**Title:** Combining functional traits with dendrochronology reveals that tree height and hydraulics shape growth responses across droughts in a temperate broadleaf forest

**Authors:** Ian R. McGregor1,2, Ryan Helcoski1, Norbert Kunert1,3, Alan J. Tepley1,4, Erika B. Gonzalez-Akre1, Valentine Herrmann1, Joseph Zailaa1,5, Atticus E.L. Stovall1,6,7, Norman A. Bourg1, William J. McShea1, Neil Pederson8, Lawren Sack9,10, Kristina J. Anderson-Teixeira1,3\*

**Author Affiliations:**

1. Conservation Ecology Center; Smithsonian Conservation Biology Institute; National Zoological Park, Front Royal, VA 22630, USA
2. Center for Geospatial Analytics; North Carolina State University; Raleigh, NC 27607, USA
3. Center for Tropical Forest Science-Forest Global Earth Observatory; Smithsonian Tropical Research Institute; Panama, Republic of Panama
4. Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta, Canada
5. Biological Sciences Department; California State University; Los Angeles, CA 90032, USA
6. Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22903, USA
7. NASA Goddard Space Flight Center; Greenbelt, MD 20771, USA
8. Harvard Forest, Petersham, MA 01366, USA
9. Department of Ecology and Evolutionary Biology; University of California, Los Angeles; Los Angeles, CA 90095, USA
10. Institute of the Environment and Sustainability; University of California, Los Angeles; Los Angeles, CA 90095, USA

\*corresponding author: [teixeirak@si.edu](mailto:teixeirak@si.edu); +1 540 635 6546

|  |  |  |  |
| --- | --- | --- | --- |
| Text | word count | other | n |
| Total word count (excluding summary, references and legends) | currently ~5855 (strict limit 6,500) | No. of figures | 2 (both colour) |
| Summary | currently 194 (limit 200) | No. of Tables | 5 |
| Introduction | currently ~1468 | No of Supporting Information files | 6 |
| Materials and Methods | currently ~2162 |  |  |
| Results | currently ~674 |  |  |
| Discussion | currently ~1551 (limit 30% of total (not strict), or 1950 if manuscript reaches word limit) |  |  |
| Acknowledgements | currently ~124 |  |  |

### Summary

* As climate change is driving increased drought frequency and severity in many forested regions around the world, mechanistic understanding of factors conferring drought resistance in trees is increasingly important. The dendrochronological record provides a window through which we can understand how tree size and species’ traits shape the species’ growth responses during droughts.
* We analyzed tree-ring records for twelve species of an oak-hickory forest - representing 97% of woody productivity - in the 25.6-ha ForestGEO plot in Virginia (USA) to test hypotheses for how tree size, microenvironment characteristics, and species’ traits shaped drought responses across the three strongest regional droughts over a 60-year period (1950 - 2009).
* Individual-level drought resistance decreased with tree height, which was the dominant size-related variable affecting drought response. Resistance was greater among species whose leaves lost turgor (wilted) at more negative water potentials, and whose leaves experienced less shrinkage upon desiccation. However, there was substantial variation in the best predictor variables across the three drought periods.
* We conclude that hydraulic traits and tree height can explain variation in the tree ring record spanning historical droughts. Thus, these factors can be useful for predicting future drought responses under climate change.

*Key words*: annual growth; canopy position; drought; Forest Global Earth Observatory (ForestGEO); leaf hydraulic traits; temperate broadleaf deciduous forest; tree height; tree-ring

### Introduction

Forests play a critical global role in climate regulation [@bonan\_forests\_2008], yet there remains enormous uncertainty as to how the terrestrial carbon (C) sink, which is dominated by forests, will respond to climate change [@friedlingstein\_climatecarbon\_2006]. An important aspect of this uncertainty lies with physiological responses of trees to drought [@kennedy\_implementing\_2019]. In many forested regions around the world, the risk of severe drought is increasing [@trenberth\_global\_2014]; [Dai et al. 2018](https://link.springer.com/article/10.1007/s40641-018-0101-6)), often despite increasing precipitation [@intergovernmental\_panel\_on\_climate\_change\_climate\_2015]. Droughts, exasperated by climate change, have been affecting forests worldwide [@allen\_global\_2010], and are expected to continue as one of the most important drivers of forest change in the future [@allen\_underestimation\_2015]. Understanding and modeling forest responses to drought requires elucidation of how tree size, microenvironment, and species’ traits jointly influence individual-level drought resistance, and the extent to which their influence is consistent across droughts. However, it has proved difficult to resolve the many factors affecting tree growth during drought with available forest census data, which only rarely captures extreme drought, and with tree-ring records, which rarely represent many species and size classes at a single site and are not necessarily associated with ecological data. The aim of this study was to pair tree-ring and forest plot data to test how tree size and traits shaped growth responses to historical droughts.

