

Drought impact on forest growth and mortality in the southeast USA: an analysis using Forest Health and Monitoring data

RYAN J. KLOS,¹ G. GEOFF WANG,^{1,4} WILLIAM L. BAUERLE,² AND JAMES R. RIECK³

¹Department of Forestry and Natural Resources, Clemson University, Clemson, South Carolina USA 29634-0317

²Department of Horticulture and Landscape Architecture, Colorado State University, Fort Collins, Colorado USA 80523-1173

³Department of Experimental Statistics, Clemson University, Clemson, South Carolina USA 29634-0313

Abstract. Drought frequency and intensity has been predicted to increase under many climate change scenarios. It is therefore critical to understand the response of forests to potential climate change in an effort to mitigate adverse impacts. The purpose of this study was to explore the regional effects of different drought severities on tree growth and mortality. Specifically, we investigated changes in growth and mortality rates across the southeastern United States under various drought and stand conditions using 1991–2005 Forest Health and Monitoring (FHM) plot data from Alabama, Georgia, and Virginia. Drought effects were examined for three species groups (pines, oaks, and mesophytic species) using the Palmer drought severity index (PDSI) as an indicator of drought severity. Stand variables, including total basal area, total tree density, tree species richness, slope, and stand age, were used to account for drought effects under varying stand conditions. The pines and mesophytic species exhibited significant reductions in growth rate with increasing drought severity. However, no significant difference in growth rate was observed within the oak species group. Mean mortality rates within the no-drought class were significantly lower than those within the other three drought classes, among which no significant differences were found, for both pines and mesophytic species. Mean mortality rates were not significantly different among drought classes for oaks. Total basal area, total tree density, and stand age were negatively related to growth and positively related to mortality, which suggests that older and denser stands are more susceptible to drought damage. The effect of basal area on growth increased with drought severity for the oak and mesophytic species groups. Tree species richness was negatively related to mortality for the pine and mesophytic species groups, indicating that stands with more species suffer less mortality. Slope was positively related to mortality within the mesophytic species group, and its effect increased with drought severity, indicating a higher mortality on sites of greater slope during severe-drought conditions. Our findings indicate that pines and mesophytic species are sensitive to drought, while oaks are tolerant of drought. The observed differential growth and mortality rates among species groups may alter the species composition of southeastern U.S. forests if drought episodes become more frequent and/or intense due to climate change. The significant effects of stand conditions on drought responses observed in our study also suggest that forest management may be used as a tool to mitigate drought effects.

Key words: drought; forest inventory and analysis; growth; mortality; Palmer drought severity index (PDSI); southeastern United States.

INTRODUCTION

Extensive forest areas across the southeastern United States have experienced several severe droughts in recent years (e.g., 1954–1957, 1986–1989, and 1998–2001) as indicated by the Palmer drought severity index (PDSI; Palmer 1965). The droughts during the 1950s and 1980s significantly affected tree growth and mortality (Buell et al. 1961, Small 1961, Elliott and Swank 1994, Olano and Palmer 2003). However, the effects of the 1998–2001 drought have not yet been documented. Climate change induced by global warming due to elevated concentra-

tions of greenhouse gases could potentially increase drought frequency and/or intensity (Neilson et al. 1989, Hanson and Weltzin 2000, Adams and Kolb 2004) and impact forest ecosystems across the United States, possibly through changes in distribution of tree species and forest types (Allen and Brashears 1998; see Plate 1). For example, Engelbrecht et al. (2007) found that species distributions are directly related to drought sensitivity in the Tropics. Provided that species distributions are influenced by drought sensitivity, potential shifts in precipitation patterns and climate change will alter the composition, structure, and function of future forests. Many climate change scenarios suggest that more frequent and/or intense drought episodes are expected across the southeastern United States, and

Manuscript received 19 February 2008; revised 12 June 2008; accepted 18 July 2008. Corresponding Editor: A. D. McGuire.

⁴ Corresponding author. E-mail: gwang@clemson.edu

potential evapotranspiration is predicted to exceed summer precipitation (Smith and Tirpak 1990). Therefore, it is important to understand the effect of drought on forest health and productivity.

Drought is a disturbance that influences the composition and structure of forest communities but is more difficult to understand than other disturbance types (e.g., fire, harvesting, etc.) because of complex relationships associated with species-specific sensitivity to drought, competitive interactions, and site variability (Elliott and Swank 1994). Although the effects of major perturbations such as fire, hurricanes, and harvesting on forest composition have been extensively explored (e.g., Oliver and Larson 1996, Batista et al. 1998, Donnegan and Rebertus 1999, Kembell et al. 2006), the effects of less intense but more extensive disturbances such as drought are not well understood. Droughts cause less forest mortality compared to other major disturbances but have a profound effect on forest ecosystems as they can affect vast areas, modify tree dynamics, and alter competitive relations among tree species (Olano and Palmer 2003). Drought episodes have been found to increase tree mortality (Fahey 1998, Condit et al. 1999), and their effects are not confined only to xeric sites. Drought can directly affect trees by reducing growth and vigor or cause mortality. Drought can also indirectly affect trees by predisposing trees to damage from other abiotic (e.g., fire) or biotic (e.g., disease and pathogens) factors (Olano and Palmer 2003).

