

## Drought-induced Growth Response of Longleaf Pine in the Alabama Fall Line Hills

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**Abstract** - Knowledge of tree-growth response to extreme climatic events, such as drought, is useful for forest managers to model the effects of future disturbances, and to develop management plans that mitigate the detrimental impacts. We analyzed the effects of an exceptional drought on *Pinus palustris* (Longleaf Pine) radial growth in the Alabama Fall Line Hills, based on site conditions and tree age. Results indicated that radial-growth response to drought was not influenced by site condition as we initially hypothesized, but was influenced by tree age. Management for resiliency to disturbance in Longleaf Pine ecosystems should consider the complexity of individual tree-growth response as a function of age and growing conditions.

### Introduction

Moisture availability is often a limiting factor in forest productivity. Projected increases in global temperature are expected to coincide with more frequent and severe drought events in the southeastern US (Seager et al. 2009, Walsh et al. 2014). Prior studies have analyzed the relationships between climate and radial growth in *Pinus palustris* Mill. (Longleaf Pine) woodlands (Bhuta et al. 2009, Devall et al. 1991, Foster and Brooks 2001, Henderson and Grissino-Mayer 2009). However, growth response of Longleaf Pine to exceptional drought is poorly understood. Little is known about the influence of growing conditions (e.g., stand density) on the growth response of Longleaf Pine to drought, and the same is true for most tree species; yet, this understanding is important for the development of forest-management systems in a changing climate.

Longleaf Pine woodlands are one of the most endangered forest ecosystems in the US (Noss et al. 1995). It is estimated that Longleaf Pine occupied ~37 million ha in the eastern US prior to European settlement (Landers et al. 1995). Agricultural clearing, industrial logging, and fire suppression reduced the distribution of this forest type to less than 3% of its original range (Frost 2007, Jose et al. 2007). Fire-restored Longleaf Pine-dominated woodlands are typically characterized by widely spaced canopy trees, a relatively open midstory, and one of the most diverse herbaceous layers outside of the tropics (Jose et al. 2007, Peet 2007). The structure and composition of Longleaf Pine woodlands is critical habitat for many threatened and endangered species such as *Leuconotopicus borealis* Vieillot (Red-cockaded Woodpecker; Brockaway and Lewis 1997). Restoration of Longleaf Pine woodlands is hypothesized to promote resiliency to future disturbances, including

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extreme climatic events that are expected to become increasingly common (Easterling et al. 2000, Meehl et al. 2007). Johnsen et al. (2009) found that Longleaf Pine growing in restored stands (reduced tree density and a prescribed fire program) were more resistant to windthrow during Hurricane Katrina than *Pinus elliotii* Englem. (Shortleaf Pine) and *Pinus taeda* Mill. (Loblolly Pine). Showalter and Turchin (1993) found that thinned Longleaf Pine stands were less susceptible to beetle infestations than unthinned stands. Structural restoration of Longleaf Pine woodlands facilitates establishment of herbaceous species that are more drought-tolerant than woody species that may inhabit un-burned sites (Ford et al. 2008). Furthermore, Longleaf Pine has been noted to require lower per-tree water and have a higher stomatal sensitivity to soil moisture than other pine species (Brantley et al. 2017, Gonzalez-Benecke et al. 2011).

The overarching goal of this study was to quantify the growth response of Longleaf Pine following an exceptional drought in 2007. The specific objectives of this study were to examine the relationships between moisture availability and radial growth, and compare the response to the 2007 drought in growth of Longleaf Pine individuals (1) on sites with different stem densities and understory characteristics and (2) of various ages. We hypothesized that Longleaf Pine individuals occurring on the unmanaged site would be less resilient to the 2007 drought because of the higher density of trees and greater competition for resources. We also hypothesized that older trees would be more sensitive to drought conditions compared to younger trees, which are generally more vigorous. Our results provide insight on the effects of drought on Longleaf Pine growth among individuals of various ages occurring on different site conditions.

