**Title:** Tree height and hydraulic traits 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 Stovall1,6 Norman A. Bourg1 William J. McShea1? Neil Pederson7 Lawren Sack8 Kristina J. Anderson-Teixeira1,3\*

**Author Affiliations:**

1. Conservation Ecology Center; Smithsonian Conservation Biology Institute; National Zoological Park, Front Royal, VA, USA
2. Center for Tropical Forest Science-Forest Global Earth Observatory; Smithsonian Tropical Research Institute; Panama, Republic of Panama
3. Biological Sciences Department; California State University; Los Angeles, CA, USA

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

**coauthors, fill in middle initials and affiliations, if missing**\*

|  |  |  |  |
| --- | --- | --- | --- |
| text | word count | other | n |
| Total word count (excluding summary, references and legends) | currently ~6442 (strict limit 6,500) | No. of figures | 2 (both colour) |
| Summary | currently 200 (limit 200) | No. of Tables | 5 |
| Introduction | currently ~1339 | No of Supporting Information files | 6 |
| Materials and Methods | currently ~1604 |  |  |
| Results | currently ~1558 |  |  |
| Discussion | currently ~1866 (limit 30% of total (not strict), or 1950 if manuscript reaches word limit) |  |  |
| Acknowledgements | currently ~73 |  |  |

### Summary

* As the climate changes, driving increased drought in many forested regions around the world, mechanistic understanding of factors conferring drought resistance in trees is increasingly important. Yet it remains unclear how tree size and species’ traits interactively shape tree growth responses during droughts.
* In this study, we analyze tree-ring records for twelve species representing 97% of woody productivity in the 25.6-ha ForestGEO plot in Virginia (USA) to determine how tree size, microhabitat, and species’ traits interactively shape drought responses across the three strongest droughts over a 60-year period (1950 - 2009).
* Individual-level drought resistance decreased with tree height, whereas crown position explained little additional variation and root water access did not confer additional resistance. Resistance was lower among species whose leaves had higher percent loss of area upon dehydration and lost turgor at less negative water potential. However, there was substantial variation in the best predictor variables across given droughts.
* We conclude that height–as opposed to canopy position, root water access, or species’ traits–is the primary factor through which tree size mediates drought response, that leaf hydraulic traits are useful indicators of drought sensitivity, and that directions but not strengths of responses are consistent across droughts.

*Key words*: canopy position; drought; Forest Global Earth Observatory (ForestGEO); leaf hydraulic traits; temperate broadleaf deciduous forest; tree growth; tree height; tree-ring [5-8] *Five to eight key words (in alphabetical order) . Words that are in the title can, and should, be among these.*

### Introduction

Forests globally play a critical 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 in responses to drought ([*Kennedy et al. 2019*](https://doi.org/10.1029/2018MS001500)). In many forested regions around the world, the risk of severe drought is increasing [@trenberth\_global\_2014], sometimes despite increasing precipitation [@intergovernmental\_panel\_on\_climate\_change\_climate\_2015]. Global change-type droughts have been affecting forests worldwide [@allen\_global\_2010], and are expected to continue severely impacting forests around the world [@allen\_global\_2010]; **REFS**). During drought, larger trees generally suffer greater reductions in growth and increases in mortality (e.g., @bennett\_larger\_2015; @stovall\_tree\_2019], resulting in disproportionate impacts on forest C storage [@meakem\_role\_2018]. As a result, forest drought responses stand to strongly impact forest feedbacks to climate change (*e.g., McDowell et al. 2016(*[*doi:10.1038/nclimate2873*](doi:10.1038/nclimate2873)*); Charney et al. 2016 (doi: 10.1111/ele.12650)*). Yet, accurate characterization of drought responses remains a modeling challenge ([*Kennedy et al. 2019*](https://doi.org/10.1029/2018MS001500))– in part because some of the mechanisms underlying drought responses remain unclear (**REF**). Understanding forest responses to drought requires increased functional understanding of how tree size, microhabitat, and species’ traits jointly confer individual-level vulnerability or resistance, and the extent to which their influence is consistent across droughts.