Sustainable forest management requires an understanding of how forests respond to environmental stress and how these responses change with stand conditions. Therefore, understanding how drought affects trees of different species and size on different sites and stand conditions is critical to successfully mitigate its impact on the sustainability of forest ecosystems. The objective of this study was to draw on Forest Health and Monitoring (FHM) data collected between 1991 and 2005 to assess the effects of drought severity on tree growth and mortality across the southeastern United States using the PDSI as an indicator of drought severity. Specifically, the study was to address the following two questions: (1) How did drought severity affect growth and mortality? (2) Did the drought effects vary with stand condition? Previous studies have examined the effects of drought on tree growth and mortality on a local scale and without explicit consideration of drought severity. This study was intended to explore the regional effects of different drought severities on tree growth and mortality across the southeastern United States based on the extensive data set of the FHM program.

METHODS

Forest Health and Monitoring plot data from Alabama, Georgia, and Virginia for the period of 1991–2005 were used for analyses in this study. The FHM plots from other states within the southeastern

United States were not used as these plots were not established prior to 1998 and thus would have had only one re-measurement within our period of study.

The FHM program, which is a subset of the Forest Inventory and Analysis (FIA) program managed by the United States Department of Agriculture (USDA) Forest Service, is responsible for the monitoring and assessment of the trends in the health of the U.S. forests. The FIA field plots consist of four 168.3 m² fixed-radius subplots and four 13.5 m² microplots (Miles 2000, Rogers 2002). Tree level data were measured for trees >12.45 cm dbh within each subplot.

For our analyses, we examined trees with dbh >12.45 cm and were sampled across the entire subplot. For each subplot measurement, basal area (in square meters per hectare), density (number of trees per hectare), tree species richness (number of species per subplot), tree species diversity, and stand age (in years) were calculated at the subplot level. Slope (as a percentage) and slope position class were obtained for each subplot. Tree species diversity was calculated for each subplot measurement as Shannon's index (Shannon 1948).

Subplots that were subjected to harvesting or experienced a land use change during the study period were excluded from the data set. A total of 308 plots and 921 subplots were used in the analyses. Trees that exhibited a decrease in dbh during re-measurement were corrected, and a zero growth was assumed. To avoid effects from other resource limitations (e.g., light), suppressed trees were identified using the crown position parameter (i.e., understory and overtopped) and were removed from growth analyses.

For each re-measurement period, annual tree growth rate (in square centimeters per centimeter per year) was calculated for each tree relative to tree size using the following equation:

$$G = \frac{(ba_2 - ba_1)/dbh_1}{t} \quad (1)$$

where G is the annual relative growth rate (in square centimeters per centimeter per year), ba_1 is the tree basal area at the previous measurement (in square centimeters), ba_2 is the tree basal area at current measurement (in square centimeters), dbh_1 is the diameter at breast height at the previous measurement (in centimeters), and t is the number of growing seasons between measurements (in years). Kloeppel et al. (2003) used this growth metric, which allows for comparison of basal area increment among various tree sizes. The growing season was defined as May–September. Since there were five months in the defined growing season, each month represented 0.2 of the total growing season. The number of growing seasons between measurements was calculated based on the number of growing-season months.

Annual mortality rates within a subplot were calculated for each species for each re-measurement period. The total basal area removed between measurements was calculated for each species. Trees defined as dead

and those not re-measured were considered removed due to mortality. Mortality was expressed as a percentage and calculated using

$$M_i = \frac{(m_i/ba_{i,t}) \times 100\%}{t} \quad (2)$$

where M_i is the annual relative mortality rate of species i (as a percentage per year), m_i is the mortality of species i (in square meters per hectare), $ba_{i,t}$ is the basal area of species i at the previous measurement (in square meters per hectare), and t is the number of growing seasons between measurements (in years).

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, while negative values indicate a moisture deficit or drought. Annual growing-season 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 calculated for the period between 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 measurements. Drought classes were defined using the minimum growing-season PDSI values between plot measurements (Table 1). These categories correspond to those defined and used by NOAA.

Three species groups were used for subsequent analyses: (1) pine (*Pinus*), (2) oak (*Quercus*), and (3) mesophytic species. The mesophytic species group includes maple (*Acer*), birch (*Betula*), beech (*Fagus*), sweetgum (*Liquidambar*), yellow poplar (*Lirodendron*), and magnolia (*Magnolia*). These three species groups were identified to represent an array of site moisture gradients, with pines typically occurring on dry ridges and mesophytic species typically occurring on moist lower lying areas.

The mixed model procedure PROC MIXED in the SAS statistical software (SAS Institute 1990) was used to examine the relationships between the dependent variables (i.e., growth and mortality) and the independent variables (i.e., drought class and stand variables). The mixed-model approach used the plot as a blocking factor and the year of re-measurement as a nested factor. The stand variables analyzed included total basal area, total tree density, tree species richness, tree species diversity, stand age, slope, and slope position class for each subplot. Preliminary analyses revealed that strong

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 drought	-3.9 to -2.9
4	severe drought	< -3.9

Note: Forest Health and Monitoring (FHM) plot data from Alabama, Georgia, and Virginia, USA, for the period of 1991–2005 were used for analyses in this study.

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 dependent and independent variables were linearized using the log transformation to remove curvature from the data and improve the fit of the model. The dependent variables (i.e., growth and mortality) were transformed using

$$Y' = \log(Y + 0.5) \quad (3)$$

where Y' is the transformed dependent variable (growth or mortality) and Y is the untransformed dependent variable (growth or mortality).

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

$$X' = \log(X + 0.001) \quad (4)$$

where X' is the transformed independent variable (total basal area, total tree density, tree species richness, stand age, or slope) and X is the untransformed independent variable (total basal area, total tree density, tree species richness, stand age, or slope).