Many studies have shown that within species, large trees tend to be more affected by drought. Greater growth reductions for larger trees was first shown on a global scale by @bennett\_larger\_2015, and numerous subsequent studies have reinforced this finding (*e.g.*, @stovall\_tree\_2019; @hacket-pain\_consistent\_2016). It has yet to be resolved which of several potential underlying mechanisms drive this pattern. First, tree height may be a primary driver. Taller trees face the biophysical challenge of lifting water greater distances against the effects of gravity and friction [@mcdowell\_relationships\_2011; @mcdowell\_darcys\_2015; @ryan\_hydraulic\_2006; @couvreur\_water\_2018]. Vertical gradients in stem and leaf traits–including smaller and thicker leaves (higher leaf mass per area-LMA), greater resistance to hydraulic dysfunction (i.e., more negative water potential at 50% loss of hydraulic conductivity, ), and lower hydraulic conductivity at greater heights [@couvreur\_water\_2018; @koike\_leaf\_2001; @mcdowell\_relationships\_2011]–enable trees to become tall [@couvreur\_water\_2018]. Indeed, tall trees require wood of greater hydraulic efficiency in their basal portions, such that xylem conduit diameters are wider in taller trees within and across species [@olson\_plant\_2018; @liu\_hydraulic\_2019], making large trees more vulnerable to embolism during drought [@olson\_plant\_2018]. Traits conducive to efficient water transport may also lead to poor ability to recover from, or re-route, water around embolisms [@roskilly\_conflicting\_2019]. Second, larger trees may have lower drought resistance because they tend to occupy more exposed crown positions, where they are exposed to higher solar radiation, greater wind speeds, and lower humidity (e.g., @koike\_leaf\_2001; @kunert\_revised\_2017). Subcanopy trees tend to fare better specifically due to the benefits of a buffered environment [@pretzsch\_drought\_2018]. Potentially counteracting the biophysical challenges faced by large trees, their larger root systems confer a potential advantage in terms of allowing greater access to water; however, it appears that this effect is usually insufficient to offset the costs of height and/or crown exposure. A final mechanism that could mediate tree size-related responses to drought is how species, and their associated hydraulic traits, are distributed with respect to size [@meakem\_role\_2018; @liu\_hydraulic\_2019]. Understanding the mechanisms driving the greater growth reductions of larger trees during drought will require sorting out the interactive effects of height, canopy position, root water access, and species’ traits.

Debates have also arisen regarding the traits that would influence tree growth responses to drought. Commonly-measured traits including wood density () and leaf mass per area () have been linked to drought responses in some temperate deciduous forests [@abrams\_adaptations\_1990; @guerfel\_impacts\_2009; @hoffmann\_hydraulic\_2011] and other forest biomes around the world [@greenwood\_tree\_2017]. However, in other cases these traits could not explain drought tolerance ([Maréchaux et al. 2019](https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.13321)), or the direction of response was not always consistent; for instance, higher has been associated with greater drought resistance at a global scale [@greenwood\_tree\_2017] but correlated negatively with tree performance during drought in a broadleaf deciduous forest in the southeastern United States [@hoffmann\_hydraulic\_2011]. Thus, their role may be controlled by indirect correlations with other traits within life-history strategies [@hoffmann\_hydraulic\_2011]. Recent work has shown a great potential for hydraulic traits to predict growth and mortality responses. Hydraulic traits including water potentials at which percent loss conductivity surpass a certain threshold (, , ) and hydraulic safety margin have enabled prediction of drought performance [@anderegg\_hydraulic\_2018] but are time-consuming to measure and therefore infeasible for predicting or modeling drought responses in highly diverse forests (*e.g.*, in the tropics). More rapidly measurable leaf hydraulic traits with direct linkage to plant hydraulic function can explain greater variation in plant distribution and function [@medeiros\_extensive\_2019]. These include leaf area shrinkage upon desiccation (; [@scoffoni\_leaf\_2014]) and the leaf water potential at turgor loss point (), *i.e.,* the water potential at which leaf wilting occurs [@bartlett\_correlations\_2016]. The abilities of both and to explain tree performance under drought remains untested.