## Methods

### Study site

We collected tree-ring and forest-inventory data in the Oakmulgee Ranger District of the Talladega National Forest in west-central Alabama from January to June 2017 (Fig. 1). The Oakmulgee Ranger District is situated in the Fall Line Hills, which is a transition zone between the Coastal Plain and Appalachians Highlands physiographic realms (Shankman and Hart 2007). The Fall Line Hills region of Alabama is characterized by steep, dissected slopes with sandy soils (Fenneman 1938). The geology is composed of the Tuscaloosa Coker and Gordo formations. The Coker formation primarily consists of micaceous very fine to medium sand, micaceous clay and gravel beds of quartz and chert. The Gordo formation is composed of cross-bedded and gravelly sands, carbonaceous clay, and chert and quartz pebbles (Szabo et al. 1988). Soils in the study area are in the Maubila and Luverne complex (USDA–NRCS 2017). The climate of the region is humid mesothermal, with long, hot summers and short, mild winters (Thorntwaite 1948), a mean annual temperature of 17.4 °C, a lowest monthly mean of 7.2 °C in January, and a highest monthly mean of 26.9 °C in July. Mean annual precipitation is 1369 mm; the highest and lowest amounts of rain occur in March (mean = 155.7 mm) and October (mean = 70.1 mm), respectively (PRISM 2017).

The Oakmulgee Ranger District is located within the central Longleaf Pine belt in Alabama as defined by Harper (1943). The area was settled by Europeans in the 1820s, logged extensively in the early 1900s by the Kaul Lumber Company, and acquired by the federal government to be managed by the USDA Forest Service in 1935 (Cox and Hart 2015). Prior to European settlement, Native Americans inhabited areas around the Black Warrior River, located to the north and west of the study site. Moundville, a social and political center of the Mississippian Indians until 1700, is located 13 km from the border of the Oakmulgee Ranger District (Maxham 2000). A current priority on the Oakmulgee Ranger District is management for re-introduction of Longleaf Pine to suitable sites currently dominated by Loblolly Pine and xeric hardwood species (USDA Forest Service 2005). Management for Longleaf Pine in the Oakmulgee Ranger District may involve regeneration harvests, site preparation, outplanting of Longleaf Pine, thinning of undesirable tree species, and prescribed burning on a 3–5-y rotation. (USDA Forest Service 2005). Some sites suitable for Longleaf Pine woodlands have remained unmanaged, resulting in mixed pine–hardwood stands with remnant Longleaf Pine individuals.

### Field methods

We used georeferenced forest-inventory data provided by the USDA Forest Service to select potential study sites. We chose potential study sites in the same subwatershed and composed of the same soil type (USDA–NRCS 2017). Once we identified potential study sites, we conducted ground reconnaissance to ensure that Longleaf Pine stems occurred on sites that were not actively managed (i.e., unthinned and unburned), henceforth referred to as the unmanaged sites. When