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

$$\begin{aligned}
 Y' = & \text{PDSI}_i + b_1\text{BA}' + b_2\text{DEN}' + b_3\text{SR}' + b_4\text{AGE}' \\
 & + b_5\text{SLOPE}' + b_6i\text{PDSI}_i \times \text{BA}' + b_7i\text{PDSI}_i \times \text{DEN}' \\
 & + b_8i\text{PDSI}_i \times \text{SR}' + b_9i\text{PDSI}_i \times \text{AGE}' + b_{10i}\text{PDSI}_i \\
 & \times \text{SLOPE}' + \varepsilon_P + \varepsilon_{Y(P)} + \varepsilon_{D_i \times P}
 \end{aligned} \quad (5)$$

where Y' is the transformed dependent variable (growth or mortality), PDSI_i is the drought class (1, no drought; 2, mild drought; 3, moderate drought; 4, severe drought), BA' is the transformed total basal area, DEN' is the transformed total tree density, SR' is the transformed species richness, AGE' is the transformed stand age, SLOPE' is the transformed slope, $\text{PDSI}_i \times \text{BA}'$ is the interaction effect of BA' by drought class, $\text{PDSI}_i \times \text{DEN}'$ is the interaction effect of DEN' by

TABLE 2. Parameter estimates of the growth model for the pine species group.

Effect	Estimate	SE	P
PDSI 1	1.010	0.074	<0.001*
PDSI 2	0.978	0.076	<0.001*
PDSI 3	0.949	0.076	<0.001*
PDSI 4	0.924	0.078	<0.001*
BA'	-0.114	0.025	<0.001*
DEN'	-0.079	0.025	0.002*
SR'	0.009	0.017	0.582
AGE'	-0.365	0.033	<0.001*
SLOPE'	-0.004	0.003	0.153

Note: Abbreviations are: PDSI, drought class according to the Palmer drought severity index; BA', transformed total basal area; DEN', transformed total tree density; SR', transformed tree species richness; AGE', transformed stand age; and SLOPE', transformed slope.

* Significant at $P < 0.05$.

drought class, $PDSI_i \times SR'$ is the interaction effect of SR' by drought class, $PDSI_i \times AGE'$ is the interaction effect of AGE' by drought class, $PDSI_i \times SLOPE'$ is the interaction effect of SLOPE' by drought class, ε_P is the error associated with the plot, $\varepsilon_{Y(P)}$ is the error associated with the plot measurement year, $\varepsilon_{D_i \times P}$ is the error associated with the interaction of drought class by plot, and $b_1, b_2, b_3, b_4, b_5, b_{6i}, b_{7i}, b_{8i}, b_{9i}$, and b_{10i} 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. 5 would be

$$X' = PDSI_i + b_1 BA' + b_2 DEN' + b_3 SR' + b_4 AGE' + b_5 SLOPE' + \varepsilon_P + \varepsilon_{Y(P)} + \varepsilon_{D_i \times P} \quad (6)$$

where all terms are as defined previously in Eq. 5.

The least significant difference (LSD) test was used to determine differences among the drought classes for each of the dependent variables. If an interaction effect was significant for a stand variable, the LSD test was used to determine differences among the drought classes for that variable. Significant differences were identified using a P value of 0.05. The coefficient of determination (R^2) was obtained using the PROC CORR procedure in the SAS statistical software (SAS institute 1990) to determine the correlation between the observed and predicted values of the model. The correlation coefficient was then squared to determine R^2 .

RESULTS

Growth models

The pine model exhibited no significant interaction effects, while the oak and mesophytic models exhibited a significant interaction effect for total basal area ($P = 0.021$ and 0.016 , respectively). Therefore, the interaction effect for total basal area was included in the growth model for the oak and mesophytic species groups. The

parameter estimates of the growth models for the pine, oak, and mesophytic species groups are presented in Tables 2, 3, and 4, respectively. The sample sizes for the pine, oak, and mesophytic species models were 5552, 2972, and 2905, respectively. The coefficients of determination (R^2) for the pine, oak, and mesophytic species models were 0.568, 0.423, and 0.320, respectively.

Stand age was significant for all three species groups. Total basal area was significant within the pine model, oak model (for the no-drought [1], moderate [3], and severe [4] drought classes), and mesophytic species model (for the no-drought [1], mild [2], and moderate [3] drought classes). Total tree density was also significant within the pine and oak models. Note that the parameter estimates for these significant stand variables were negative within all three species groups. Since the oak and mesophytic species models exhibited a significant interaction effect for total basal area, indicating that the effect of basal area differed among drought classes, the LSD test was used to determine differences among drought classes that exhibited a significant parameter estimate for basal area. For the oak species group, a significant difference was found between the no-drought (1) and severe-drought (4) classes ($P = 0.020$). For the mesophytic species group, significant differences were found between the no-drought (1) and moderate-drought (3) classes ($P = 0.002$) and between the mild (2) and moderate (3) drought classes ($P = 0.028$). It appeared that the effect of basal area increased with increasing drought severity, with higher basal area resulting in greater reduction of growth rate for both oak and mesophytic species groups.

All three species groups showed a general decrease in mean annual growth rate with increasing drought severity (Fig. 1). For the pine group, significant differences were found between the no-drought class (1) and the three drought severities (2–4) ($P = 0.023$, <0.001 , and <0.001 , respectively) and between the mild-drought (2) and severe-drought (4) classes ($P = 0.029$). For the mesophytic species group, significant differences were observed between the no-drought (1) and severe-

TABLE 3. Parameter estimates of the growth model for the oak species group.