The long time frame captured in tree-ring data enables us to address the question of whether tree size and species’ traits have similar influence across different drought events, or whether that influence is more strongly predicted by community-level responses to variable drought severity, duration, and timing based on tree size and traits. Tree growth responses vary with drought characteristics such as timing and atmospheric demand [@dorangeville\_drought\_2018], but the question of how tree size and species’ traits impact growth responses across droughts still remains. While tree-ring studies provide long-term records of tree responses to multiple droughts (e.g., @lloret\_components\_2011; @dorangeville\_drought\_2018), they generally focus on species-level or taxa responses, and do not consider the roles of tree size and microenvironment. The ecological field-based studies that have shaped our understanding of the role of tree size and microenvironment in forest drought responses generally examine only a single drought and tend to focus disproportionately on the most extreme droughts with dramatic impacts (*e.g.*, @allen\_global\_2010; @bennett\_larger\_2015; @stovall\_tree\_2019; @anderegg\_meta-analysis\_2016). Thus, our knowledge of forest responses to more moderate but frequent droughts - e.g., those with historical return intervals of one to two decades - remains limited. There is evidence that the degree to which larger trees are more impacted by drought increases with the severity of drought conditions [@bennett\_larger\_2015; @stovall\_tree\_2019], so the influence of tree size may be less in weaker–but more common–droughts. Thus, while we expect many of the mechanisms shaping drought responses to be universal, we have little understanding of how tree size and traits interact with drought characteristics, and the extent to which their influence is consistent across droughts.

To yield a functional understanding of how tree size, microenvironment characteristics, and species’ traits collectively shape drought responses, we tested a series of hypotheses and associated specific predictions (Table 1) based on the combination of tree-ring records from three droughts events (1966, 1977, 1999), species functional and hydraulic trait measurements, and forest census data from a plot in Virginia (USA). First, we focus on the role of tree size and its interaction with microenvironment. We test whether, consistent with most forests globally, larger-diameter trees tend to have lower drought resistance () in this forest, which is in a region (eastern North America) represented by only two studies in @bennett\_larger\_2015. We then test hypotheses designed to disentangle the relative importance of tree height; crown exposure; and soil water availability, which should be greater for larger trees in dry but not in perpetually wet microsites. Second, we focus on the role of species’ functional and hydraulic traits, testing the hypothesis that species’ traits-–particularly leaf hydraulic traits-–predict . We test predictions that drought resistance is correlated with wood density–either postively [@greenwood\_tree\_2017] or negatively [@hoffmann\_hydraulic\_2011]– and positively correlated with specific leaf area, but that hydraulic leaf traits including and are better predictors. We expect that ring-porous species would have greater drought resistance than semi-ring and diffuse-porous species, as has been previously observed [@kannenberg\_linking\_2019; @elliott\_forest\_2015; @friedrichs\_species-specific\_2009].

### Materials and Methods

*Study site*

Research was conducted at the 25.6 ha ForestGEO (Forest Global Earth Observatory) study plot at the Smithsonian Conservation Biology Institute (SCBI) in Virginia, USA (38°53’36.6“N, 78°08’43.4”W) [@bourg\_initial\_2013; @andersonteixeira\_ctfs-forestgeo\_2015]. SCBI is located in the central Appalachian Mountains at the northern boundary of Shenandoah National Park. Elevations range from 273-338m above sea level with a topographic relief of 65m [@bourg\_initial\_2013]. Climate is humid temperate, with mean annual temperature of 12.7C and precipitation of 1005 mm during our study period (1960-2009; source: CRU TS v.4.01; @harris\_updated\_2014). Dominant tree taxa within this secondary forest include *Liriodendron tulipifera*, oaks (*Quercus* spp.), and hickories (*Carya* spp.).

*Data collection and preparation*

All analysis beyond basic data collection was performed using R version 3.5.3 [@R-base].

Within or just outside the ForestGEO plot, we collected data on a suite of variables including tree size, microenvironment characteristics, and species traits (Table 2). The SCBI ForestGEO plot was measured in 2008, 2013, and 2018 following standard ForestGEO protocols, whereby all free-standing woody stems 1cm diameter at breast height (DBH) were mapped, tagged, measured at DBH, and identified to species [@condit\_tropical\_1998]. From this census data, we used measurements of DBH from 2008 to calculate historical DBH and data for all stems 10cm to analyze functional trait composition relative to tree height (all analyses described below). Census data are available through the ForestGEO data portal (www.forestgeo.si.edu).

