative to diffuse porous responses and the magnitude of the decline increased with subsequent drought events. However, in the decade following drought events, ring porous species grew significantly faster than diffuse porous species. These findings add to a number of studies reporting inconsistent evidence that forest growth responses can be predicted consistently by wood anatomy.

Our study suggests that a multitude of factors were at play in determining annual growth rates on the site, including droughts, insect and disease outbreaks, and local land management practices. The complexity of tree- and stand-level factors interact with climate to influence the short- and long-term growth responses. These legacy effects of drought and disturbance along with the continuing mesophication of the southern Appalachians in response to changes in land use and management has shiftrf forest composition and structure. For hardwood forest management in the southeastern USA and beyond, understanding species composition and relative biomass values will be critical in predicting how forests respond to future droughts, hurricanes, and insect or disease outbreaks.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2023.109358.

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