Effect	Estimate	SE	P
PDSI 1	0.585	0.081	<0.001*
PDSI 2	0.549	0.096	<0.001*
PDSI 3	0.651	0.109	<0.001*
PDSI 4	0.849	0.148	<0.001*
PDSI 1 \times BA'	-0.053	0.023	0.020*
PDSI 2 \times BA'	-0.038	0.039	0.326
PDSI 3 \times BA'	-0.116	0.055	0.033*
PDSI 4 \times BA'	-0.290	0.102	0.005*
DEN'	-0.100	0.030	0.001*
SR'	-0.003	0.028	0.925
AGE'	-0.131	0.034	<0.001*
SLOPE'	-0.005	0.003	0.124

Note: For explanations of parameter abbreviations, see Table 2.

* Significant at $P < 0.05$.

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

Effect	Estimate	SE	P
PDSI 1	0.456	0.086	<0.001*
PDSI 2	0.472	0.098	<0.001*
PDSI 3	0.633	0.108	<0.001*
PDSI 4	0.270	0.129	0.036*
PDSI 1 × BA'	-0.088	0.028	0.002*
PDSI 2 × BA'	-0.114	0.042	0.007*
PDSI 3 × BA'	-0.245	0.051	<0.001*
PDSI 4 × BA'	-0.007	0.074	0.927
DEN'	-0.033	0.032	0.297
SR'	0.041	0.030	0.179
AGE'	-0.157	0.033	<0.001*
SLOPE'	-0.002	0.003	0.437

Note: For explanations of parameter abbreviations, see Table 2.

* Significant at $P < 0.05$.

drought (4) classes ($P < 0.001$) and between the mild- (2) and severe-drought (4) classes ($P = 0.015$). No significant differences were observed among drought classes within the oak species group.

Mortality models

The pine and oak models exhibited no significant interaction effects, while the mesophytic species model exhibited a significant interaction effect for slope ($P = 0.003$). Therefore, the interaction effect for slope was included in the mortality model for the mesophytic species group. The parameter estimates of the mortality models for the pine, oak, and mesophytic species groups are presented in Tables 5, 6, and 7, respectively. The sample sizes for the pine, oak, and mesophytic species models were 1314, 1275, and 1854, respectively. The coefficients of determination (R^2) for the pine, oak, and mesophytic species models were 0.669, 0.471, and 0.463, respectively. Total tree density and tree species richness were significant within the pine and mesophytic species models. Total basal area and stand age were significant within the oak model. Slope was only significant for the severe-drought class (4) within the mesophytic species model, indicating that stands of greater slope experi-

enced greater mortality at the severe-drought class. Note that the parameter estimates for total tree density, total basal area, and slope were positive, while estimates for tree species richness and stand age were negative.

The pine and mesophytic species groups showed a general increase in mean annual mortality rate with increasing drought severity, but the oak species group did not (Fig. 2). Significant differences were found between the no-drought class (1) and the three drought classes (2–4) for the pine ($P = <0.001$, 0.047, and 0.015, respectively) and mesophytic species ($P = <0.001$, 0.007, and 0.005, respectively) groups, but not among the three drought classes (2–4). For the oak species group, the mild-drought class (2) significantly differed from the no-drought and severe-drought classes (1 and 4; $P = <0.001$ and 0.032, respectively).

DISCUSSION

Growth

Among the stand variables included in the growth models, total basal area, total tree density, and stand age were found to exhibit a significant effect on growth. All of these significant stand variables produced negative parameter estimates, indicating that they adversely affected growth under climatic drought. It is likely that stands with higher total basal area and tree density exhibit more intense competition among trees for resources (i.e., light, moisture, nutrients, growing space, etc.). Trees growing under these higher competitive environments may express lower growth rates due to resource limitations. In addition, Wang et al. (2006) found older as compared to younger open-grown white spruce trees to be more sensitive and less capable of recovering from drought stress. These results indicate that trees in older stands and/or stands with intense competition (i.e., dense stands) are more susceptible to reduced growth rates during drought. Therefore, forest management may be used to mitigate drought effects through alteration of these stand characteristics.

A general decrease in mean relative growth rate was observed with increasing drought severity. However, this

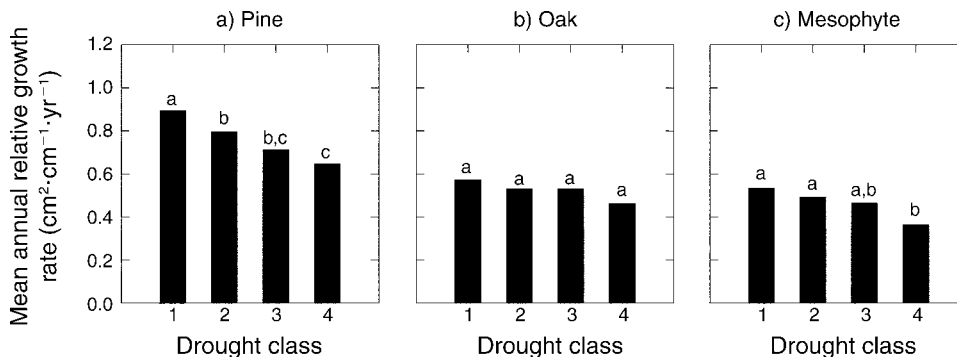


FIG. 1. Mean annual relative growth rates by drought class for the (a) pine, (b) oak, and (c) mesophytic species groups. For each species group, the results of the least significant difference test are indicated with letter designations shown above each bar. Significant differences were determined using a P value of 0.05.

TABLE 5. Parameter estimates of the mortality model for the pine species group.

