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1 *Running Head:* Long-term drought-induced morbidity

2

3 *Title:* Multi-year drought-induced morbidity preceding tree death in Southeastern US forests

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11

12 *Abstract.* Recent forest diebacks combined with threats of future drought focus attention on the  
 13 extent to which tree death is caused by catastrophic events as opposed to chronic declines in  
 14 health that accumulate over years. While recent attention has focused on large-scale diebacks,  
 15 there is concern that increasing drought stress and chronic morbidity may have pervasive impacts  
 16 on forest composition in many regions. Here we use long-term, whole-stand inventory data from  
 17 Southeastern US forests to show that trees exposed to drought experience multi-year declines in  
 18 growth prior to mortality. Following a severe, multi-year drought, 72% of trees that did not  
 19 recover their pre-drought growth rates died within 10 years. This pattern was mediated by local  
 20 moisture availability. As an index of morbidity prior to death, we calculated the difference in  
 21 cumulative growth after drought relative to surviving conspecifics. The strength of drought-  
 22 induced morbidity varied among species and was correlated with drought tolerance. These  
 23 findings support the ability of trees to avoid death during drought events but indicate shifts that  
 24 could occur over decades. Tree mortality following drought is predictable in these ecosystems  
 25 based on growth declines, highlighting an opportunity to address multi-year drought-induced  
 26 morbidity in models, experiments, and management decisions.

27

28 *Key words:* tree, drought, mortality, morbidity, long-term, forest, adaptive management

29

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## INTRODUCTION

31           The risk of tree mortality from drought stress threatens forest structure and function at  
32 multiple time scales (Anderegg et al. 2013a, Choat et al. 2012, Dietze and Moorcroft 2011) with  
33 potentially important ecological and economic consequences. The expectation of increasing  
34 frequency and severity of drought events in the future (Li et al. 2011, Dai 2012) may require  
35 novel forest policy and management practices (Millar et al. 2007, Puettmann 2011). However,  
36 attributing tree mortality to discrete drought events can be difficult because tree mortality rates  
37 are typically low and many of the long-term data sets used to analyze drought effects have  
38 intervals of multiple years between measurements (Klos et al. 2009, Metcalf et al. 2009). These  
39 challenges create uncertainties in efforts to predict and model drought-induced tree mortality  
40 (McDowell et al. 2011). This study provides information on the time scale of tree decline  
41 following severe drought across sites and species.

42           Tree mortality trends during and after drought can be obscured by the multiple,  
43 interacting factors that contribute to declining health (Franklin et al. 1987), termed morbidity.  
44 For example, trees that die during drought are often susceptible before the drought occurs (Ogle  
45 et al. 2000, Macalady and Bugmann 2014). Species are expected to differ in their vulnerability  
46 and exposure to stress within a site, which can create variation among individuals in mortality  
47 risk (Clark et al. 2010). Trees also have multiple ways to avoid stress during drought (e.g.,  
48 resistance to cavitation, stomatal control, xylem refilling [Meinzer et al. 2010, McDowell et al.  
49 2011]), although these mechanisms can progressively degrade over time and multiple drought  
50 events (Anderegg et al. 2013a). Additionally, drought events could incite morbidity and increase  
51 future mortality risk for surviving trees (Pedersen 1998). The extent to which morbidity induced  
52 by and following drought could contribute to mortality across species and environments has not

53 been quantified. If extensive, drought-induced morbidity may signal risks for forests beyond  
 54 well-publicized die-off events (Archaux and Walters 2006, Franklin et al. 1987).