One fundamental question regarding forest responses to drought is what drives the observed tendency for large trees to suffer more during drought. @bennett\_larger\_2015 showed that in forests globally, large trees suffer greater growth reductions during drought, and numerous subsequent studies have reinforced this finding (e.g., @stovall\_tree\_2019; @hacket-pain\_consistent\_2016]. However, @bennett\_larger\_2015 quantified tree size based on DBH, which has no direct mechanistic meaning. This study proposed two major mechanisms–besides the tendency for bark beetles to preferentially attack larger trees [@pfeifer\_observations\_2011]–for the observed greater drought growth reductions of large trees. First, taller trees face greater 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], which becomes a greater liability during drought [@zhang\_size-dependent\_2009]. Second, larger trees may have lower drought resistance because they are more often in the canopy, where they are exposed to higher solar radiation, greater wind speeds, lower humidity, and lower CO\_2\_ concentrations [@koike\_leaf\_2001; **REFS-KAT**). Alternatively, the generally supressed status of subcanopy trees may be insufficient to override the benefits of their buffered environment during drought. Potentially counteracting the biophysical challenges faced by large trees, their larger root systems confer an 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 [@bennett\_larger\_2015]. A final mechanism that could mediate tree size-related responses to drought is how hydraulic traits are distributed with respect to size [@meakem\_role\_2018]. The pattern observed by @bennett\_larger\_2015 could be caused if the larger size classes were dominated by species less adapted to handle drought, be it through avoidance, resistance, or resilience. Alternatively, larger size classes may be dominated by species that are better adapted to inherently greater biophysical challenges–as is the case in tropical moist forests of Panama, where larger size classes contain greater proportions of deciduous species [@condit\_quantifying\_2000; @meakem\_role\_2018]. Understanding the mechanisms underlying the tendency for larger trees to suffer more during drought will require sorting out the interactive effects of height, canopy position, root water acess, and species’ traits.

A second fundamental question regarding forest responses to drought is how species’ traits – alone and in interaction with tree size – influence drought response. Xylem architecture plays a role, with diffuse porous species tending to be more drought-sensitive than ring-porous species [@kannenberg\_linking\_2019; @elliott\_forest\_2015; @friedrichs\_species-specific\_2009], but does not differentiate species beyond broad classes. Commonly-measured traits including wood density () and leaf mass per area () have been linked to drought responses in temperate deciduous forests [@abrams\_adaptations\_1990; @guerfel\_impacts\_2009; @hoffmann\_hydraulic\_2011] and other forest biomes around the world [@greenwood\_tree\_2017]. However, the direction of response is not always consistent; wood density correlated negatively with drought tree performance in a broadleaf deciduous forest in the southeastern United States [@hoffmann\_hydraulic\_2011] but positively or with no effect at a global scale [@greenwood\_tree\_2017; @anderegg\_hydraulic\_2018). Hydraulic traits including water potentials at which percent loss conductivity passes a certain threshold (, , ) and hydraulic safety margin tend to be more successful at predicting 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, including leaf area shrinkage upon dessication (; [@scoffoni\_leaf\_2014]) and the osmotic potential at turgor loss point ()–i.e., the water potential at which leaf wilting occurs [@bartlett\_correlations\_2016] – are emerging as traits with potential to explain greater variation in plant distribution and function than the more commonly-measured and [@medeiros\_extensive\_2019]. The ability of and to explain tree performance under drought remains untested.

A final fundamental question regarding forest responses to drought is whether tree size and species’ traits have similar influence across droughts, or whether variability in factors such as drought severity, duration, and timing interact with tree size and traits such that components of the community respond differently across droughts. No two droughts are the same, and tree growth responses vary with drought characteristics such as timing and atmospheric demand [@dorangeville\_drought\_2018]. However, we are not aware of any studies that compare how tree size and species’ traits mediate growth responses across droughts. While tree-ring studies provide long-term records of tree responses to multiple droughts (e.g., [@lloret\_components\_2011; @dorangeville\_drought\_2018] **REFS**), these do not test for differential trait effects across periods of water shortage [@dorangeville\_drought\_2018] and generally focus on species-level responses, which preclude consideration of the roles of tree size and microenvironment. The ecological 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 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 modest but frequent droughts–e.g., those with historical return intervals on the order of a decade–remains more limited. While the tendency for larger trees to suffer more certainly predominates [@bennett\_larger\_2015], there are exceptions (*e.g.*, **REFS??**). There is also evidence that the degree to which larger trees are impacted more by drought increases with the severity of drought conditions [@bennett\_larger\_2015; @stovall\_tree\_2019]. [*Are there any studies showing interactions of drought type with traits?*] Thus, while we expect many of the fundamental mechanisms shaping drought responses to be universal, we have little undertanding of how tree size and traits interact with drought characteristics to result in differential responses across droughts.