Effect	Estimate	SE	<i>P</i>
PDSI 1	-0.438	0.161	0.007*
PDSI 2	-0.251	0.165	0.130
PDSI 3	-0.304	0.168	0.070
PDSI 4	-0.203	0.184	0.271
BA'	-0.035	0.080	0.661
DEN'	0.185	0.075	0.014*
SR'	-0.155	0.069	0.024*
AGE'	0.007	0.055	0.903
SLOPE'	0.018	0.010	0.063

Note: For explanations of parameter abbreviations, see Table 2.

* Significant at $P < 0.05$.

decrease was not significant among drought classes for the oak species group, suggesting that oaks can maintain their growth rates during drought episodes because of their drought tolerance. Similarly, Elliott and Swank (1994) also found that the radial growth of *Quercus prinus* and *Quercus coccinea* was not affected by drought. Oaks may achieve drought tolerance 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). Deep roots of oaks allow access to moisture from deeper soil layers, which have less soil moisture variability during drought episodes and can sustain a moisture supply during drought events. Moisture deficit results in a reduction of leaf area since cell expansion is highly sensitive to water deficit (Boyer 1988). Lower leaf area, in turn, causes a reduction in growth rate because of lower amounts of carbon-fixing tissue. Drought tolerance allows oak species to maintain leaf area and photosynthetic rates during the period of increasing soil moisture deficit and atmospheric drought (Abrams et al. 1990, Weber and Gates 1990). Since water stress changes carbon allocation from shoots to roots to increase root production and moisture acquisition (Steinberg et al. 1990, Kramer and Boyer 1995), species such as oaks with carbohydrate reserves and deep roots may have the ability to avoid significant changes in carbon allocation and thus maintain aboveground growth rates during periods of water deficit. Epron et al. (1995), Backes and Leuschner (2000), and Leuschner et al. (2000) found that oaks are more drought tolerant than beech trees because physiological functions (i.e., leaf conductance, stem hydraulic conductivity, photosynthesis, stem diameter growth, and fine root vitality) of oaks were less drought sensitive than beech and deep roots of oaks maintain a water supply during drought periods. The pine species group appears to be more sensitive to drought because a reduced growth rate was observed during a mild drought, while a reduction of growth rate was not observed until a moderate drought for the mesophytic

TABLE 6. Parameter estimates of the mortality model for the oak species group.

Effect	Estimate	SE	<i>P</i>
PDSI 1	-0.232	0.184	0.207
PDSI 2	-0.025	0.186	0.891
PDSI 3	-0.136	0.190	0.473
PDSI 4	-0.243	0.204	0.234
BA'	0.142	0.062	0.023*
DEN'	0.040	0.091	0.663
SR'	-0.095	0.093	0.311
AGE'	-0.097	0.041	0.019*
SLOPE'	0.000	0.008	0.986

Note: For explanations of parameter abbreviations, see Table 2.

* Significant at $P < 0.05$.

species group. However, both species groups exhibited significantly impaired growth rates during moderate and severe-drought episodes. Drought sensitivity of pines was unexpected because pines typically occur on dry sites or ridge tops and are thus expected to tolerate drought. Because PDSI measures moisture availability and long-term (cumulative) meteorological drought, it is likely that the same PDSI value may have different impacts on tree growth and mortality, depending on local site conditions. In the southeastern United States, pines naturally occur on dry sites of excessive drainage and poor soil water-holding capacity, which provides no effective buffer to the meteorological drought. Therefore, a small change in PDSI could have a greater impact on pine growth and mortality. It should be noted that although pines exhibited a reduction in growth rate with increasing drought severity, growth rates were still higher than those observed for oaks and mesophytic species. Drought sensitivity of mesophytic species may be related to their drought-sensitive physiological functions reported by Epron et al. (1995) and Leuschner et al. (2000, 2001). Since mesophytic species do not possess deep roots and carbohydrate reserve characteristics of oaks, changes in carbon allocation from shoots to roots during periods of moisture stress may further

TABLE 7. Parameter estimates of the mortality model for the mesophytic species group.

Effect	Estimate	SE	<i>P</i>
PDSI 1	-0.507	0.139	<0.001*
PDSI 2	-0.401	0.143	0.005*
PDSI 3	-0.372	0.146	0.011*
PDSI 4	-0.262	0.154	0.088
BA'	-0.065	0.052	0.213
DEN'	0.183	0.068	0.007*
SR'	-0.158	0.073	0.031*
AGE'	0.004	0.031	0.887
PDSI 1 × SLOPE'	0.002	0.007	0.769
PDSI 2 × SLOPE'	-0.017	0.013	0.206
PDSI 3 × SLOPE'	0.014	0.020	0.487
PDSI 4 × SLOPE'	0.088	0.028	<0.001*

Note: For explanations of parameter abbreviations, see Table 2.

* Significant at $P < 0.05$.

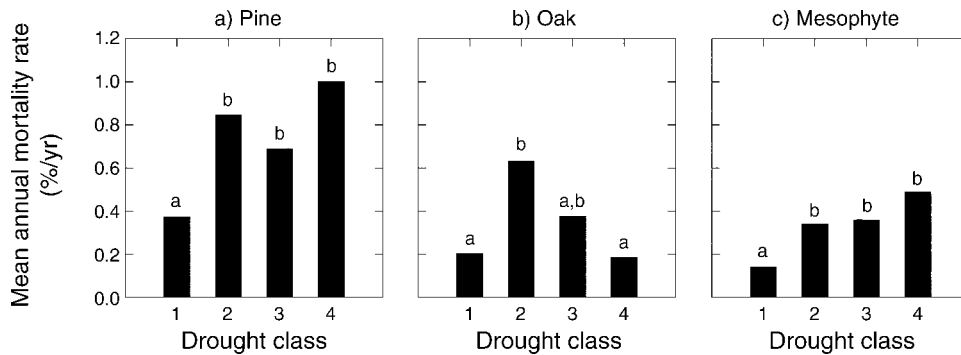


FIG. 2. Mean annual mortality rates by drought class for the (a) pine, (b) oak, and (c) mesophytic species groups. For each species group, the results of the least significant difference test are indicated with letter designations shown above each bar. Significant differences were determined using a P value of 0.05.