55 Here, we assess tree decline following drought with whole-stand data of annual tree  
 56 records from forests in two regions of the Southeastern US, including >28,000 trees from 35  
 57 species over 20 years (1993–2012). We tracked individual trees for up to a decade after a severe,  
 58 prolonged drought in 2000–2002 across two distinct climatic zones, the Piedmont Plateau (MAT  
 59 = 15.5°C, MAP = 1140 mm) and the southern Appalachian Mountains (MAT = 12.6°C, MAP =  
 60 1805 mm). We test the hypothesis that mortality can follow a progressive, drought-induced  
 61 decline in growth by examining the effects of post-drought recovery and local moisture  
 62 availability on decadal tree survival after this drought. We consider the factors that contributed to  
 63 recovery for the trees that survived. Then we use these responses to develop a new index that  
 64 quantifies trends in morbidity leading up to death across species, based on the difference in  
 65 cumulative growth between comparable individuals that survived and died.

66  
 67 METHODS

68 Observations of individual trees come from long-term demographic monitoring plots in  
 69 the southern Appalachian Mountains (Coweeta Hydrologic Laboratory, Macon County) and the  
 70 Piedmont Plateau (Duke Forest, Orange County) of North Carolina. Data on individual tree  
 71 growth (Clark et al. 2007) and survival (Wyckoff and Clark 2002, Metcalf et al. 2009) were  
 72 collected from each plot over a period of 8 to 21 years. Each tree has a unique observation  
 73 history, and data models are fit to observations to trace each individual's growth and survival  
 74 probability annually. From 28,879 measured trees, 5,818 died during the study. Further details on  
 75 field methods, models, and diagnostics can be found in Clark et al. (2010). Each individual was

76 exposed to the site-level environmental conditions as well as local environmental variation. We  
 77 used the topographic wetness index ( $\omega_i$ ), calculated with local elevation data, as an indicator of  
 78 tree moisture availability. The topographic wetness index describes local drainage patterns in a  
 79 catchment and provides a relative measure of soil moisture availability in these forests (Moore et  
 80 al. 1993, Hwang et al. 2009, Berdanier and Clark *unpublished data*). We also considered the  
 81 influence of local basal area, calculated as the summed basal area of neighbors within 10m of  
 82 each tree, and the change in local basal area over the study period.

83 Individual growth rates were quantified with estimates of annual diameter increment (cm  
 84  $\text{yr}^{-1}$ ). For relative growth vigor preceding mortality ( $\gamma$ ), we identified all individuals that died  
 85 during the study and, for each individual that died ( $i$ ), we selected conspecific trees (same  
 86 species, same plot) that survived for the entire study ( $j$ ) and calculated the average growth rate in  
 87 each year ( $g_i$ ). Then, we took the log ratio of the growth rate for each dead tree ( $g_{t,i}$ ) versus the  
 88 growth rate of the average conspecific in each year prior to their death,  $\gamma_{t,i} = \ln(g_{t,i}/\overline{g_{t,j}})$ .  
 89 Negative vigor values indicate growth rates that are lower in dead trees than in surviving trees.

90 For comparisons of individual growth before and after drought ( $\rho$ , an indicator of  
 91 recovery or morbidity), we averaged the post-drought growth rates across surviving years (for  
 92 trees that died) or the remainder of the study (for trees that survived) for each individual to  
 93 estimate growth after drought ( $\overline{g_{post,l}}$ ). Then, we calculated the average pre-drought growth rate  
 94 for each individual ( $\overline{g_{pre,l}}$ ) and used the log ratio of average growth rates after and before the  
 95 drought as an index of recovery  $\rho_i = \ln(\overline{g_{post,l}}/\overline{g_{pre,l}})$ . Here, negative values indicate lower  
 96 growth after the drought than before the drought. We assumed recovery if post-drought growth  
 97 rate ratios were greater than the 10<sup>th</sup> percentile of surviving trees. We tested the effects of

98 individual growth recovery ( $\rho_i$ ) and individual wetness conditions ( $\omega_i$ ) on decadal survival ( $s_i$ )  
 99 following the 2000–2002 drought with a Bayesian logistic regression,

100  $s_i \sim \text{Bernoulli}(\pi_i),$

101  $\text{logit}(\pi_i) = \beta_0 + \beta_1 \rho_i + \beta_2 \omega_i + \beta_3 \rho_i \omega_i.$

102 Parameters were fit across species and sites that were exposed to and survived the 2000–2002  
 103 drought ( $n = 11,662$ ). For surviving trees, we examined the effect of tree size (natural log of  
 104 individual diameter) and the change in local basal area (natural log of basal area loss within 10m)  
 105 on individual growth recovery with a Bayesian linear regression. We used uninformative normal  
 106 priors on all regression parameters and ran 50,000 MCMC iterations with the *MCMCpack* library  
 107 in R to generate posterior estimates of each parameter.

