Drought impact on forest regeneration in the Southeast USA

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Abstract. Elevating concentrations of atmospheric greenhouse gases are now widely acknowledged as a major cause of global warming. A warmer climate could increase the frequency, duration, and/or severity of drought and, in turn, could alter the composition, structure, and biogeography of forests in many regions. To explore the regional effects of different drought severities on forest regeneration, we investigated changes in sapling growth and density across the southeastern United States under various drought and stand conditions using 1991–2005 Forest Health and Monitoring plot data from Alabama, Georgia, and Virginia. Drought effects were examined on three species groups (pine, oak + hickory, and mesophytic species) using the Palmer Drought Severity Index. Stand and site variables, including total basal area, total stand density, tree species richness, slope, and stand age, were used to account for drought effects under varying stand conditions. The oak + hickory and mesophytic species groups exhibited significant reductions in annual growth rate with increasing drought severity. However, no significant difference in annual growth rate was observed within the pine species group. Chi-square analysis showed that annual mortality rate was significantly dependent on drought severity for each species group but annual recruitment rate was only significantly dependent on drought severity for the oak + hickory group. Total basal area, tree species richness, and stand age had a negative effect on growth in one or more species groups. The observed differential dynamics of sapling growth, mortality, and recruitment among species groups may alter the trend of forest regeneration in southeastern U.S. forests because of the predicted increases in intensity and frequency of droughts in the future. The significant effects of stand conditions on drought responses observed in our study also suggest that appropriate forest management strategies may be useful to maintain structure features of understory saplings for southeastern U.S. forests.

Key words: drought; Forest Health and Monitoring; Forest Inventory and Analysis; growth; mortality; Palmer Drought Severity Index (PDSI); recruitment; sapling.

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INTRODUCTION

Elevating concentrations of greenhouse gases in the atmosphere are now widely acknowledged as a major cause of global warming, increasing global mean temperature by 0.85°C over the period 1880–2012 (IPCC 2013). A warmer climate could increase the frequency, duration, and/or severity of drought (Hanson and Weltzin 2000, Adams and Kolb 2004, reviewed in Allen et al. 2010), which, in turn, could alter the composition, structure, and biogeography of forests in many regions (Allen and Brashears 1998, Phillips et al. 2009, Van Mantgem et al. 2009, reviewed in Allen et al. 2010, Peng et al. 2011, Martínez-Vilalta et al. 2012, Schuster and Oberhuber 2013, Vicente-Serrano et al. 2014). Drought not only directly affects trees by reducing growth and
vigor, but also indirectly predisposes them to damage from other abiotic (e.g., fire) or biotic (e.g., disease and pathogens) agents (Olano and Palmer 2003, reviewed in Allen et al. 2010, Floyd et al. 2015). For example, Allen et al. (2010) presented the first global assessment of recent tree mortality attributed to drought and heat stress, concluding that drought-induced tree mortality due to climate change may have already been co-occurring in at least some of the world's forested ecosystems. Consequently, it is likely that forest vulnerability to drought will increase, even in environments that are not normally considered water-limited. Overall, their review pointed to amplified tree mortality due to drought in forests worldwide.