reduce stem diameter growth (Steinberg et al. 1990, Kramer and Boyer 1995). Our results also support those reported by Elliott and Swank (1994) in which the radial growth of *Liriodendron tulipifera* decreased during a drought episode, but contrast those reported by Olano and Palmer (2003) in which growth rates of smaller trees were higher during a drought episode within an old-growth Appalachian forest. Olano and Palmer (2003) also found that growth rates of larger size trees did not exhibit a significant change in growth rate during drought and attributed their findings to high mortality rates during the pre-drought and drought periods. Unlike Elliott and Swank (1994) and Olano and Palmer (2003), who examined localized effects of drought on growth and mortality regardless of drought severity, our study investigated the regional effects of drought in the southeastern United States under different drought severities. Contrasting results may be attributed to accounting for drought severity and stand conditions at a regional scale while ignoring site conditions at the local scale.

Mortality

Among the stand variables tested in the mortality models, total tree density, species richness, total basal area, stand age, and slope were found to exhibit a significant effect on mortality. Total tree density, basal area, and slope produced significant positive parameter estimates, indicating that mortality was higher in stands of greater density, basal area, or slope. Tree species richness and stand age produced negative parameter estimates, indicating that mortality was lower in stands of higher tree species richness or older stands. Trees within stands of higher total basal area and/or density likely experience an increased competition for resources (i.e., light, moisture, nutrients, growing space, etc.). Severe competition may result in resource limitation, which can cause mortality if carbohydrate reserves are exhausted. Our results suggest that dense stands may be more sensitive to drought and would likely suffer greater mortality rates if drought frequency and/or intensity

increase with climate change. Stands of higher tree species richness (i.e., more tree species per unit area) could mitigate competition for resources because different species possess different resource requirements and together can fully exploit available resources through mechanisms such as nitrogen fixation, hydraulic lift, and nutrient sharing via mycorrhizal networks (Read 1997, Caldwell et al. 1998, Fridley 2001). Therefore, our findings that stands of higher tree species richness experienced less mortality is not unexpected. Traditional plantation forestry that promotes monoculture environments may prove detrimental with increasing drought severity and frequency under global warming. Therefore, forest management should promote greater tree species richness in order to mitigate the negative impacts of drought and reduce mortality rates. Stand age was significant within the oak model and produced a negative parameter estimate, indicating that less mortality was observed in older oak stands during drought. Older oak trees possess larger carbohydrate reserves, which may benefit oak survival during drought. Slope was significant for the severe-drought class within the mesophytic model, indicating that the drought effect varied with site conditions for the mesophytic species group. Mesophytic stands on a greater slope are more susceptible to mortality during severe-drought conditions. Available moisture is likely limited on sites of a greater slope and becomes further limiting under severe-drought conditions. Mesophytic tree species do not have the morphological adaptations (i.e., deep roots) to cope with the increased moisture stress and subsequently suffer higher mortality rates during drought conditions (Leuschner et al. 2000). As a result, drought may limit the distribution of mesophytic species to lower slopes and coves, especially when drought frequency and/or intensity increase with climate change. The current distribution of mesophytic species may be further depleted due to climate change caused by drought sensitivity of mesophytic tree recruitment (Ibáñez et al. 2007).



PLATE 1. Lake Hartwell, a massive 22 675-ha lake straddling the Georgia–South Carolina state line, is near the epicenter of a recent drought in the southeastern United States. The drought started in early 2006. At the time of this picture (December 2008), the lake water line was nearly 5.5 m below normal levels. Much of the lake dried up, as shown by the boat ramp resting on a dry lake bottom. Photo credit: G. G. Wang.

A general increase in mean relative mortality rate was observed with increasing drought severity for the pine and mesophytic species groups. These findings are similar to those reported by Olano and Palmer (2003) in which higher mortality rates were observed for *Fagus grandifolia*, *Tilia americana*, *Acer saccharum*, and *Aesculus flava* during a drought episode. Slow-growing trees may be experiencing greater stress and, therefore, are more likely to suffer mortality during an additional stress (i.e., drought; Fahey 1998). As both the pine and mesophytic species groups exhibited a decrease in growth rate with increasing drought severity, it is expected that they will also suffer higher mortality rates. Significantly lower mortality rates observed within the no-drought class, coupled with no differences in mortality rate among the three drought classes, for both the pine and mesophytic species groups, indicate that pines and mesophytic species are sensitive to drought and suffer higher mortality rates during drought episodes, regardless of severity. Mean relative mortality rates did not increase with drought severity for the oak species group, indicating that oaks exhibit drought tolerance and can avoid mortality during drought episodes, regardless of severity. Similar to the results of the growth analyses, oaks exhibit drought tolerance

because their physiological functions are less drought-sensitive than mesophytic species (Epron et al. 1995, Leuschner et al. 2000, 2001). If drought frequency and/or intensity increase with climate change, mesophytic and pine stands will suffer higher mortality rates, which may allow possible invasion of drought-tolerant species such as oaks, provided that regeneration of these drought-tolerant species is not inhibited by drought. Higher mortality rates in pine stands during more frequent and/or intense drought episodes may change the fire regime within these stands as fuel accumulation will increase. Pine stands typically occur on dry ridges and would be more susceptible to higher intensity fires than mesophytic stands, which typically occur on moist low-lying areas. Higher intensity fires may change many closed-canopy pine stands into a pine savanna with a well-developed grasses and herbs layer. Pines might also migrate downslope to less xeric sites if frequent and severe drought prevails in the region.