We analyzed tree-ring data (cambial growth increment) from 571 trees representing the twelve species contributing the most to woody aboveground net primary productivity (), which together comprised 97% of study plot between 2008 and 2013 [@helcoski\_growing\_2019] (Figure S1). Cores were collected within the ForestGEO plot at breast height (1.3m) in 2010-2011 or 2016-2017 using a 5mm increment borer. In 2010-2011, cores were collected from randomly selected live trees of species with at least 30 individuals 10cm DBH [@bourg\_initial\_2013]. In 2016-2017, cores were collected from all trees found dead in the annual mortality census [@gonzalezakre\_patterns\_2016]. Cores were sanded, measured, and cross-dated using standard procedures, as detailed in [@helcoski\_growing\_2019]. The resulting chronologies were published in association with @helcoski\_growing\_2019 (DOI: 10.5281/ zenodo.2649302).

For each cored tree, we combined tree-ring records and allometric equations of bark thickness to retroactively calculate DBH for the years 1950-2009. Prior DBH was estimated using the following equation:

Here, denotes the year of interest, denotes ring width derived from cores, and denotes bark thickness. Bark thickness was estimated from species-specific allometries based on the bark thickness data from the site [@andersonteixeira\_size-related\_2015]. Specifically, we used linear regression equations on log-transformed data to relate bark thickness to diameter inside bark from 2008 data (Table S1), which were then used to determine bark thickness in the retroactive calculation of DBH.

Height measurements (, n=1518 trees) were taken by several researchers between 2012 to 2019. Measurement methods included manual [@stovall\_assessing\_2018; @neon\_national\_2018], digital rangefinders [@andersonteixeira\_size-related\_2015; @neon\_national\_2018], and automatic, ground-based LiDAR [@stovall\_terrestrial\_2018]. Rangefinders used either the tangent method (Impulse 200LR, TruPulse 360R) or the sine method (Nikon ForestryPro) for calculating heights. Both methods are associated with some error [@larjavaara\_measuring\_2013], but in this instance there was no clear advantage of one or the other. Measurements from the National Ecological Observatory Network (NEON) were collected nearby the ForestGEO plot following standard NEON protocol, whereby vegetation of short stature was measured with a collapsible measurement rod, and taller trees with a rangefinder [@neon\_national\_2018]. Species-specific height allometries were developed (Table S2) using logarithmic regression (). For species with insufficient height data to create reliable species-specific allometries, heights were calculated from an equation developed using all height measurements.

Crown position ()–a categorical variable including dominant, co-dominant, intermediate, and suppressed–was recorded for all cored trees that remained standing during the growing season of 2018 following the protocol of @jennings\_assessing\_1999. While some tree crowns undoubtedly changed position in the 52 years between the 1966 drought and our observations in 2018, in this case the bias would be unlikely to result in false acceptance of our hypothesis (i.e., type I error unlikely; type II error possible). An analysis of crown position relative to height (Fig. 2d) and height changes since the beginning of the study period indicated that changes were fairly small relative to differences among canopy positions (Fig. S3), with average tree height growth confined to ~0.82m from 1966 to 1977, ~1.45m from 1977 to 1999, and ~1.97m from 1999 to 2018. Dominant and co-dominant trees were similar in height (Figs. 2d, S3).

Topographic wetness index (TWI) was calculated using the dynatopmodel package in R (Figure S1) [@R-dynatopmodel]. Originally developed by @beven\_physically\_1979, TWI was part of a hydrological run-off model and has since been used for a number of purposes in hydrology and ecology [@sorensen\_calculation\_2006]. TWI calculation depends on an input of a digital elevation model (DEM), and from this yields a quantitative assessment defined by how “wet” an area is, based on areas where run-off is more likely. From our observations in the plot, the calculation of TWI performed comparatively better at categorizing wet areas than the calculation of a distance matrix from a stream shapefile.

Hydraulic traits were collected in August 2018 (Table 3). We sampled small sun-exposed branches within eight meters of the ground from three individuals of each species in and around the ForestGEO plot. Sampled branches were re-cut under water at least two nodes above the original cut and re-hydrated overnight in covered buckets under opaque plastic bags before measurements were taken. Rehydrated leaves taken towards the apical end of the branch (n=3 per individual: small, medium, and large) were scanned, weighed, dried at 60 C for 48 hours, and then re-scanned and weighed. Leaf area was calculated from scanned images using the LeafArea R package [@R-LeafArea]. was calculated as the ratio of leaf dry mass to fresh area. was calculated as the percent loss of area between fresh and dry leaves. was calculated for ~1cm diameter stem samples (bark and pith removed) as the ratio of dry weight to volume, which was estimated using Archimedes’ displacement. We used the rapid determination method of @bartlett\_rapid\_2012 to estimate water potential at turgor loss point (). Briefly, two 4mm diameter leaf discs were cut from each leaf, tightly wrapped in foil, submerged in liquid nitrogen, perforated 10-15 times with a dissection needle, and then measured using a vapour pressure osmometer (VAPRO 5520, Wescor, Logan, UT, USA). Osmotic potential () given by the osmometer was used to estimate () using the equation [@bartlett\_rapid\_2012].