Effects of drought on the composition and structure of forest communities may be more difficult to understand than other disturbance types (e.g., fire, harvesting) because of complex relationships associated with species-specific sensitivity to drought, competitive interactions, past growth trends, and site variability (Elliott and Swank 1994, Fensham and Holman 1999, Lloret et al. 2004, Floyd et al. 2009, Linares et al. 2011, Morán-López et al. 2014, Sergent et al. 2014, Vicente-Serrano et al. 2014). Even for the same species, differences in age/size (Cavender-Bares and Bazzaz 2000, He et al. 2005, Niinemets and Valladares 2006, Schuster and Oberhuber 2013), provenance (e.g., Wellstein and Cianfaglione 2014), site condition (e.g., Abrams et al. 1998), and drought severity (e.g., Klos et al. 2009) could result in different responses. For example, Cavender-Bares and Bazzaz (2000) found that Quercus rubra seedlings (basal stem diameter < 1 cm) were more susceptible to drought than mature trees because seedlings closed their stomata earlier during the drought, whereas mature trees avoided the drought conditions by accessing deeper water supplies and adjusting water-use efficiency. Wellstein and Cianfaglione (2014) found that although extreme durations of drought exceeded the tolerance of Quercus pubescens of all provenances (Bulgaria, Germany, Hungary, and Italy), plants of Italian provenance showed the highest capacity of whole-individual survival, and those of Bulgarian provenance showed the highest maintenance of the apex under extreme drought. Klos et al. (2009) explored the impacts of drought severity, defined by Palmer Drought Severity Index (PDSI; Palmer 1965), on the growth and mortality of trees (diameter at breast height [dbh] > 12.45 cm) in the southeastern United States and reported that the pines and mesophytic species exhibited significant reductions in growth when drought severity increased from mild (−2.9 < PDSI < −1.9) to severe (PDSI < −3.9), but no reduction in oak species growth was detected with increasing drought severity.

Across the southeastern United States, extensive forest areas have experienced several severe droughts over the past three decades (e.g., 1986–1989, 1998–2001, and 2005–2006) as indicated by PDSI (Klos et al. 2009, Seager et al. 2009). Many climate change scenarios suggest that the frequency, duration, and intensity of drought episodes are expected to increase across the southeastern United States, and potential evapotranspiration is predicted to exceed summer precipitation, caused by projected higher temperatures (Karl et al. 2009). Increasing our understanding of the effects of drought on trees of different species and ages is therefore important to better understand and forecast population and community dynamics for southeastern U.S. forests. Furthermore, sustainable forest management requires an understanding of how forests respond to drought stress and how these responses change with various stand conditions. Therefore, understanding how drought affects trees of different species and age/size classes growing under different site and stand conditions is critical to successfully mitigate the negative impact of climate change.

Previous studies have examined the effects of drought on tree growth and mortality at various spatial scales in the southeastern United States (e.g., Olano and Palmer 2003, Klos et al. 2009, Floyd et al. 2015). However, the impact of drought severity on forest regeneration has not been studied over a large geographical area. Therefore, the objective of this study was to explore Forest Health and Monitoring (FHM) data collected between 1991 and 2005 to assess the effect of drought severity on tree sapling (2.54 cm ≤ dbh ≤ 12.45 cm) dynamics across the southeastern United States using the PDSI as an indicator of drought severity. Specifically, the study attempted to address the following two questions: (1) “How did drought severity affect tree sapling growth, mortality, and recruitment?” and (2) “Did the drought effect vary with stand conditions?”

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DATASETS AND METHODS

Datasets

Forest Health and Monitoring (FHM) plot data from the southeastern United States were not used because these plots were not established prior to 1998 and thus would have only one re-measurement within our study period. These plots were initially established through the FHM program, which was developed in 1990 and later became a part of the Forest Inventory and Analysis program managed by the United States Department of Agriculture (USDA) Forest Service. The FHM program is designed to monitor, assess, and report on the long-term status, changes, and trends in United States Forest Health (USDA Forest Service 2004). The FHM field plots consist of four 168.3-m² fixed-radius subplots, each of which contains four 13.5-m² nested microplots (USDA Forest Service 2004). All trees with a dbh greater than 12.45 cm were measured within the subplots, and all the seedlings and saplings with 2.54 cm ≤ dbh ≤ 12.45 cm were measured within the microplots (Miles 2002, Rogers 2002).

For our analyses, we examined sapling (2.54 cm ≤ dbh ≤ 12.45 cm) data collected from each microplot and stand and site variables measured or derived from subplot tree (dbh > 12.45 cm) data. Stand variables included total basal area (m²/ha), stand density (no. trees/ha), tree species richness (no. species/subplot), tree species diversity, and stand age (yr). Site variables included slope (%) and slope position class. Tree species diversity in each subplot was calculated using Shannon’s index (Shannon 1948). Subplots that were subjected to timber harvest, catastrophic disturbance, or experienced a land-use change during the study period were excluded from the dataset. A total of 259 plots and 608 subplots were used in the analyses.