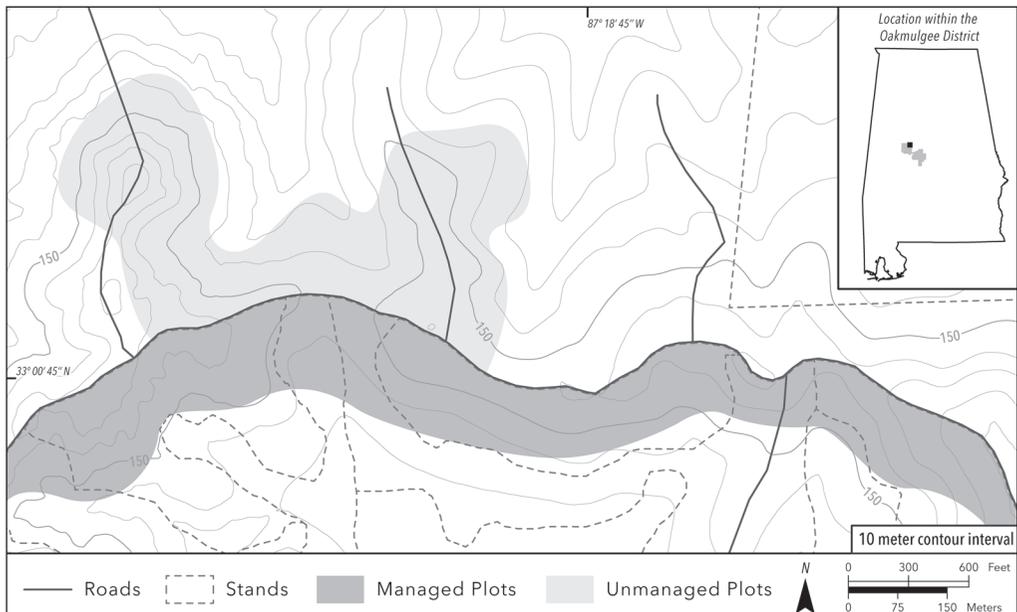


Figure 1. Location of the 2 treatments (managed and unmanaged) in the Oakmulgee Ranger District of the Talladega National Forest, AL. Forest-inventory plots and focal Longleaf Pine plots were established in the 2 treatment areas.

we confirmed the presence of Longleaf Pine on an unmanaged site, we chose a managed Longleaf Pine woodland site (i.e., thinned and burned on a 3–5-y rotation) directly adjacent for comparison. The thinning operation on the managed site occurred in the 1980s; the free thinning was used to reduce tree density and favor Longleaf Pine dominance. The prescribed fire program was also implemented at this time (data provided by USDA Forest Service). To objectively quantify species composition and stand structure, we established twenty 0.04-ha plots on both the managed and unmanaged sites (40 independent plots). We spaced all plots at 30-m intervals along mid-slope positions. On each plot, we recorded species, measured diameter at breast height (dbh; 1.37 m above the soil surface), and assigned crown positions of all trees  $\geq 5$  cm dbh.

To quantify Longleaf Pine growth response to drought, we established thirty 0.04-ha plots on managed and unmanaged sites for a total of 60 plots (these 60 plots were distinct from the 40 used to quantify general stand conditions described above). Each plot had a single Longleaf Pine, which was either dominant or codominant in the canopy, at plot center, referred to as the focal Longleaf Pine stem. On the unmanaged site, we established plots based on the first overstory Longleaf Pine encountered while walking transects through the site, regardless of any other conditions. We selected focal Longleaf Pine on the managed site to match the range of stem dbh of Longleaf Pine on the unmanaged site by walking parallel to the slope contours and selecting trees that were within the dbh range of the 30 focal Longleaf Pine individuals from the unmanaged site. On each plot, we measured dbh and extracted 2 cores from the focal Longleaf Pine tree. For all trees  $\leq 5$  cm dbh, we also recorded species, measured dbh, and assigned crown classes (dominant, codominant, intermediate, and overtopped) based on relative crown height and position (Oliver and Larson 1996).

### **Analytical methods**

To quantify species composition and structural characteristics of the study stands, we analyzed standard descriptions of the tree layer (live woody stems  $\geq 5$  cm dbh) based on the 20 plots established on each site for this purpose. We calculated density (stems  $\text{ha}^{-1}$ ), relative density (contribution to total trees), dominance (basal area;  $\text{m}^2 \text{ha}^{-1}$ ), relative dominance (contribution to total basal area), and relative importance (sum of relative density and relative dominance) for each species. We prepared tree-core samples for analysis using the methods outlined by Stokes and Smiley (1996). We prepped all cores by first air-drying, then glueing to wooden mounts with cells vertically aligned, and finally sanding all cores with progressively finer-grit sand-paper (Orvis and Grissino-Mayer 2002). We dated tree rings on all cores to the calendar year of establishment, and employed pith estimators when the pith was not present but showed significant ring curvature to estimate establishment date (Villalba and Veblen 1997). We measured raw ring-widths to the nearest 0.001 mm using a Velmex measuring stage interfaced with the software Measure J2X (VoorTech Consulting, Holderness, NH). We visually compared and statistically analyzed the measurement series using segmented time-series correlation analysis with the software COFECHA to ensure that each annual ring was assigned to the

proper year of formation (Grissino-Mayer 2001). The software program flagged all segments that fell below the pre-determined threshold ( $r^2 = 0.32$ ,  $P > 0.01$ ). We re-inspected flagged samples for errors and re-dated them, if necessary.