To characterize how environmental conditions vary with height, data were obtained from the National Ecological Observation Network (NEON) tower located <1km from the study area. We used data on wind speed, relative humidity, and air temperature, all measured over a vertical profile spanning from 7.2 m height to above the top of the tree canopy (31.0 or 51.8m, depending on censor), for the years 2016-2018 [@noauthor\_national\_2018]. After filtering for missing and outlier values, the data were consolidated to represent the mean values per sensor height per day. The range of these means were then aggregated at a monthly scale.

*Identification of drought years*

We identified droughts within the time period 1950-2009, defining drought [@slette\_how\_2019] as events with both anomalously dry peak growing season climatic conditions and widespread reductions in tree growth, i.e., to focus on droughts that substantially impacted the forest community. We identified ). These were the years with driest conditions during May-August (MJJA), the current-year months to which annual growth was most sensitive for trees at this site ( @helcoski\_growing\_2019). We considered two metrics of moisture deficit: NOAA Divisional Data’s Palmer Drought Severity Index (PDSI) and the difference between monthly potential evapotranspiration () and precipitation (); data obtained from the ForestGEO Climate Data Portal (<https://github.com/forestgeo/Climate>) in August 2018, with monthly PET and PRE sourced from Climatic Research Unit high-resolution gridded dataset (CRU TS v.4.01; @harris\_updated\_2014). The driest years were identified through ranking mean MJJA or for the time period from driest to wettest. Three of the five years between 1950 and 2009 with greatest moisture deficit () during MJJA consistently ranked as the three driest in terms of : 1966, 1977, and 1999, which had mean MJJA of 83, 87, and 80 mm mo-1, respectively (Table S3). The years 1964 and 2007 also ranked among the five lowest (84 and 82 mm mo-1, respectively), but were not among the lowest in terms of PDSI and were thus not identified as candidate years for inclusion as top drought years (Table S3). We defined years with widespread growth reduction (“pointer years”) as those where >25% of the cored trees experienced >30% reduction in basal area increment () relative to the previous 5 years, following the drought resistance () metric of [@lloret\_components\_2011]. values <1 and >1.0 indicate growth reductions and increases respectively. Pointer years were identified using the pointRes package [@R-pointRes] in R. Four years met our criteria: 1966, 1977, 1991, and 1999. We excluded 1991 (26.5% of trees experienced >30% growth reduction, mean resistance= -13.8%), as it was not among the driest of the time period (Table S3). Rather, the severity of growth reduction may be explained in part by defoliation by gypsy moths (*Lymantria dispar* L.) from approximately 1988-1995, which strongly impacted *Quercus* spp. [@twery\_effects\_1991]. ). The droughts differed in intensity and prior onset (Fig. S2, Table S3). The 1966 drought was preceded by two years of moderate drought during the growing season and severe to extreme drought starting the previous fall and in August reached the minimum growing season (-4.82) among of any of the three droughts. The 1977 drought was the least intense throughout the growing season, and was preceded by 2.5 years of near-normal conditions, making it the mildest of the three droughts. The 1999 drought was preceded by wetter than average conditions until the previous June, but reached the lowest PDSI during May-July.

*Statistical Analysis*

For each drought period, we calculated drought resistance () as the ratio of BAI during drought to the mean BAI over the five years preceding the drought [@lloret\_components\_2011]. Thus, <1 indicates reduced growth under drought. Analyses focused on testing the predictions presented in Table 1, with as the response variable. The general statistical model for hypothesis testing was a mixed effects model (lme4 package from @R-lme4) with as the response variable, tree nested within species as a random effect, and one or more independent variables as fixed effects. We used AICc (AICcmodavg package from @R-AICcmodavg) to assess model selection, and conditional/marginal R-squared to assess model fit.

Models were run for all drought years combined (with year as a fixed effect) and for each drought year independently. To determine the relative importance of the traits alone, we first tested the predictor variables independently against both height and given height’s substantial influence. Variables were considered to have significant influence on when AICc was reduced by 2 relative to the corresponding null model lacking that variable (Table 4).

We then determined the best full models for predicting for each individual drought year and for all years combined. Candidate variables were selected, based on the single-variable tests, as those whose addition to a corresponding null model improved fit (at dAICc 1.0) in at least one drought (Table 4). We compared models with all possible combinations of candidate variables and identified the full set of models within dAICc=1 of the very top model (that with lowest AICc), henceforth referred to as “full models”. When a variable appeared in all top models and the sign of the coefficient was consistent across models, this was counted as support for/ rejection of the associated prediction by the full models. If the variable appeared in only some of the models, we considered this partial support/rejection.