108 To calculate cumulative morbidity for each individual that died ( $\chi_i$ ), we first summed the  
 109 growth between the drought and eventual mortality ( $d_i$ ),  $G_i = \sum_{t=2003}^{d_i} g_{i,t}$ . Next, we summed the  
 110 growth for each surviving conspecific ( $j, i$ ) over the same time period and took the average across  
 111 survivors,  $G_{j,i} = \overline{\sum_{t=2003}^{d_i} g_{j,t}}$ . Then, we calculated the log ratio of the cumulative growth for the  
 112 average conspecific over the time period versus that of each dead tree,  $\chi_i = \ln(G_{j,i}/G_i)$ . We  
 113 generated summary statistics for each species that had at least 10 dead individuals with these  
 114 individual measures and compared these values to a species drought-tolerance index that  
 115 incorporates information on physiological responses to water stress and habitat occurrence  
 116 observations (Niinemets and Valladares 2006).

117 RESULTS

118 Three severe drought events occurred during the 20 year study, including a prolonged  
 119 drought in 2000–2002 that was preceded by a decade of mesic conditions on average. During this  
 120 drought, the June-July-August Palmer Drought Severity Index (JJA PDSI) in the Appalachian



121 Mountains exceeded the 90<sup>th</sup> percentile of 100-year drought severity and the 2002 JJA PDSI in  
 122 the Piedmont Plateau was in the 96<sup>th</sup> percentile. Survival rates remained high across these events  
 123 and showed no relationship with drought severity between censuses (Appendix A, Table A1). In  
 124 contrast, we found decreased growth during drought years across sites and species (Appendix A,  
 125 Table A2). For the trees that died during drought years (n = 823, 14% of total deaths), 87% had  
 126 pre-drought growth rates that were below the average for conspecific individuals in the same  
 127 stands over periods of 2 to 5 years. Declining growth rates suggest that these trees were  
 128 susceptible for multiple years before the drought, consistent with tree-ring observations during  
 129 drought events in other ecosystems (e.g. Macalady and Bugmann 2014). For the remaining trees  
 130 that survived the drought, we examined whether drought exposure further affected their long-  
 131 term growth and survival.

132 We compared the health statuses of trees that survived and died after droughts to account  
 133 for pre-drought risk. Tree mortality can follow declines in radial stem growth over multiple years  
 134 (Waring 1987, Wyckoff and Clark 2002), which we observed as a decline in vigor compared to  
 135 conspecific trees (Fig. 1). We examined if the growth rates of trees changed following drought  
 136 and, if so, whether it was associated with a decline in survival. We found that decadal survival  
 137 for trees that were exposed to the 2000–2002 drought was positively related to both post-drought  
 138 recovery ( $\beta_1 = 5.64$ , 95% credible interval [CI] = 5.26–6.05) and tree moisture availability ( $\beta_2 =$   
 139 0.14, 95% CI = 0.08–0.19), a relationship that was consistent across sites and species. Decadal  
 140 survival was independent of local basal area before the drought, consistent with findings in other  
 141 studies (Klos et al. 2009, Floyd et al. 2009, Ganey and Vojta 2011).