For each re-measurement, annual sapling growth rate (cm²-cm⁻¹-yr⁻¹) was calculated for each sapling relative to sapling size using the following equation:

\[ G = \frac{(ba_2 - ba_1)/dbh_1}{t} \]

where \( G \) is the annual relative growth rate (cm²-cm⁻¹-yr⁻¹), \( ba_1 \) is the sapling basal area at previous measurement period (cm²), \( ba_2 \) is the sapling basal area at current measurement period (cm²), \( dbh_1 \) is the dbh at previous measurement period (cm), and \( t \) is the number of growing seasons between two sequential measurement periods (yr).

Annual sapling mortality rates within a subplot were calculated for each species and each re-measurement period based on the total sapling basal area removed between two sequential measurement periods. Saplings recorded as dead and missing (thus not re-measured) were considered removed due to mortality. Mortality was expressed as a percent and calculated using

\[ M_i = \frac{(m_i/ba_{i1}) \times 100%}{t} \]

where \( M_i \) is the annual relative mortality rate of species \( i \) (% per yr), \( m_i \) is the mortality of species \( i \) (m²/ha), \( ba_{i1} \) is the basal area of species \( i \) at previous measurement period (m²/ha), and \( t \) is the number of growing seasons between two sequential measurement periods (yr).

Annual sapling recruitment rates within each subplot were calculated for each species and for each re-measurement period, where saplings defined as ingrowth on each microplot were considered recruitments. Recruitment rate was expressed as the number of saplings per hectare per year using

\[ R_i = \frac{r_i}{t} \]

where \( R_i \) is the annual recruitment rate of species \( i \) (no. ha⁻¹-yr⁻¹), \( r_i \) is the recruited sapling density of species \( i \) (no. ha⁻¹), and \( t \) is the number of growing seasons between two sequential measurement periods (yr).

Monthly PDSI values for 1991–2005 for each of the counties in which FHM plots were located...
were obtained from the National Oceanic and Atmospheric Administration (NOAA). The 1998–2001 drought was quite variable across the southeast region in terms of severity and duration as indicated by the PDSI values. The PDSI is calculated based on precipitation, temperature, and local available moisture content of the soil (Olano and Palmer 2003). Positive values indicate adequate moisture availability, and negative values indicate a moisture deficit or drought.

Annual growing-season PDSI averages were calculated for each plot/county during the study period. Preliminary analyses indicated that growing-season PDSI averages were more correlated with growth and mortality than annual PDSI averages. For each re-measurement, mean and minimum PDSI values were derived for the period between two sequential measurements. Preliminary analyses revealed that the minimum PDSI (i.e., the most severe growing-season drought) was more correlated with growth and mortality than the mean PDSI between two sequential measurement periods. Drought classes were defined using the minimum growing-season PDSI values between plot measurements (Table 1). Those categories correspond to those defined and used by NOAA.

Three species groups were identified for subsequent analyses: (1) pine (Pinus), (2) oak (Quercus) + hickory (Carya), and (3) mesophytic species. The mesophytic species group includes maple (Acer), birch (Betula), beech (Fagus), ash (Fraxinus), sweetgum (Liquidambar), yellow poplar (Liriodendron), magnolia (Magnolia), tupelo (Nyssa), and sassafras (Sassafras). These species groups represented an array of site moisture gradients, with pines typically occurring on dry ridges, mesophytic species on moist lower-lying areas, and oaks and hickories in between the two. The detailed information on species and the number of subplots for each group and each drought class are given in Appendix S1: Tables S1–S3.

**Statistical analyses**

The mixed-model procedure PROC MIXED (SAS 9.1, SAS Institute 2004) in the SAS statistical software was used to examine the relationships between sapling annual relative growth rate and the independent variables (i.e., drought class and stand and site variables). The mixed-model approach used the plot as a blocking factor and the year of re-measurement as a nested factor (to account for the hierarchical structure of the data). The stand and site variables analyzed included total basal area, total stand density, tree species richness, tree species diversity, stand age, slope, and slope position class for each subplot. Preliminary analyses revealed that strong correlations existed between tree species richness and tree species diversity and between slope and slope position class. Therefore, tree species diversity and slope position class were excluded from the final analyses.