Conclusion

This study presented the regional effects of drought severity on growth and mortality for the pine, oak, and mesophytic species groups within the southeastern United States. These effects were observed using forest

inventory data collected through the FHM program. Our findings indicate that pines and mesophytic species are sensitive to drought as they exhibited a significant reduction in growth rate and elevated mortality rate with increasing drought severity. In contrast, oaks exhibited no significant change in either growth or mortality rates with increasing drought severity, suggesting that oaks are tolerant of drought. The observed drought tolerance of oaks may favor a potential forest composition shift toward oak-dominated forests if drought episodes become more frequent and/or intense, provided that oak regeneration is not affected by drought events. Similarly, with more frequent and severe drought, pines could also migrate downslope to less xeric sites at the expense of mesophytic species. Our study also found that stand conditions, such as density and species richness, were significantly related to both growth and mortality rate of canopy trees. Through alteration of stand conditions, forest management could potentially be used to mitigate drought effects, especially if drought episodes become more frequent and/or intense due to climate change. Recommendations that can be drawn from this study to mitigate the future impact of drought include: (1) forest management activities should attempt to reduce competitive stress within stands of high productivity (i.e., greater basal area or density), (2) forest stands should be scheduled for harvest near minimum rotation age where possible, (3) silviculture activities should avoid creation of monocultures and encourage establishment of multiple species, and (4) the observed growth rate reduction and elevated mortality rates should be accounted for in the calculation of sustainable harvest levels. However, these recommendations are based solely on the premise of losing forest growth potential as a result of drought occurrence, and they must be considered and evaluated in conjunction with other sustainable management objectives. For example, thinning of highly competitive sites will result in a short-term accumulation of fuel loads and increased fire risk, which will contradict management goals to minimize fire hazard. However, a short-term accumulation of fine fuel loads may be preferred in the long run, resulting in a healthy forest stand of improved growth and vigor and consequently reduced susceptibility to large-scale coarse woody debris accumulation from insect and disease damage (Turchin et al. 1999, Waring and O'Hara 2005). Another example is the recommendation to schedule the harvest of forests near minimum rotation age, which may interact with objectives to sequester carbon. Biomass production efficiency slows as trees age. Therefore, harvesting of forests near minimum rotation age may improve carbon sequestration on managed forests through (1) locking up standing carbon in forest products and (2) enhanced efficiency of carbon fixation in regenerating forests (USDA 2004, Cason et al. 2006). Future research should focus on the effect of drought on regeneration of these

forests to provide more insight on the impact of drought and consequently improve mitigation measures.

ACKNOWLEDGMENTS

This study was funded by the U.S. Department of Agriculture (USDA) Forest Service. We express gratitude to Sonja Oswalt at the USDA Southern Research Station in Knoxville, Tennessee, for her assistance in the acquisition of Forest Health and Monitoring (FHM) data.

LITERATURE CITED

- Abrams, M. D. 1990. Adaptations and responses to drought in *Quercus* species of North America. *Tree Physiology* 7:227–238.
- Abrams, M. D., and M. E. Kubiske. 1990. Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin: influence of light regime and shade tolerance rank. *Forest Ecology and Management* 31:245–253.
- Abrams, M. D., J. C. Schultz, and K. W. Kleiner. 1990. Ecophysiological responses in mesic versus xeric hardwood species to an early-season drought in central Pennsylvania. *Forest Science* 36:970–981.
- Adams, H. D., and T. E. Kolb. 2004. Drought responses of conifer ecotone forests of northern Arizona: tree ring growth and leaf $\delta^{13}\text{C}$. *Oecologia* 140:217–225.
- Allen, C. D., and D. D. Brashears. 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences (USA)* 95:14839–14842.
- Backes, K., and C. Leuschner. 2000. Leaf water relations of competitive *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. trees during four years differing in soil drought. *Canadian Journal of Forest Research* 30:335–346.
- Batista, W. B., W. J. Platt, and R. E. Macchiavelli. 1998. Demography of a shade-tolerant tree (*Fagus grandifolia*) in a hurricane-disturbed forest. *Ecology* 79:38–53.
- Boyer, J. S. 1988. Cell enlargement and growth-induced water potentials. *Physiologia Plantarum* 73:311–316.
- Buell, M. F., H. F. Buell, J. A. Small, and C. D. Monk. 1961. Drought effect on radial growth of trees in the William L. Hutcheson Memorial Forest. *Bulletin of the Torrey Botanical Club* 88:176–180.
- Caldwell, M. M., T. E. Dawson, and J. H. Richards. 1998. Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia* 113:151–161.
- Cason, J. D., D. L. Grebner, A. J. Londo, and S. C. Grado. 2006. Potential for carbon storage and technology transfer in the southeastern United States. *Journal of Extension* 44:4FEA6.
- Condit, R., P. S. Ashton, N. Manokaran, J. V. LaFrankie, S. P. Hubbell, and R. B. Foster. 1999. Dynamics of the forest communities at Pasoh and Barro Colorado: comparing two 50 ha plots. *Philosophical Transactions of the Royal Society B*. 354:1739–1748.
- Donnegan, J. A., and A. J. Rebertus. 1999. Rates and mechanisms of subalpine forest succession along an environmental gradient. *Ecology* 80:1370–1384.
- Elliott, K. J., and W. T. Swank. 1994. Impact of drought on tree mortality and growth in a mixed hardwood forest. *Journal of Vegetation Science* 5:229–236.
- Engelbrecht, B. M. J., L. S. Comita, R. Condit, T. Kursar, M. T. Tyree, B. L. Turner, and S. B. Hubbell. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* 447:80–83.
- Epron, D., D. Godard, G. Cornic, and B. Genty. 1995. Limitations of net CO_2 assimilation rates by internal resistances to CO_2 transfer in leaves of two species (*Fagus*