Here, we combine tree-ring records covering three droughts (1966, 1977, 1999), species functional and hydraulic trait measurements, and forest census data from a 25.6-ha ForestGEO plot in Virginia (USA) to test a series of hypotheses and associated specific predictions (Table 1) designed to yield functional understanding of how tree size, microenvironment, and species’ traits collectively shape drought responses. First, we focus on the role of tree size and its interaction with microenvironment. We confirm that, consistent with most forests globally, larger-diameter trees tend to have lower drought resistance in this forest, which is in an ecoregion represented by only one study in [@bennett\_larger\_2015] (*H1.0*). We then test hypotheses designed to disentangle the relative importance of tree height (*H1.1*), crown exposure (*H1.2*), and root water access, which should be greater for larger trees in dry but not in perpetually wet microsites (*H1.3*). Second, we focus on the role of species’ functional and hydraulic traits and their interaction with tree height. We hypothesize that drought resistance will follow observed patterns in relation to wood density (negative effect; @hoffmann\_hydraulic\_2011), specific leaf area (positive effect), and xylem architecture (*i.e.*, ring or diffuse/ semi-ring porous), but that hydraulic leaf traits including and will prove better predictors (*H2.1*). We then test whether these traits correlate with tree height (*H2.2*), potentially driving the observed tendency for taller trees to suffer more during drought (*H2.3*). Finally, we focused on variability among droughts, asking how community resistance varied across droughts (*H3.1*) and whether the factors confirming vulnerability or resistance varied across droughts (*H3.2*).

### 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 edge of Shenandoah National Park. Elevations range from 273-338m above sea level [@gonzalezakre\_patterns\_2016] 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 include tulip poplar (*Liriodendron tulipifera*), oaks (*Quercus* spp.), and hickories (*Carya* spp.).

*Data collection and preparation*

Within or just outside the ForestGEO plot, we collected data on a suite of variables including tree size, microenvironemnt, and species traits (Table 2). The SCBI ForestGEO plot was censused 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 these census data, we used measurements of DBH from 2008 to calculate historical DBH, tree location in the plot to determine the topographic wetness index, and data for all stems 10cm to analyze functional trait composition relative to tree height (all analyses described below). Census data, which were last updated in 2019, are available through the ForestGEO data portal (www.forestgeo.si.edu).

We analyzed tree-ring data from 571 trees representing the twelve species contributing 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 obtained in 2010-2011 or 2016-2017 from a breast height of 1.3m using a 5mm increment borer. In 2010-2011, cores were collected from randomly selected live trees of species with at least 30 individuals of DBH 10cm [@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 have been published in association with @helcoski\_growing\_2019: (ITRDB; GitHub/Zenodo). **Ryan, have you heard back from ITRDB? We should also cite GitHub/Zenodo here.**

For each 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 without 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, and are archived in a public [GitHub repository](https://github.com/SCBI-ForestGEO/SCBI-ForestGEO-Data/tree/master/tree_dimensions/tree_heights). Measurement methods included manual [@stovall\_assessing\_2018, NEON], digital rangefinders [@andersonteixeira\_size-related\_2015], and automatic 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. Species-specific height allometries were developed (Table S2). For species with insufficient height data to create reliable species-specific allometries, heights were calculated from an equation developed using all height measurements.