The annual relative growth rate and independent variables were linearized using the log transformation to remove curvature from the data and improve the fit of the model. The annual relative growth rate was transformed using the following equation:

\[
G^* = \ln(G + 0.25);
\]

where \(G^*\) is the transformed annual relative growth rate and \(G\) is the untransformed annual relative growth rate.

The independent variables (i.e., total basal area, total stand density, tree species richness, stand age, and slope) were transformed using

\[
X^* = \log(X + 1)
\]

where \(X^*\) is the transformed independent variable and \(X\) is the untransformed independent variable.

For each of the independent variables, interaction effects between the stand and site variables and drought classes were examined to determine whether the effect of the stand and site variables was the same for each of the drought classes. The mixed model used to determine interaction effects is shown in the following equation:

**Table 1. Drought severity classification based on the minimum growing-season Palmer Drought Severity Index (PDSI).**

| Drought class       | Severity                  | PDSI   |
|---------------------|---------------------------|--------|
| 1                   | No drought                | >−1.9  |
| 2                   | Mild drought              | −2.9 to −1.9 |
| 3                   | Moderate to severe drought| ≤−2.9  |
where $G^*$ is the transformed annual relative growth rate, $\text{PDSI}_i$ is the drought class ($i = 1$, no drought; $i = 2$, mild drought; $i = 3$, moderate to severe drought), $\text{BA}^*$ is the transformed total basal area, $\text{DEN}^*$ is the transformed total stand density, $\text{SR}^*$ is the transformed species richness, $\text{AGE}^*$ is the transformed stand age, $\text{SLOPE}^*$ is the interaction effect of $\text{BA}^*$ by drought class, $\text{PDSI}_i \times \text{BA}^*$ is the interaction effect of $\text{BA}^*$ by drought class, $\text{PDSI}_i \times \text{SR}^*$ is the interaction effect of $\text{SR}^*$ by drought class, $\text{PDSI}_i \times \text{AGE}^*$ is the interaction effect of $\text{AGE}^*$ by drought class, $\text{PDSI}_i \times \text{SLOPE}^*$ is the interaction effect of $\text{SLOPE}^*$ by drought class, $e_{\text{YEAR(PLOT)}}$ is the error associated with the plot measurement year, $e_{\text{PDSI}_i \times \text{PLOT}}$ is the error associated with the interaction of drought class by plot, and $b_1, b_2, b_3, b_4, b_5, b_6, b_7, b_8, b_9, b_{10}$ are parameter coefficient estimates.

If an interaction effect was significant (i.e., $P$ value $< 0.05$), it was included in the model. Otherwise, a single term was used in the model to represent the effect of the stand variable regardless of drought class. Therefore, the simplest form of Eq. 6 would be

$$G^* = \text{PDSI}_i + b_1 \text{BA}^* + b_2 \text{DEN}^* + b_3 \text{SR}^* + b_4 \text{AGE}^* + b_5 \text{SLOPE}^* + e_{\text{YEAR(PLOT)}} + e_{\text{PDSI}_i \times \text{PLOT}}$$

where all terms are as defined previously in Eq. 6.

The Fisher’s least significant difference (LSD) test was used to determine differences among the drought classes for annual relative growth rate. If an interaction effect was significant for a stand variable (i.e., $P < 0.05$), the LSD test was used to determine differences among the drought classes for that variable. The coefficient of determination ($R^2$) was determined for each model using the PROC CORR procedure (SAS 9.1, SAS Institute 1990), which was calculated from the correlation between the observed and predicted values of the model. The correlation coefficient was then squared to determine $R^2$.

For annual mortality and recruitment rates, over 70% of sampled subplots for each species groups were recorded as zero, and therefore, these data did not meet the normality required for mixed model. After separating annual mortality and recruitment rates into two classes: zero or no-zero, we used two-way chi-square analysis to determine whether annual mortality and recruitment rates are dependent on drought class using procedure PROC FREQ (SAS 9.1, SAS Institute 1990).