Basal area increment (BAI) is a common metric used to calculate secondary tree-growth (West 1980). BAI represents overall tree growth better than other measures, such as radial-ring growth, because it accounts for decreased ring-width with age and increased tree diameter (Biondi and Qeadan 2008, Husch et al. 2003). In other studies, BAI has been shown to approach a constant level in healthy, mature trees (Duchesne et al. 2002, Valentine and Mäkelä 2005), and decline when trees experience stress, such as moisture stress induced by drought (Phipps and Whittton 1988). We calculated BAI based on the methods outlined by Phipps and Field (1989):

$$BAI_t = \pi(R_t^2 - R_{t-1}^2)$$

and

$$R_{t-1} = R_t - w_t,$$

where  $w_t$  is total ring width and  $R_t$  is radius length at year  $t$ .

To quantify the impact of the 2007 drought, we determined percent growth reduction by calculating the percent change in raw BAI in 2007 from the mean BAI of the previous 10 y (1997–2006). We also calculated the 2008 BAI growth reduction to account for the possible lag in response by some individuals. We calculated recovery time for each individual by determining the number of years subsequent to the 2007 drought that were less than that of the mean annual growth of the 10 y prior to drought. Disturbance-history studies commonly use 10-y mean growth (e.g., Fraver and White 2005, Hart et al. 2012, Nowacki and Abrams 1997), which mitigates variability in short-term growth trends associated with climatic variability. We acknowledge that the 2000 drought may have influenced mean BAI during this 10-y window. However, we suspect that almost any 10-y window in these individuals would contain some influence of drought based on the frequency of these events in the region. We used independent-sample  $t$ -tests to determine if the 2007 and 2008 BAI percent growth-reduction and recovery time of the Longleaf Pine individuals were statistically different between individuals on the managed (i.e., thinned and burned) and those on unmanaged sites, and between individuals  $\geq 80$  y and those  $\leq 55$  y of age. We employed an age threshold because potential differences in radial growth may not manifest in trees of similar ages. Of the 60 Longleaf Pine trees analyzed, we removed 22 from analysis of age-related trends because they were between 56 and 79 years of age. We also tested for a significant difference between growth response to the 2000 drought on the managed and unmanaged site because of the difference in seasonality between the 2 drought events (the 2000 drought occurred in late summer and early fall and the 2007 drought occurred in spring and early summer). We used independent-sample  $t$ -test to test for a significant difference in growth reduction as a function of treatment to the 2000 drought. We also tested radial-growth response for the 2000 and 2007 droughts, regardless of treatment.

We used the Palmer drought severity index (PDSI) to determine the relationship between Longleaf Pine radial growth and drought. PDSI is a regional metric that uses temperature and precipitation to determine water balance, and includes a regional calculation of soil-water storage based on the Thornthwaite evapotranspiration model (Palmer 1965). We acquired PDSI values for the Upper Plains Climatological Division of Alabama for the years 1980–2016 (NDIS 2017). We selected these 36 y to ensure that use of chronologies from all 60 individuals could be used in the correlation analysis (i.e., common life span of samples). We used standard Pearson correlation to analyze the relationship between PDSI and annual BAI values in the 60 Longleaf Pine individuals. We analyzed BAI and PDSI for a 21-mo period (previous March to current November) because previous and current growing conditions can affect productivity (Meldahl et al. 1999). We conducted all correlation analyses in SAS v. 9.4. All data met the assumption of homoscedasticity.

## Results and Discussion

### Forest composition

The managed site contained 9 tree species and was dominated by Longleaf Pine, which represented 92% of trees ha<sup>-1</sup> and 97% of basal area ha<sup>-1</sup>. The site contained 304 stems ha<sup>-1</sup> and had a total basal area of 21.29 m<sup>2</sup> ha<sup>-1</sup>. The remaining 8% of trees/ha were primarily hardwood species with 1 Loblolly Pine stem. (Table 1). The majority (72%) of recorded trees on the managed site were in canopy dominant or codominant positions. The remaining 28% had crowns that were in subcanopy positions (intermediate or overtopped). Mean dbh of trees measured in our plots on the managed site was 27.7 cm.