All data, code, and results are available through the SCBI-ForestGEO organization on GitHub (<https://github.com/SCBI-> ForestGEO: SCBI-ForestGEO-Data and McGregor\_climate-sensitivity-variation repositories), with static versions corresponding to data and analyses presented here archived in Zenodo (DOIs: 10.5281/zenodo.3604993 and [TBD], respectively).

### Results

*Community-level drought responses*

At the community-level, trees showed substantial growth reductions in all three droughts, with mean values of 0.86, 0.84, and 0.86 for 1966, 1977, and 1999 droughts, respectively (Fig. 1b). In each drought, roughly 30% of the cored trees experienced , 29% of trees in 1966, 32% in 1977, and 27% in 1999. However, some individuals exhibited increased growth, i.e., , 26% of trees in 1966, 22% in 1977, and 26% in 1999.

*Tree size, microenvironment, and drought resistance*

Larger-diameter trees showed stronger growth reductions during drought, although there was no significant effect during 1977 or 1999 individually (Tables 1, 4). The only significant effect was in 1966, one of the driest years? and the year preceded by drought. The same held true for in single-variable tests (Tables 1, 4). When combined with other predictor variables in the full models, appeared, with negative coefficient, in all full models for the three droughts combined, in the 1966 model, and in one of the two 1999 models (Tables 1, 5).

Crown position varied as expected with (dominant > co-dominant > intermediate > suppressed), but with substantial variation (Fig. 2d). Yet, crown position was a much poorer predictor of than was in the single-variable tests (Table 4), lending little overall support to the hypothesis that trees with more exposed crowns have lower (Table 1). When was included in the model, was a significant predictor in the 1999 drought, with lowest for suppressed and then intermediate trees. Crown position was included in some of the full models (Table 5). In 1977, where was not included in the full model, dominant trees had the lowest , and suppressed the highest. In contrast, in full models including both and (all droughts and 1999), the lowest was in suppressed, followed by intermediate, trees.

In the non-drought years for which we have vertical profiles in climate data (2016-2018), taller trees–or those in dominant crown positions– were generally exposed to higher evaporative demand during the peak growing season months (May-August; Fig. 2). Specifically, maximum daily wind speeds were significantly higher above the top of the canopy (40-50m) than within and below (10-30m) (Fig. 2a). Relative humidity was also somewhat lower during June-August, ranging from ~50-80% above the canopy and ~60-90% in the understory (Fig. 2b). Air temperature did not vary across the vertical profile (Fig. 2c).

Resistance was negatively correlated with (Tables 4-5), rejecting the idea that trees in moist microsites would be less affected by drought. Nevertheless, we tested for a negative interaction, which could indicate that smaller trees (with smaller rooting volume) are more susceptible to drought in drier microenvironments with a deeper water table. This hypothesis was rejected as the interaction was never significant and had a consistently positive coefficient (Table 4).

*Species’ traits and drought resistance*

Hydraulic traits, including , , and , were linked to drought responses (Tables 1,4,5). In the single-variable tests, and never significantly associated with (Table 4) and were excluded from the full models. In contrast, , , and all explained modest amounts of variation (dAIC > 1.0) in at least one drought (Table 4). was a strong predictor for the 1966 drought and all droughts combined, with consistently negative coefficients (Table 4). Similarly, was consistently included, with negative coefficient, in full models for the three droughts combined and for the 1966 and 1977 droughts individually (Table 5). was not come out significant in any single-variable tests; however, coefficients were consistently negative (Table 4) and was included in the top full model for all droughts combined and for the 1977 and 1999 droughts individually (Table 5). Xylem porosity was not significant for all droughts combined and had contrasting effects in the individual droughts: whereas ring-porous species had higher than diffuse- and semi-ring- porous species in the 1966 and 1999 droughts, they had lower in 1977 (Tables 4,5).