**RESULTS**

**Growth**

The pine and mesophytic species models exhibited no significant interaction effects, while the oak + hickory species model exhibited significant interactions between drought severity classes and total basal area ($P = 0.042$) as well as between drought severity classes and stand age ($P = 0.039$), indicating that the effects of drought severity classes on sapling growth depended on total basal area and stand age. The parameter estimates of the growth models for the pine, oak + hickory, and mesophytic species models were 694, 978, and 1669, respectively (Appendix S1: Table S1). The

| Effect       | Estimate | SE    | $P$   |
|--------------|----------|-------|------|
| PDSI1        | 1.6164   | 0.1873| <0.0001† |
| PDSI2        | 1.5155   | 0.2090| <0.0001† |
| PDSI3        | 1.4344   | 0.2172| <0.0001† |
| BA*          | -0.6286  | 0.2026| 0.0021† |
| DEN*         | -0.0543  | 0.1498| 0.7173 |
| SR*          | 0.0474   | 0.3174| 0.8815 |
| AGE*         | -0.6618  | 0.1786| 0.0002† |
| SLOPE*       | 0.1329   | 0.0751| 0.0784 |

**Note:** $\text{PDSI}_1$, no drought (Palmer Drought Severity Index $[\text{PDSI}] > -1.9$); $\text{PDSI}_2$, mild drought ($\text{PDSI}$ from $-1.9$ to $-2.9$); $\text{PDSI}_3$, moderate to severe drought ($\text{PDSI} < -2.9$); $\text{BA}^*$, transformed total basal area; $\text{DEN}^*$, transformed total stand density; $\text{SR}^*$, transformed tree species richness; $\text{AGE}^*$, transformed stand age; and $\text{SLOPE}^*$, transformed slope.

† Significant at $P = 0.05$. 
Table 3. Parameter estimates of the growth model for the oak + hickory species group.

| Effect          | Estimate | SE     | P     |
|-----------------|----------|--------|-------|
| PDSI1           | 0.4587   | 0.4443 | 0.3029|
| PDSI2           | 0.8181   | 0.7691 | 0.2899|
| PDSI3           | 1.5134   | 0.9956 | 0.1303|
| PDSI1 × BA*     | 0.0451   | 0.3166 | 0.8868|
| PDSI2 × BA*     | 0.2687   | 0.3906 | 0.4918|
| PDSI3 × BA*     | −0.1250  | 0.4128 | 0.7621|
| DEN*            | −0.2470  | 0.2596 | 0.3417|
| SR*             | −0.8155  | 0.5163 | 0.1149|
| PDSI1 × AGE*    | −0.9284  | 0.3221 | 0.0042†|
| PDSI2 × AGE*    | −1.7515  | 0.5927 | 0.0034†|
| PDSI3 × AGE*    | 0.2924   | 0.6979 | 0.6755|
| SLOPE*          | −0.1926  | 0.1278 | 0.1339|

Note: PDSI1, no drought (Palmer Drought Severity Index [PDSI] > −1.9); PDSI2, mild drought (PDSI from −1.9 to −2.9); PDSI3, moderate to severe drought (PDSI < −2.9); BA*, transformed total basal area; DEN*, transformed total stand density; SR*, transformed tree species richness; AGE*, transformed stand age; and SLOPE*, transformed slope.

† Significant at P = 0.05.

The coefficient of determination ($R^2$) for the pine, oak + hickory, and mesophytic species models was 0.805, 0.563, and 0.654, respectively.

Stand age negatively affected the growth within the pine, oak + hickory (only for the no-drought and mild-drought classes), and mesophytic species models. Stand basal area only negatively affected growth within the pine species model, while tree species richness only negatively affected growth within the mesophytic species model. Since the oak + hickory species model exhibited significant interactions between drought severity classes and total basal area as well as between drought severity classes and stand age, the Fisher’s LSD test was used to determine differences among drought severity classes that exhibited a significant parameter estimate for total basal area and stand age, respectively. However, we found no significant difference between the no-drought (1) and mild-drought (2) classes ($P = 0.1831$) for stand age.