Crown positions were recorded in the field during the growing season of 2018 following the crown position protocol of @jennings\_assessing\_1999, whereby positions were ranked as dominant, codominant, intermediate, or suppressed. As there was no way to retroactively estimate crown position, we assumed that 2018 crown position was reflective of each tree’s position over the past 60 years. While some trees undoubtedly changed position, an analysis of crown position relative to height (Fig. 2) and height change since the beginning of the study period indicated that change was likely slow (Fig. S3). Specifically, average tree height growth was confined to <0.5m from 1966 to 1977, ~1m from 1977 to 1999, and **# (IAN)** from 1999 to 2018.

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 at SCBI (Table 3). In August 2018, we sampled small sun-exposed branches from three individuals of each species in and around the ForestGEO plot. Samples were re-cut under water by at least two notes and re-hydrated overnight in buckets covered with opaque plastic bags before measurements. Rehydrated leaves (n=3 per indivdiual) 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 (**citation**). 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. 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]. Data and R scripts for hydraulic traits are available at [**create new public GitHub repo for hydraulic traits, archive in Zenodo, give DOI**].

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, for the years 2016-2018 [@noauthor\_national\_2018]. After filtering for missing and outlier values, the data was consolidated to represent the mean values per sensor height per day.

*Identification of drought years*

We identified droughts within the time period 1950-2009, defining drought [@slette\_how\_2019] as events with widespread reductions in tree growth and anomalously dry peak growing season climatic conditions. Specifically, candidate drought years were defined as those where >25% of the cored trees experienced >30% reduction in basal area increment (BAI) relative to the previous 5 years, following the drought resistance () metric of [@lloret\_components\_2011], and identified using the pointRes package [@R-pointRes] in R (version 3.5.3). Separately, we identified the years with driest conditions during May-August, which stood out in the analysis of [@helcoski\_growing\_2019] as the current-year months to which annual growth was most sensitive for trees at this site. We considered two metrics of moisture deficit: NOAA Divisional Data’s Palmer Drought Severity Index (PDSI) and the difference between monthly potential evapotranspiration (PET) and precipitation (PRE). These data were 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 May-August PDSI or [PET-PRE] for the time period from driest to wettest.

*Analysis*

For each drought period, we calculated drought resistance () as the ratio of BAI during drought to that of the five previous years [@lloret\_components\_2011]. Analyses focused on testing the predictions presented in Table 1, most of which consider 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 fit. Models were run for all drought years combined (with year as a fixed effect) and for each drought year independently. We first tested the predictor variables independently, counting a variable as useful for predicting when AICc was reduced by 2 relative to the appropriate null model lacking that variable (Table 4). Because height had a substantial influence on , we included it in the null model for testing other variables (Table 4).

Second, for each drought year and for all years combined, we determined the best multivariate models for predicting . All variables with dAICc > 1.0 in any model (drought years combined or any individual drought) were used as candidate variables for each scenario’s best model. We compared models with all possible combinations of candidate variables and identified the full set of models within dAICc=2 of the top model (that with lowest AICc). These were counted as the “top multivariate models”. When a variable appeared in all of these 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 multivariate models. If the variable appeared in only some of the models, we considered this partial support.

### Results

*Focal droughts and their characteristics*

In the 60-year period between 1950 and 2009, there were three droughts that met our criteria of anomalously dry climatic conditions coupled with substantial reductions in tree growth for at least some portions of the community: 1966, 1977, and 1999 (Figs. 1, S2). We excluded one year (1991) meeting the growth reduction criteria (26.5% of trees experienced >30% growth reduction, mean resistance= -13.8%) because this year was not among the driest in terms of May-August [PET-PRE] or PDSI (Table S3). Rather, the severity of growth reduction may be explained by defoliation by gypsy moths (*Lymantria dispar* L.) from approximately 1988-1995, which most strongly impacted *Quercus* spp. (*Cite Shenandoah paper, if accepted*). Climatically, these droughts included three of the five years between 1950 and 2009 with greatest moisture deficit (PET-PRE) during the peak growing season months of May-August, which are the months to which annual tree growth at this site is most sensitive [@helcoski\_growing\_2019]. Specifically, 1966, 1977, and 1999 had mean MJJA PET-PRE of 83.37, 86.97, and 80 mm mo-1, respectively. The years 1964 and 2007 also ranked in the top five driest (PET-PRE =83.87 and 82.13 mm mo-1), but were not among the lowest in terms of PDSI and were not identified as a pointer years (Table S3).