The unmanaged site contained 20 tree species, with a greater density of *Quercus* (oak) and other hardwood species relative to the managed site (Table 2). Loblolly Pine was the most important species, comprising 52% relative density and 66% relative dominance. The site contained 25 Longleaf Pine stems ha<sup>-1</sup> representing 4%

Table 1. Density, dominance, and importance (sum of relative density and relative dominance) measures for all live stems  $\geq 5$  cm dbh on a managed (thinned and burned) site on the Oakmulgee Ranger District of the Talladega National Forest, Alabama.

Species	Density (stems/ha)	Relative density (%)	Dominance (m <sup>2</sup> /ha)	Relative dominance (%)	Relative importance
<i>Pinus palustris</i> Mill.	279	91.8	20.57	96.6	188.4
<i>Nyssa sylvatica</i> Marshall	8	2.5	0.23	1.1	3.6
<i>Quercus falcata</i> Michx.	6	2.1	0.22	1.0	3.1
<i>Quercus marilandica</i> Münchh.	4	1.2	0.15	0.7	1.9
<i>Quercus coccinea</i> Münchh.	3	0.8	0.05	0.2	1.1
<i>Quercus stellata</i> Wangenh.	1	0.4	0.02	0.1	0.5
<i>Liquidambar styraciflua</i> L.	1	0.4	0.02	0.1	0.5
<i>Quercus laevis</i> Walter	1	0.4	0.01	0.1	0.5
<i>Pinus taeda</i> L.	1	0.4	0.01	0.1	0.5
Total	304	100.0	21.29	100.0	200.0

of stems and 3% of total basal area  $\text{ha}^{-1}$ . Oaks represented 17% of the stems  $\text{ha}^{-1}$  and 11% of the basal area  $\text{ha}^{-1}$ . On the unmanaged site, stem density ( $P < 0.05$ ) and basal area ( $P < 0.05$ ) were higher and mean diameter of trees was lower ( $P < 0.05$ ). The unmanaged site also had more trees in subcanopy positions (39%) than the managed site. The majority (71%) of individuals in canopy dominant and codominant positions were Loblolly Pine.

### Climate–growth relationships

The BAI of Longleaf Pine trees showed a significant positive relationship to PDSI in current July ( $r = 0.394$ ,  $P < 0.05$ ), August ( $r = 0.449$ ,  $P < 0.05$ ), September ( $r = 0.459$ ,  $P < 0.05$ ) and previous November ( $r = 0.362$ ,  $P < 0.05$ ) (Fig. 2). These significantly positive relationships indicated that Longleaf Pine responded positively to increased moisture conditions during the late summer months. Henderson and Grissino-Mayer (2009) found the strongest correlation of Longleaf Pine radial growth to PDSI occurred between July and November. Similarly, Devall et al. (1991) found that current August precipitation and February PDSI were the best predictors of Longleaf Pine productivity. Knapp et al. (2016) found that latewood growth in Longleaf Pine was strongly correlated to summer rainfall, which includes tropical cyclone precipitation. We acknowledge that growth response to the 2007 drought based on treatment effects might elicit a significant difference if only

Table 2. Density, dominance, and importance (sum of relative density and relative dominance) measures for all live stems  $\geq 5$  cm dbh on an unmanaged (no active management) site of the Oakmulgee Ranger District of the Talladega National Forest, Alabama.