Although all three species groups showed a general decrease in mean annual growth rate with increasing drought severity (Fig. 1), significant effects of drought severity classes on sapling growth were detected for the oak + hickory and mesophytic species groups but not the pine species group. For the oak + hickory species group, significant differences were found between the no-drought class (1) and the two drought severities (2—3; $P = 0.0163$ and 0.0132, respectively). For the mesophytic species group, significant differences were also found between the no-drought class (1) and the two drought severities (2—3; $P = 0.0178$ and 0.0009, respectively).

Mortality and recruitment

The sample sizes of sapling mortality analyses for the pine, oak + hickory, and mesophytic species groups were 306, 532, and 836, respectively (Appendix S1: Table S2). The chi-square analysis showed that annual sapling mortality rate was significantly dependent on drought severity class for all three species groups (Table 5). For each species group, the proportion of sampled subplots in which sapling mortality was detected consistently increased with increasing drought classes, indicating sapling mortality increased with drought severity (Fig. 2). However, annual recruitment rate was significantly dependent on drought class only for the oak + hickory species group, but not for the pine and mesophytic species groups (Table 5). Within the oak + hickory species group, the proportion of subplots that had sapling recruitment was higher for two drought classes (Fig. 3). The sample sizes of sapling recruitment analyses for the pine, oak + hickory, and mesophytic species groups were 343, 593, and 957, respectively (Appendix S1: Table S3).

Table 4. Parameter estimates of the growth model for the mesophytic species group.

| Effect         | Estimate | SE     | P     |
|----------------|----------|--------|-------|
| PDSI1          | 0.4835   | 0.3649 | 0.1861|
| PDSI2          | 0.1641   | 0.3923 | 0.6799|
| PDSI3          | −0.0653  | 0.4000 | 0.8704|
| BA*            | −0.2794  | 0.2664 | 0.2945|
| DEN*           | −0.0133  | 0.2280 | 0.9534|
| SR*            | −1.1274  | 0.3827 | 0.0033†|
| AGE*           | −0.8950  | 0.2539 | 0.0005†|
| SLOPE*         | −0.0097  | 0.1018 | 0.9244|

Note: PDSI1, no drought (Palmer Drought Severity Index [PDSI] > −1.9); PDSI2, mild drought (PDSI from −1.9 to −2.9); PDSI3, moderate to severe drought (PDSI < −2.9); BA*, transformed total basal area; DEN*, transformed total stand density; SR*, transformed tree species richness; AGE*, transformed stand age; and SLOPE*, transformed slope.

† Significant at $P = 0.05$. 
DISCUSSION

Growth

Drought is one of many stress factors that affect the establishment, growth, and mortality of trees (Peters et al. 2015). Given that the recent trend of increasing frequency of drought conditions across the southeastern United States is projected to continue into the future, understanding the species-specific responses of trees with different age/size classes is important both to predicting the dynamics of forest composition and structure in the future and to implementing sustainable forest management practices. Our results indicate that drought effects on sapling growth differed among the three species groups. Although a general decrease in mean relative growth rate was observed with increasing drought severity, the lack of significant differences in growth among drought classes for the pine species group suggested that pine saplings maintained their growth rates during the drought episodes occurred within the study period. In the southeastern United States, pines naturally occur on dry sites of excessive drainage and poor soil water-holding capacity, and as a result, a certain degree of drought tolerance of pine saplings was expected. Protection from forest canopy may have also reduced the impact of drought, giving understory saplings some advantage in drought resistance (Garcia-Plazaola and Becerril 2000, Olano and Palmer 2003). However, a significant decrease in growth was detected for saplings of the oak + hickory species group during the drought episodes.

Fig. 1. Annual relative growth rates (mean ± 1 SE) by drought class for the pine (a), oak + hickory (b), and mesophytic species (c) groups. For each species group, the results of the least significant difference test are indicated with letter designations shown above each drought class.