142 Trees that survived the drought but died within the next 10 years had lower growth rates  
 143 on average for the rest of their lives than they did prior to drought (54 and 71% of pre-drought



144 levels in the Piedmont Plateau and Appalachian Mountains) (Fig. 2). This pattern held regardless  
 145 of the post-drought time interval examined, although it was exacerbated following exposure to  
 146 additional droughts (Appendix A, Fig. A1). Similar to the trees that died during drought and  
 147 consistent with our observation of multi-year declines prior to death (Fig. 1), 64% of the trees  
 148 that died in the next 10 years had pre-drought growth rates that were lower than the average  
 149 surviving conspecific. Those trees were performing poorly compared to their neighbors prior to  
 150 the drought and experienced further growth declines after the drought. Trees that survived for  
 151 over 10 years following the drought resumed pre-drought growth patterns and had higher growth  
 152 rates than before the drought on average while trees that ultimately died showed continued  
 153 morbidity. For the trees that survived, their growth recovery was positively related to both tree  
 154 size (posterior mean effect = 0.129, 95% CI = 0.121–0.137) and, less strongly, the loss of  
 155 neighbor basal area over the study period (posterior mean effect = 0.016, 95% CI = 0.007–  
 156 0.024). Of all trees that did not recover pre-drought growth rates, 72% died within 10 years.

157 Survival was higher for trees in wet local environments than those in dry areas, in  
 158 agreement with another study in this region (Klos et al. 2009). The negative effect of declining  
 159 growth on survival was amplified in dry locations, based on the positive interaction between  
 160 drought recovery and tree moisture availability from the topographic wetness index ( $\beta_3 = 0.38$ ,  
 161 95% CI = 0.20–0.56). In contrast, survival in the relatively mesic period preceding this drought  
 162 (1993–1999) responded similarly to growth declines but showed no association with the  
 163 topographic wetness index (Appendix A, Table A3). While the multi-year declines in growth  
 164 preceding mortality are similar between the two distinct time periods, these declines were  
 165 greatest for trees in dry local environments only after the drought.

166 Our morbidity measure quantifies the cumulative differences in growth between trees that  
 167 die and comparable survivors and provides an index for the risk of mortality from growth stress  
 168 following drought. The cumulative morbidity for trees that were exposed to the 2000-2002  
 169 drought and ultimately died varied by species (Fig. 3), with most species showing a pattern of  
 170 decline that extended for multiple years. Averaged across species, mortality risk increased when  
 171 the cumulative diameter growth fell below 54% of the growth of surviving conspecifics (range  
 172 across species = 21–125%), consistent with our observation that mortality is a multi-year process  
 173 (Fig 1). The only species that experienced mortality at growth rates above surviving conspecifics  
 174 on average (negative morbidity) was *Tsuga canadensis*, which is currently experiencing rapid  
 175 declines by an exotic insect that equally targets healthy trees (Nuckolls et al. 2009). The average  
 176 species morbidity index values were correlated with a species drought-tolerance index ( $r = 0.713$ ,  
 177 Fig. 4) (Niinemets and Valladares 2006), where species characterized as drought intolerant were  
 178 relatively unable to withstand large cumulative depressions in growth prior to mortality.

180 DISCUSSION

181 Our results demonstrate a pattern of multi-year declines in tree growth following a severe  
 182 drought across sites in the Southeastern US. These declines were related to a reduced survival  
 183 probability over the following decade and associated with local drought severity. While most of  
 184 the trees that were unable to recover from this stress ultimately died, the cumulative morbidity  
 185 that trees experienced prior to death varied among species (Fig. 3), indicating possible shifts in  
 186 species composition under different climate scenarios. Dying trees that have high morbidity prior  
 187 to death are under stress relative to surviving conspecifics and are prone to die in the years after  
 188 drought because of their inability to recover (Fig. 2), especially if they experience subsequent

189 droughts. The finding that drought can set in motion protracted morbidity leading to eventual  
 190 death suggests that drought frequency and severity may already be changing forest composition  
 191 and structure beyond regions where large diebacks are observed (Allen et al. 2010). For most  
 192 species here, drought stress contributes to deteriorating health over multiple years, exacerbated  
 193 by dry habitats.