### Discussion

Tree size, microenvironment, and hydraulic traits shaped tree growth responses across three droughts in our study site? (Table 1). The greater susceptibility of larger trees to drought, similar to forests worldwide [@bennett\_larger\_2015], was driven primarily by their height rather than crown exposure [@liu\_effect\_1993; @stovall\_tree\_2019]. There was a marginal additional effect of crown exposure, with a tendency for lowest among the most exposed (dominant) and suppressed trees. The negative effect of height on held after accounting for species’ traits. Drought sensitivity was not consistently linked to species’ , , or xylem architecture, but was negatively correlated with the leaf hydraulic traits (, ) in the top overall model and the top models for two of the three individual droughts [@scoffoni\_leaf\_2014;@bartlett\_correlations\_2016; @medeiros\_extensive\_2019]. Indeed, this is the first report to our knowledge linking and to growth reduction during drought. The direction of responses was mostly consistent across droughts, supporting the premise that they were driven by fundamental physiological mechanisms. However, the strengths of each predictor varied across droughts (Tables 4-5), indicating that drought characteristics interact with tree size, microenvironment, and traits to shape which individuals are most affected. These findings significantly advance our knowledge of the factors that confer vulnerability or resistance on trees during drought.

The droughts considered here were of a magnitude that has occurred with an average frequency of approximately one per 10-15 years (Fig. 1a, @helcoski\_growing\_2019) and had substantial impacts on tree growth (Fig. 1b). These droughts were classified as severe (1977) or extreme (1966, 1999) according to the PDSI metric and have been linked to tree mortality in the eastern United States [@druckenbrod\_redefining\_2019]; however, extreme, multiannual droughts or so-called “megadroughts”, droughts of 10 years or more, of the type that have triggered massive tree die-off in other regions (e.g., @allen\_global\_2010; @stovall\_tree\_2019) have not occurred in the Eastern United States within the past several decades [@clark\_impacts\_2016]. Of the droughts considered here, the 1966 drought, which was preceded by two years of dry conditions (Fig. S2), severely stressed a larger portion of trees (Fig. 1b). It may be notable that the tendency for large trees to have lowest resistance was most pronounced in this drought, consistent with other findings that this phycological response increases with drought strength [@bennett\_larger\_2015; @stovall\_tree\_2019]. Across all three droughts, the majority of trees experienced reduced growth, but a substantial portion had increased growth (Fig. 1b), potentially due to decreased leaf area of competitors during the drought. It is likely because of the moderate impact of these droughts, along with other factors influencing tree growth, that our best models characterize only a modest amount of variation: 11-13% for all droughts combined, and 21-26% for each individual drought (Table 5).

Our analysis indicates that tree height has a stronger influence on drought response than does canopy position (Tables 1,4,5). This is consistent with, and reinforces, previous findings that biophysical constraints make it impossible for trees to efficiently transport water to great heights and simultaneously maintain strong resistance and resilience to drought-induced embolism [@olson\_plant\_2018; @couvreur\_water\_2018; @roskilly\_conflicting\_2019]. However, the collinearity between the two variables (Fig. 2d) makes it impossible to confidently partition causality. Taller trees are more likely to be in dominant canopy positions (Fig. 2d) and, largely as a consequence of their position relative to others, face different microenvironments (Fig. 2a-b). Even under non-drought conditions, evaporative demand and maximum leaf temperatures increase with tree height [@smith\_temperature\_1977; @bretfeld\_plant\_2018; @kunert\_revised\_2017], and such conditions would incur additional stress during drought, when solar radiation tends to be higher and less water is available for evaporative cooling of the leaves. However, some decoupling between height and canopy position is introduced by the configuration of neighboring trees (Fig. 2d) [@muller-landau\_testing\_2006], and height was an overall stronger predictor of drought response than crown position (Tables 1,4,5).

Our analysis has the limitation that canopy positions were recorded in 2018, as opposed to the years of the droughts. However, because trees would generally advance towards more dominant positions as they grow and as neighbors die, changing canopy positions would bias against the acceptance of our hypothesis. The implication is that dominant crown positions did have a marginally negative influence on , which makes sense in light of the vertical environmental gradients described above and agrees with previous studies showing greater drought sensitivity in more exposed trees [@suarez\_factors\_2004; @scharnweber\_confessions\_2019]. It is safe to assume that currently suppressed trees have always been in the understory, and their relatively low (after accounting for height effects) is real, perhaps as a result of competition (*[Sohn et al. 2016](https://www.sciencedirect.com/science/article/pii/S0378112716304029)*). The observed height-sensitivity of , together with the lack of advantage to large stature in drier topographic positions, agrees with the concept that physiological limitations to transpiration under drought shift from soil water availability to the plant-atmosphere interface as forests age [@bretfeld\_plant\_2018], such that tall, dominant trees are the most sensitive in mature forests. Additional research comparing drought responses of young and old forest stands, along with short and tall isolated trees, would be valuable for more clearly disentangling the roles of tree height and crown exposure.