Table 5. The results of the chi-square analysis for the pine, oak + hickory, and mesophytic species groups.

| Species group     | Mortality Chi-square | P      | Recruitment Mortality Chi-square | P      |
|-------------------|----------------------|--------|---------------------------------|--------|
| Pine              | 13.4795              | 0.0012 | 3.4768                          | 0.1758 |
| Oak + hickory     | 35.4802              | <0.0001| 8.2213                          | 0.0164 |
| Mesophytic species| 39.282               | <0.0001| 2.6086                          | 0.2714 |

† Significant at P = 0.05.
suggesting that oak + hickory saplings were more sensitive to drought than pine saplings. In contrast to our results, previous studies reported that the growth rates of mature trees (dbh > 12.45 cm) of the pine species group were sensitive to drought (Klos et al. 2009), whereas the growth rates of mature trees of the oak species group were drought tolerant (Elliott and Swank 1994, Klos et al. 2009). These contradictory results suggest that drought tolerance of trees in a forest stand depends not only on species-specific adaptation but also on their stem size (and thus their canopy position). Previous studies have demonstrated that trees of different sizes or ages responded to drought differently. For example, Wang et al. (2006) found that older, open-grown white spruce trees were more sensitive and less capable of recovering from drought stress. In addition, He et al. (2005) found that saplings (2.8 cm ≤ basal stem diameter ≤ 6.0 cm) of Acer rubrum exhibited no growth reduction, saplings (3.8 cm ≤ basal stem diameter ≤ 8.5 cm) of Betula papyrifera exhibited increased radial growth, whereas mature trees of both species experienced growth reductions during a drought event. However, the degree of growth reduction depended on species and their associated successional status as well as community types, ranged from ~18% for A. rubrum and Acer saccharum and <5% for B. papyrifera and Betula alleghaniensis (He et al. 2005).

In general, the difference between saplings and mature trees has been considered to be due, in part, to the fact that saplings and mature trees may occupy different microhabitats and depend
on different water resources (Donovan and Pappen 1998, Cavender-Bares and Bazzaz 2000, Treyger and Nowak 2011). As their shoot and root systems develop, seedlings and saplings become more integrated into the environment and therefore less sensitive to small-scale fluctuations in environmental factors. Consequently, mature trees may be buffered against changes in soil moisture because of their rooting patterns, and against changes in temperature and nutrient availability by their large above- and belowground mass, enabling them to better access resources (Elliott and Swank 1994, Bazzaz et al. 1996). Furthermore, previous studies have also shown that plants are capable of adjusting water-use efficiency during their development. In a study on two co-occurring Mediterranean oaks, Mediavilla and Escudero (2004) found that the seedlings (basal stem diameter < 1 cm) of Quercus rotundifolia and Quercus faginea showed a less conservative water-use strategy, in comparison with mature trees, with a relatively high stomatal conductance and lower stomatal sensitivity to soil and atmospheric drought.

 Similarly to the results reported for mature trees (reported by Klos et al. 2009), the growth rate of saplings of the mesophytic species group was also significantly affected by drought. The consistency in their drought sensitivity across developmental stages is largely expected for mesophytic species because of their drought-sensitive physiological functions (Epron et al. 1995, Leuschner et al. 2000, 2001). Unlike oaks, mesophytic species lacks deep roots and large carbohydrate reserves, and changes in carbon allocation from shoots to roots during periods of moisture stress typically reduce stem diameter growth (Steinberg et al. 1990, Kramer and Boyer 1995). Our results contrast those reported by Olano and Palmer (2003) in which growth rates of smaller trees (5 cm < dbh < 20 cm) of two mesophytic species (A. saccharum and Fagus grandifolia) were significantly higher during a drought episode within an old-growth Appalachian forest in North Carolina, due to a reduction in asymmetric competition.