Species	Density (stems/ha)	Relative density (%)	Dominance ( $\text{m}^2/\text{ha}$ )	Relative dominance (%)	Relative importance
<i>Pinus taeda</i> L.	360	51.9	16.07	66.2	118.1
<i>Liriodendron tulipifera</i> L.	46	6.6	2.15	8.8	15.4
<i>Acer rubrum</i> L.	46	6.6	0.76	3.1	9.7
<i>Quercus montana</i> Willd.	35	5.0	0.91	3.7	8.7
<i>Quercus rubra</i> L.	36	5.2	0.69	2.8	8.0
<i>Liquidambar styraciflua</i> L.	35	5.0	0.62	2.5	7.6
<i>Pinus palustris</i> Mill.	25	3.6	0.77	3.2	6.8
<i>Oxydendrum arboreum</i> (L.) DC.	31	4.5	0.53	2.2	6.7
<i>Quercus alba</i> L.	18	2.6	0.48	2.0	4.6
<i>Quercus falcata</i> Michx.	14	2.1	0.26	1.1	3.1
<i>Quercus nigra</i> L.	10	1.4	0.21	0.9	2.2
<i>Nyssa sylvatica</i> Marshall	8	1.2	0.25	1.0	2.2
<i>Cornus florida</i> L.	10	1.4	0.16	0.7	2.1
<i>Carya glabra</i> (Mill.) Sweet	5	0.7	0.25	1.0	1.7
<i>Quercus stellata</i> Wangenh.	4	0.5	0.04	0.2	0.7
<i>Juniperus virginiana</i> L.	2	0.3	0.05	0.2	0.6
<i>Sassafras albidum</i> (Nutt.) Nees	2	0.3	0.04	0.2	0.5
<i>Fagus grandifolia</i> Ehrh.	2	0.3	0.03	0.1	0.5
<i>Vaccinium arboreum</i> Marshall	2	0.3	0.03	0.1	0.5
<i>Magnolia macrophylla</i> Michx.	2	0.3	0.02	0.1	0.4
Total	694	100	24.29	100	200

latewood growth were measured rather than whole-ring width. Longleaf Pine experiences recurrent growth flushes (Kozłowski 1971), which may explain the higher correlation in the late summer–early fall months rather than the spring months, during which precipitation is generally greater. Orvis and Grissino-Mayer (2009) speculated that early-season growth flushes in Longleaf Pine utilized stored carbohydrates during earlywood formation, reducing the effects of spring precipitation on radial growth. Therefore, in the late growing season, during a secondary flush, precipitation is likely more utilized as carbohydrates are exhausted from previous growth flushes during the early growing season. Our results concur with other studies that found that Longleaf Pine was more responsive to late summer and early fall moisture than spring moisture (Orvis and Grissino-Mayer 2009).

### Growth response to drought

We noted no significant ( $P > 0.05$ ) difference in 2007 BAI reduction between Longleaf Pine individuals on managed and unmanaged sites. Longleaf Pine individuals on the managed site showed a mean 16.4% BAI reduction in the year 2007 relative to the mean BAI of the preceding 10 y, as opposed to a 15.8% BAI reduction for individuals on the unmanaged site (Table 3). In 2008, mean BAI reduction was 14% on the managed site and 17% on the unmanaged site ( $P > 0.05$ ). The mean recovery time was 5.1 y for trees on the managed site and 4.9 y for the unmanaged site ( $P > 0.05$ ). Therefore, recovery time was nearly the same for trees on both sites (Fig. 3). Trees  $\leq 55$  y old showed a significantly greater growth reduction than trees  $\geq 80$  y old ( $P < 0.001$ ). Trees  $\leq 55$  y old showed a 18.6% growth reduction in the year 2007, and trees  $\geq 80$  y old showed a 15.0% growth reduction in the year 2007 (Table 3). Therefore, our results indicated that younger trees were more sensitive to drought conditions than older trees. The older trees in this study had larger crowns and more growing space, and, we hypothesize, better-developed root networks than