The development of tree-ring chronologies for the twelve most dominant tree species at our site [@helcoski\_growing\_2019; @bourg\_initial\_2013] gave us the sample size to compare historical drought responses across species and associated traits at a single site [see also @elliott\_forest\_2015]. Concerted measurement of leaf hydraulic traits of emerging importance [@scoffoni\_leaf\_2014; @bartlett\_correlations\_2016; @medeiros\_extensive\_2019] allowed novel insights into the role of hydraulic traits in shaping drought response. The finding that and can be useful for predicting drought responses of tree growth (Tables 1,4,5) is both novel and consistent with previous studies linking these traits to habitat and drought tolerance. Previous studies have demonstrated that and are physiologically meaningful traits linked to species distribution along moisture gradients [@medeiros\_extensive\_2019; @simeone\_coupled\_2019; @marechaux\_drought\_2015] (*Rosas et al. 2019, DOI: 10.1111/nph.15684*, [Fletcher et al. 2018](https://bsapubs.onlinelibrary.wiley.com/doi/full/10.1002/ajb2.1164)), and our findings indicate that these traits also influence drought responses. Furthermore, the observed linkage of to in this forest aligns with observations in the Amazon that is higher in drought-intolerant than drought-tolerant plant functional types and adds support to the idea that this trait is useful for categorizing and representing species’ drought responses in models (*Powell et al. 2016, DOI: 10.1111/gcb.13731*). Because both and , which can be measured relatively easily [@bartlett\_rapid\_2012; @scoffoni\_leaf\_2014], they hold promise for predicting drought growth responses across species. The importance of linking species’ traits to drought responses increases with tree species diversity; whereas it is feasible to study drought responses for all dominant species in most boreal and temperate forests (e.g., this study), this becomes difficult to impossible for species that do not form annual rings, and for diverse tropical forests. Although progress is being made for the tropics [@schongart\_dendroecological\_2017], a full linkage of hydraulic traits to drought responses would be invaluable for forecasting how little-known species and whole forests will respond to future droughts (*Powell et al. 2016, DOI: 10.1111/gcb.13731*).

As climate change drives increasing drought in many of the world’s forests [@trenberth\_global\_2014; @intergovernmental\_panel\_on\_climate\_change\_climate\_2015], the fate of forests and their climate feedbacks will be shaped by the biophysical and physiological drivers observed here. Large trees have been disproportionately impacted in forests around the world [@bennett\_larger\_2015; @stovall\_tree\_2019], and we show, at least at this site, that this is primarily driven by their height with some contributions from canopy position. The distinction is important because it suggests that height *per se* makes trees vulnerable, even if their crowns are somewhat protected by neighbors, whereas solitary trees or the dominant trees in young regrowth forests should be less vulnerable. This would suggest that, all else being equal, mature forests would be more vulnerable to drought than young forests with short trees; however, root water access may limit the young forests [@bretfeld\_plant\_2018], and species traits often shift as forests age. Early successional species at our site (*Liriodendron tulipifera*, *Quercus spp.*, *Fraxinus americana*) display a mix of traits conferring drought tolerance and resistance (Table 3), and further research on how hydraulic traits and drought vulnerability change over the course of succession would be valuable for addressing how drought tolerance changes as forests age [e.g. @rodriguez-caton\_long-term\_2015]. In the meantime, the results of this study advance our knowledge of the factors conferring drought vulnerability and resistance in a mature forest, opening the door for more accurate forecasting of forest responses to future drought.

### Acknowledgements

We especially thank the numerous researchers who helped to collect the data used here, in particular Jennifer C. McGarvey, Jonathan R. Thompson, and Victoria Meakem for original collection and processing of cores. Thanks also to Camila Medeiros for guidance on hydraulic and functional trait measurements, Edward Brzostek’s lab for collaboration on leaf sampling, and Maya Prestipino for data collection. Funding for the establishment of the SCBI ForestGEO Large Forest Dynamics Plot was provided by the Smithsonian-led Forest Global Earth Observatory (ForestGEO), the Smithsonian Institution, and the HSBC Climate Partnership. This study was funded by ForestGEO, a Virginia Native Plant Society grant to KAT and AJT, and support from the Harvard Forest and National Science Foundation which supports the PalEON project (NSF EF-1241930) for NP.

### Author Contribution

KAT, IM, and AT designed the research. Tree-ring chronologies were developed by RH under guidance of AT and NP. Trait data was collected by IM, JZ under guidance of NK and LS. Other plot data were collected by IM, AS, EGA, and NB under guidance of EGA and WM. Data analyses were performed by IM under guidance of KAT and VH. KAT and IM interpreted the results. IM and KAT wrote the first draft of manuscript, and all authors contributed to revisions.