 Although drought significantly affected the growth rate of saplings in both oak + hickory and mesophytic species groups, saplings of the oak + hickory species group exhibited less reduction in growth rates with increasing drought severity compared to the mesophytic species group (Fig. 1b, c). Oak and hickory saplings may have achieved smaller decrease in growth through leaf modifications (e.g., high stomatal density, thick leaves, and small guard cells) that increase water-use efficiency (Abrams and Kubiske 1990) and through morphological acclimations (e.g., deep roots, efficient water transport, and osmotic adjustments) that increase water uptake (Abrams 1990), when compared to saplings of mesophytic species. Thus, oak and hickory species often exhibit higher photosynthetic rates and smaller decreases in photosynthetic rates with increasing soil and atmospheric drought than co-occurring mesophytic species (Abrams 1990, Elliott and Swank 1994).

 Among the stand and site variables examined in our study, stand basal area, stand age, and tree species richness were found to exhibit a significant effect on growth in one or more species groups. All of these significant stand variables produced negative parameter estimates, indicating that they adversely affected growth under climatic drought. This finding is in general agreement with previous studies (e.g., Wang et al. 2006, Klos et al. 2009, Rais et al. 2014). It is likely that saplings within stands of higher total basal area and/or older trees also experience more intense competition for resources (i.e., light, moisture, nutrients, growing space). Similarly, stands with higher species richness in the canopy may result in more complete use of growing space by canopy trees, which would limit the development of understory saplings due to more intense resource competition from canopy trees. These results suggest that both mature trees and saplings growing under higher competitive environments may express lower growth rates due to resource limitations, which tends to further magnify the negative effect of climatic drought on growth. Therefore, forest management practices (e.g., thinning) may be used to mitigate drought effects on mature trees and saplings through the silvicultural manipulation of stand conditions aimed to reduce competition.

 Mortality and recruitment

 Drought-induced mortality has been reported around the world (e.g., reviewed in Allen et al. 2010, Peng et al. 2011, Martín-Vilalta et al. 2012). Our results showed that drought was positively correlated with sapling mortality across all

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three species groups. Similarly, for Mesa Verde National Park’s old-growth woodlands in southwestern Colorado, USA, most of the young Colorado pinon (Pinus edulis) saplings (two–five years old) that gminated in 2006–2008 have died because of the 2010–2011 drought (Floyd et al. 2015). Klos et al. (2009) reported that tree mortality of pine and mesophytic species groups increased with drought severity in the southeastern United States. Contrast to our finding, Klos et al. (2009) found that mortality of oak trees was not due to drought severity. Together, results from this study and Klos et al. (2009) suggested that the drought tolerance of oaks could change with ontogeny, with mature trees less susceptible to drought mortality.

Our results indicate that drought affected sapling recruitment only in the oak + hickory species group. However, contrary to our expectation, drought had a positive effect on sapling recruitment. Difficulty in regenerating oaks on mesic sites has been well documented in previous studies, and it is believed that competition from mesophytic species has prevented oak seedlings from being recruited into sapling size (e.g., Abrams 1992, Wang et al. 2005, Nowacki and Abrams 2008). If drought has more detrimental effects on mesophytic species than oaks in eastern deciduous forests, increasing drought frequency and intensity would give oaks a relative growth advantage. Therefore, it is possible that drought occurred during the study period had improved sapling recruitment in oak and hickory species group, especially on mesic sites. Several previous studies reported that dry environment would benefit oak regeneration, while moist environment would benefit the regeneration of mesophytic species (e.g., Olano and Palmer 2003, McEwan et al. 2011). For example, through monitoring seedling establishment of five dominant tree species: A. rubrum, Betula spp., Liriodendron tulipifera, Nyssa sylvatica, and Quercus rubra for 10 yr in the southern Appalachian Mountains, Ibáñez et al. (2007) found that warmer spring temperature was the key driver to benefit the recruitment of A. rubrum, Betula spp., and N. sylvatica; L. tulipifera, which was abundant on mesic sites, experienced highest establishment rates on sites with great soil moisture. Quercus rubra could experience higher recruitment under warmer spring temperature and drier environments. Therefore, it is likely that most of the forest stands in the southeastern United States will experience reduced regeneration due to increased sapling mortality and oak species may replace mesophytic species on the mesic sites if drought frequency and/or intensity increases with climate change due to global warming.

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