The droughts differed in intensity and prior onset (Table S3, Fig. S2). In terms of intensity during the peak growing season of the focal year, the 1999 drought was the most intense (lowest PDSI) during May-July. It was surpassed in intensity in August by the 1966 drought, which was otherwise the second most intense during the peak growing season. The 1977 was the least intense throughout the growing season. All droughts increased in intensity from May through August, but differed in the months previous. The 1966 drought was preceded by two years of moderate drought during the growing season and severe to extreme drought starting the previous fall. Similarly, the 1999 drought was preceded by severe to extreme drought starting the previous fall, but before that conditions were wetter than average until the previous June. The 1977 drought was preceded by 2.5 years of near-normal conditions, and was therefore the mildest of the three droughts by any measure.

Community-level tree growth responses to these droughts were modest, with mean resistance values of 0.86, 0.84, and 0.86 for 1966, 1977, and 1999, respectively (Fig. 1b). In each drought, roughly 30% of the cored trees suffered 30% growth reductions ( 0.7): 29.43% in 1966, 31.86% in 1977, and 26.81% in 1999. Some trees exhibited increased growth: ( > 1.0): 26.31% in 1966, 21.92% in 1977, and 25.57% in 1999.

*Tree size and drought resistance*

Overall, our analysis confirmed the tendency for larger-diameter trees to show greater reductions in growth during drought [@bennett\_larger\_2015] (*H1.0*), although there was no signficant effect for 1977 or 1999 individually (Tables 1, 4). The same held true for as a univariate predictor (*H1.1*; Tables 1, 4). When combined with other predictor variables in our multivariate models, the top models usually included an effect of , and its coefficient was consistently negative, as predicted (Tables 1, 5). We note that a non-signficant positive correlation between and for 1999 became negative in the context of the multivariate models, again supporting *H1.1* (Table 1).

Crown position was generally correlated with , but with substantial variation (Fig. 2d). Crown position was a much poorer predictor of than was (Table 4), lending little overall support to *H1.2* (Table 1). When considered alone, had a significant influence only in the 1966 drought, during which trees with dominant position? had the lowest . When considered in conjunction with , came out as a significant predictor only for the 1999 drought, during which suppressed and then intermediate trees had the lowest . Crown position was included in almost half of the top models, with mixed results as to how varied with (Table 5). Most commonly in these multivariate models, as in the univariate models (Table 4), the resistance of dominant trees was less than that of co-dominant trees but higher that of suppressed trees. Thus, was sometimes a useful predictor of , but overall had a weak effect relative to that of .

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 signficantly 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), negating the idea that trees in moist microsites would suffer less during drought. Nevertheless, we tested for a negative interaction (*H1.3*), which could indicate that smaller trees (with smaller rooting volume) have a greater tendency to suffer more in drier microenvironments with greater depth to the water table. *H1.3* was rejected; the interaction was never signficant and had a consistently positive coefficient (Table 4).

*Species’ traits, height, and drought resistance*

Our results partially supported *H2.1*: Species’ hydraulic traits –, , and –were sometimes useful in explaining variation in drought responses, whereas and were not (Tables 1,4,5). Specifically, and never significantly associated with in the univariate models (all dAIC 0.22; Table 4), and therefore these were excluded as candidate variables for the full multivariate models. In contrast, , , and all explained at least modest amounts of variation (dAIC > 1.0) in at least one drought (Table 4). Of these, was a strong predictor for the 1966 drought and overall, with consistently negative coefficients across all droughts. was never significant (dAIC 2) in the univariate models but had a consistently negative coefficient (Table 4). Whereas ring-porous species had highest overall and in the 1966 and 1999 droughts, they had lower in 1977. Results were similar in the context of multivariate models (Table 5), except that had a small positive coefficient in the one 1999 model in which it was included. , and were each included in the top overall model and in the top model for two of the three individual droughts (Table 5).