194 Our observation that mortality can be prolonged following drought events could result  
 195 from interactions between hydraulic status, carbon balance, and additional contributing factors  
 196 that lead to growth morbidity and predispose an individual to die (Pedersen 1998, McDowell et  
 197 al. 2011). For example, while trees may avoid systemic hydraulic failure over short time periods  
 198 (Fisher et al. 2006, Plaut et al. 2012), non-lethal loss of canopy conductance could be a precursor  
 199 for multi-year morbidity (Anderegg et al. 2013a). Moreover, many of the trees that died during  
 200 and after drought had lower vigor prior to the drought than surviving conspecifics, indicating  
 201 potential predisposition to drought vulnerability, possibly from interactions with pathogens,  
 202 insects, or habitat (Franklin et al. 1987, Anderegg et al. 2015).

203 The long-term nature of tree decline following drought in Southeastern US forests has  
 204 important implications for the monitoring and management of drought impacts in these  
 205 ecosystems (Anderegg et al. 2013b). The relationship between the ability to endure cumulative  
 206 morbidity prior to death and species drought tolerance (Fig. 4) highlights differing degrees of  
 207 vulnerability among species. Our cumulative morbidity measure, combined with the relationship  
 208 between growth and mortality, may provide accurate predictions for forest responses to droughts  
 209 of varying frequency and intensity in dynamic global vegetation models, which already have  
 210 strong growth modules (McDowell et al. 2011). Field monitoring and adaptive management  
 211 efforts can focus on growth morbidity as a predictor of drought mortality with particular



232 LITERATURE CITED

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319 SUPPLEMENTAL MATERIAL

320 Ecological Archives

- 321 Appendix A: Annual survival rates, pre-drought survival, and progressive declines after multiple  
 322 drought events

323 FIG. 1. Decline in growth vigor prior to death ( $\gamma$  in text). Growth rates of trees that died were  
 324 lower than those of average surviving comparable trees for multiple years prior to death (line and  
 325 dark shading shows mean  $\pm$  SE) although there was large variation across individuals (light gray  
 326 shading is 95% range).

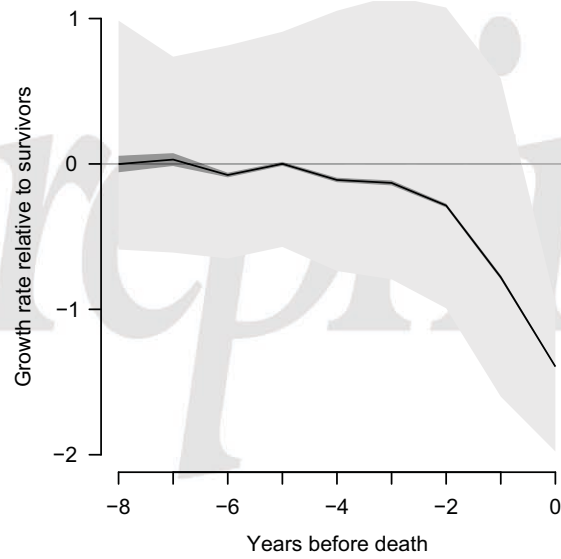
327  
 328 FIG. 2. Post-drought survival depends on growth recovery ( $\rho$  in text). Growth rates for trees that  
 329 died in the decade after drought (shaded) were lower than pre-drought levels in both the  
 330 Appalachian Mountains (top) and the Piedmont Plateau (bottom). Trees that survived throughout  
 331 the study (open) showed increased growth in years following drought on average. Vertical lines  
 332 and horizontal bars show mean  $\pm$  SE and distribution intervals range over 95% of individuals.