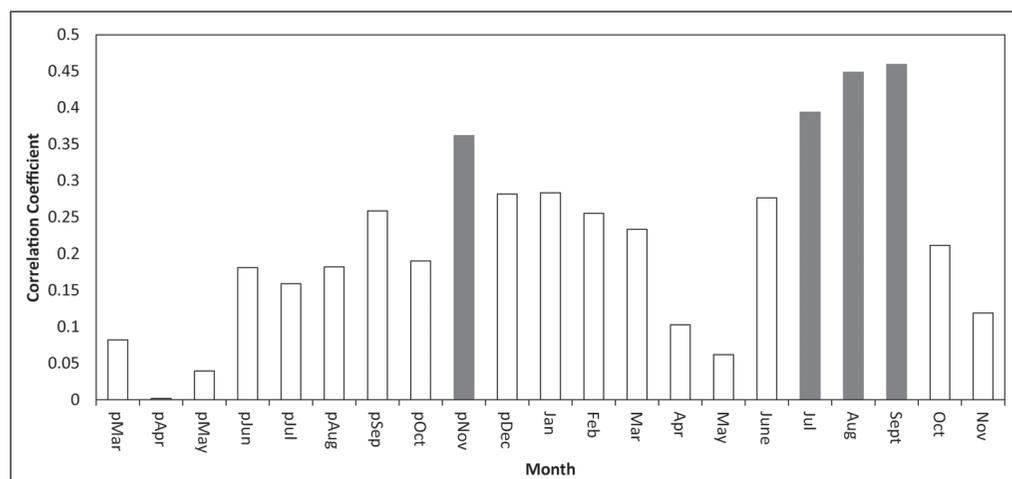


Figure 2. Correlation analysis of the BAI chronology and mean monthly PDSI among 60 Longleaf Pine individuals. Monthly abbreviations preceded by ‘p’ indicate previous year. Gray bars indicated significance values of  $P < 0.05$ .

younger trees. The larger crowns, root networks, and growing space may have led to a greater advantage in accessing water during drought conditions.

We hypothesized that Longleaf Pine would be more resilient to drought when growing in low-density stands (i.e., woodland conditions of the managed site). However, we found no significant difference in growth response to the 2007 drought of Longleaf Pine stems growing on the managed vs. unmanaged sites. We attributed growth responses of individuals on the managed site to 2 possible explanations. First, prescribed burning every 3–5 y may reduce the moisture holding capacity of the soil and duff layer (Boyer and Miller 1994, Harrington and Edwards 1999). Reduced moisture holding capacity from frequent prescribed fire is a result of exposure of bare mineral soil to rainfall and subsequent aggregate clogging of soil pores (Bower 1966). Frequent prescribed fire has also been attributed to higher moisture evaporation from the darkened soil and duff layer (Bond-Lamberty et al. 2009). Reductions in soil and duff-layer moisture-holding capacity, and the loss of organic matter, may cause higher stress during drought years (Mitchell et al.

Table 3. Average 1997–2007 basal area increment (BAI), 2007 BAI, 2007 BAI % reduction, 2008 BAI, 2008 BAI % reduction, and average recovery time among Longleaf Pine individuals based on site condition and age in the Oakmulgee Ranger District of the Talladega National Forest, AL.

	1997–2006 average BAI	2007 BAI	2008 BAI	2007 BAI reduction (%)	2008 BAI reduction (%)	Average recovery time (y)
Managed	1162.60	951.68	984.29	-16.4	-14.1	5.1
Unmanaged	1562.34	1355.87	1250.63	-15.8	-17.0	4.9
≥80 years old	1422.86	1222.26	1192.65	-15.0	-18.6	4.9
≤55 years old	1484.87	1214.04	1099.10	-18.6	-22.7	5.8

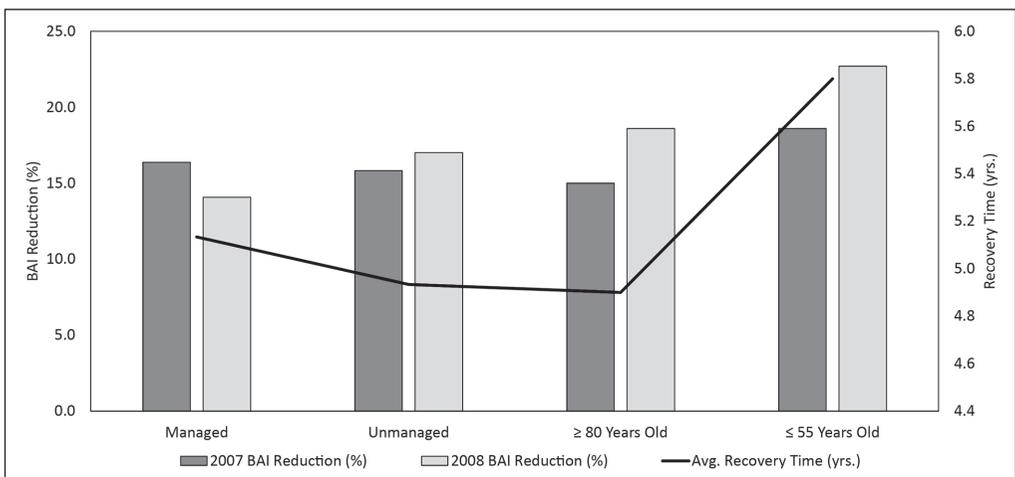


Figure 3. 2007 and 2008 average percent basal area increment (BAI) reduction and average recovery time in years of Longleaf Pine individuals based on site conditions and age. BAI reduction is shown as bars on the primary y-axis and recovery time is shown as a line on the secondary y-axis.