- sylvatica* L. and *Castanea sativa* Mill.). Plant, Cell and Environment 18:43–51.
- Fahey, T. J. 1998. Recent changes in an upland forest in south-central New York. Journal of the Torrey Botanical Society 125:51–59.
- Fridley, D. 2001. The influence of species diversity on ecosystem productivity: How, where, why? Oikos 93:514–526.
- Hanson, P. J., and J. F. Weltzin. 2000. Drought disturbance from climate change: response of United States forests. Science of the Total Environment 262:205–220.
- Ibáñez, I., J. S. Clark, S. LaDeau, and J. H. R. Lambers. 2007. Exploring temporal variability to understand tree recruitment response to climate change. Ecological Monographs 77:163–177.
- Kemball, K. J., G. G. Wang, and R. A. Westwood. 2006. Are mineral soils exposed by severe wildfire better seedbeds for conifer regeneration? Canadian Journal of Forest Research 36:1943–1950.
- Kloeppel, B. D., B. D. Clinton, J. M. Vose, and A. R. Cooper. 2003. Drought impacts on tree growth and mortality of southern Appalachian forests. Pages 43–55 in D. Greenland, D. G. Goodin, and R. C. Smith, editors. Climate variability and ecosystem response at long-term ecological research sites. Oxford University Press, New York, New York, USA.
- Kramer, P. J., and J. S. Boyer. 1995. Water relations of plants and soil. Academic Press, San Diego, California, USA.
- Leuschner, C., K. Backes, D. Hertel, F. Schipka, U. Schmitt, O. Terborg, and M. Runge. 2001. Drought response at leaf, stem and fine root levels of competitive *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. trees in dry and wet years. Forest Ecology and Management 149:33–46.
- Leuschner, C., D. Hertel, H. Coners, and V. Buttner. 2000. Root competition between beech and oak: a hypothesis. Oecologia 126:276–284.
- Miles, P. D. 2000. Using biological criteria and indicators to address forest inventory data at the state level. Forest Ecology and Management 155:171–185.
- Neilson, R. P., G. A. King, R. L. DeVelice, J. Lenihan, D. Marks, J. Dolph, B. Campbell, and G. Glick. 1989. Sensitivity of ecological landscape to global climatic change. EPA-600-3-89-073, NTIS-PB-90-120-072-AS. U.S. Environmental Protection Agency, Washington, D.C., USA.
- Olano, J. M., and M. W. Palmer. 2003. Stand dynamics of an Appalachian old growth forest during a severe drought episode. Forest Ecology and Management 174:139–148.
- Oliver, C. D., and B. C. Larson. 1996. Forest stand dynamics. Wiley, New York, New York, USA.
- Palmer, W. C. 1965. Meteorological drought. Research Paper number 45. Department of Commerce, Washington, D.C., USA.
- Read, D. 1997. Mycorrhizal fungi—the ties that bind. Nature 388:517–518.
- Rogers, P. 2002. Using forest health monitoring to assess aspen forest cover change in the southern Rockies ecoregion. Forest Ecology and Management 155:223–236.
- SAS Institute. 1990. SAS/STAT user's guide. Fourth edition. Version 6. Volumes 1 and 2. SAS Institute, Cary, North Carolina, USA.
- Shannon, C. E. 1948. A mathematical theory of communications. Bell Systems Technical Journal 27:379–423.
- Small, J. A. 1961. Drought response in William L. Hutcheson Memorial Forest, 1957. Bulletin of the Torrey Botanical Club 88:180–183.
- Smith, J. B., and D. A. Tirpak. 1990. The potential effects of global climate changes on United States. Hemisphere, New York, New York, USA.
- Steinberg, S. L., J. C. Miller, and M. J. McFarland. 1990. Dry matter partitioning and vegetative growth of young peach trees under water stress. Australian Journal of Plant Physiology 17:23–36.
- Turchin, P., J. Davidson, and J. L. Hayes. 1999. Effects of thinning on development of southern pine beetle infestations in old growth stands. Southern Journal of Applied Forestry 23:193–196.
- USDA [U.S. Department of Agriculture]. 2004. US agriculture and forestry greenhouse gas inventory, 1990–2001. Technical Bulletin number 1907. Global Change Program Office, Office of the Chief Economist, U.S. Department of Agriculture, Washington, D.C., USA.
- Wang, G. G., S. Chhin, and W. L. Bauerle. 2006. The effect of natural atmospheric CO₂ fertilization suggested by open-grown white spruce in a dry environment. Global Change Biology 12:601–610.
- Waring, K. M., and K. L. O'Hara. 2005. Silvicultural strategies in forest ecosystems affected by introduced pests. Forest Ecology and Management 209:27–41.
- Weber, J. A., and D. M. Gates. 1990. Gas exchange in *Quercus rubra* (northern red oak) during drought: an analysis of relations among photosynthesis, transpiration, and leaf conductance. Tree Physiology 7:215–225.