333  
 334 FIG. 3. Drought-induced morbidity preceding tree death ( $\chi$  in text). Post-drought growth  
 335 morbidity prior to death varied among species, with trees of many species showing cumulative  
 336 depressions in growth (positive morbidity values) compared to surviving conspecifics prior to  
 337 mortality. Vertical lines and horizontal bars show mean  $\pm$  SE and distribution intervals range  
 338 over 95% of individuals.

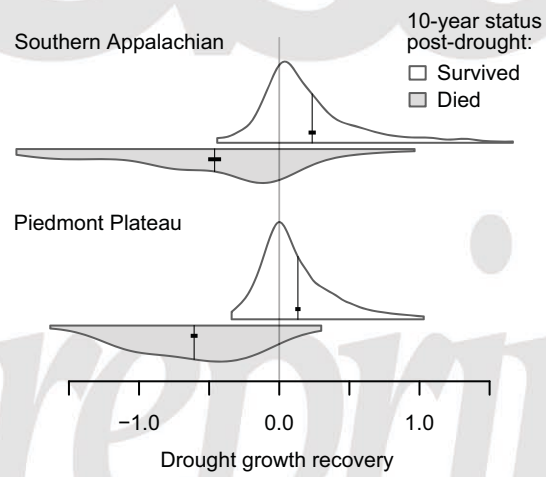
339  
 340 FIG. 4. Positive correlation between the average posterior post-drought morbidity index and  
 341 species drought tolerance index. Dashed line shows a linear regression between indices.

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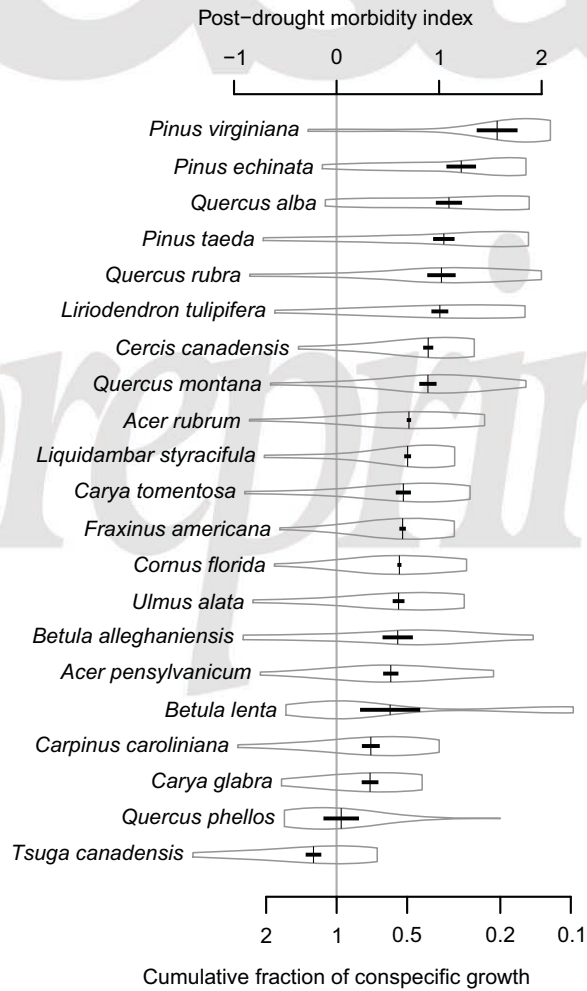
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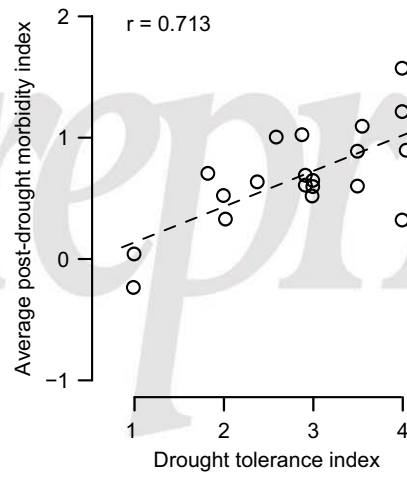


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