1999). The managed site was burned in 2006, one year before the 2007 drought. Second, the amount of light capable of reaching the understory may have increased moisture evaporation on the managed site as opposed to the mixed pine–hardwood unmanaged site (Battaglia et al. 2002). The managed Longleaf Pine stand has an open, woodland structure; thus, more light can reach the forest floor, which may increase evaporation rates thereby reducing available moisture. The structure and composition of the unmanaged site likely allowed for more canopy and midstory light-capture, and likely less soil-moisture evaporation. We acknowledge that transpiration rates may be higher in stands with higher tree density. Importantly, we note that our results suggest that management did not make the trees more sensitive to drought conditions.

Analysis of growth in relation to climate revealed that Longleaf Pines were more sensitive to PDSI in the late summer and early fall months (July–September and previous November). These relationships indicated that Longleaf Pine is more sensitive to late growing-season climatic conditions. The drought of 2007 was most severe during the spring and early summer months. Each month in 2007 received less precipitation than the 30-y normal. However, the most severe decrease in precipitation occurred during the growing season, which cumulatively lowered PDSI values into the late growing season and dormant season. Based on the climate–growth correlation results, we speculate that Longleaf Pine individuals did not significantly respond to drought conditions because the drought occurred early in the growing season, and Longleaf Pine has been found to be less sensitive to moisture conditions during the spring months. Results indicated that no significant difference occurred in radial-growth response among the 2 treatments during the 2000 and 2007 drought events. Although the 2000 drought was more severe in the months of August, September, and October, the 2007 drought had a sustained severity through the growing season into the dormant season. However, when we tested for significant difference in growth response between the 2000 and 2007 droughts, regardless of treatment, we noted a significant difference ( $P < 0.01$ ) in growth response between the 2 droughts. We found that Longleaf Pine individuals showed a significantly greater growth-reduction response to the 2000 drought than to the 2007 drought, a finding that agrees with our speculation that Longleaf Pine was more sensitive to drought conditions in the late growing season. The 2000 drought was indeed more severe in August, September, and October. Results revealed the importance of understanding not only the impacts of drought severity on tree growth, but the impacts of the timing of drought on tree growth. Our results highlight the complexity of predicting growth response to extreme climate conditions across contrasting stand conditions or management approaches.

## **Conclusion**

Tree-growth response to severe drought can be used as a predictive tool for response to future droughts. An individual tree may experience a unique response to drought conditions based on factors such as physical site conditions, stand density, or tree age. We sought to test the growth response of Longleaf Pine to an exceptional

drought in 2007 among individuals inhabiting sites of different growing conditions and ages. We hypothesized that individuals on sites with lower tree density would be less sensitive to moisture stress and thus, more resilient to drought conditions. However, we found no significant differences ( $P > 0.05$ ) in radial-growth reductions between managed (thinned and burned) and unmanaged sites. We also hypothesized that older trees would be more sensitive than younger trees, but results indicated that age did not significantly influence drought response ( $P > 0.05$ ). We speculated that prescribed-fire frequency and soil and litter moisture evaporation influenced the growth response of Longleaf Pine trees. Climate-growth correlation analysis revealed a greater BAI sensitivity to PDSI in the late summer and early fall months. The timing of the 2007 drought in the spring and early summer months may have resulted in the lack of notable growth response in Longleaf Pine stems. As management plans are developed to promote resiliency in Longleaf Pine ecosystems to future disturbances such as drought, we should consider that tree response is complex and influenced by multiple interacting variables, such as microclimatic conditions, phenology, and the temporal variability of disturbance.

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