We rejected *H2.2*, finding no evidence that taller trees had traits associated with greater drought resistance. In part because of the large sample size (**n=#** trees–all individuals of our 12 focal species 10 cm in 25.6 ha), there were significant (p<0.0001) correlations of with all species’ traits (see Table S4). However, the correlation only matched the predicted direction (*i.e.*, more drought-resistant traits associated to taller trees) in the cases of and , which were not useful predictors of . Furthermore, although correlations were statistically signifcant, trait variation within each height class overwhelmed any vertical trends (Fig. 2e-f).

Our findings supported the hypothesis (*H2.3*) that the observed tendency for larger trees to have greater growth reductions during drought (lower ) was driven by height itself, as opposed to more drought-sensitive traits in larger trees (Tables 1,5). As discussed above, there was little meaningful variation in traits with height at the community level. When and hydraulic traits were considered together in multivariate models, the effect of on was consistently negative (Table 5)–reversing a non-signficant positive - correlation in the univariate model for the 1999 drought (Table 4).

*Responses across droughts*

Our results rejected the hypothesis (*H3.1*) that overall community responses varied across droughts. Within the context of mixed effects models, there were no significant differences in across drought years (Table 4). This is consistent with the observation that the distribution of values was similar across droughts (Fig. 1b).

We found limited support for hypothesis (*H3.2*) that directions of responses varied across droughts. In the majority of cases, response directions were consistent across droughts in both univariate and multivariate models (Tables 1,4,5). However, there were a few exceptions – most commonly in the categorical variables ( and ) but also for in one multivariate model for the 1999 drought (Tables 4, 5). These differences may be random, as opposed to statistically meaningful. Among the univariate models, there was no instance where predictor variables signficantly improved the models of two different droughts (dAIC 2), but with contrasting coefficients (Table 4). Among the multivariate models, was not consistently in the top models for any drought (Table 5), and only appeared with a positive coefficient in the weakest of six models for the 1999 drought (contrasting with a negative coefficient in the univariate model; Table 4). It is likely that ring-porous species had lower than diffuse- and semi-ring- porous species in the 1977 drought, contrasting with higher resistance in 1966 and 1999 (Tables 4,5), but note that was not a signficant predictor on its own for the 1977 drought.

Our findings supported the hypothesis (*H3.3*) that the strength of predictor variables was different across the droughts (Tables 1,4,5). For instance, and had much stronger negative effects in 1966 than in the other two years, had the strongest negative effect in 1977, and (higher among ring-porous trees) was strongest in 1999 (Tables 4,5).

### Discussion

Our results reveal how tree size, microhabitat, and hydraulic traits shaped tree growth responses across three droughts in a temperate deciduous forest (Table 1). The tendencey for larger trees to suffer more, observed here as in forests around the world [@bennett\_larger\_2015], was driven primarily by their height. There was a marginal additional effect of crown exposure, with the most exposed and the most suppressed trees suffering most, consistent with observations of both greater drought sensitivity of exposed trees (e.g., [@suarez\_factors\_2004]; [@scharnweber\_confessions\_2019]) and greater sensitivity of suppressed and crowded individuals (**REFS**). There was no evidence that root water access increased drought resistance; in contrast, trees in wetter topographic positions suffered more (consistent with [@zuleta\_drought-induced\_2017]), and larger rooting volume provided no advantage in the drier microenvironments. The lower drought resistance of larger trees was not driven by any tendency for the canopy to be dominated by more drought-sensitive species. Drought sensitivity was not consistently linked to species’ , , or xylem architecture. However, drought resistance was negatively correlated with the leaf hydraulic traits (, ) in the top overall model and the top models for two of the three individual droughts, which is physiologically logical ([@scoffoni\_leaf\_2014];[@bartlett\_correlations\_2016]; [@medeiros\_extensive\_2019]) but scientifically novel in that and have not previously been linked to drought growth responses. The direction of responses was mostly consistent across droughts, indicating that they were driven by fundamental physiological mechanisms; however, the strengths of each predictor varied across droughts, indicating that specific drought characteristics interact with tree size, microenvironment, and traits to shape which individuals suffer most. These findings significantly advance our knowledge of the factors that confer vulnerability or resistance on trees during drought.

The droughts considered here were of similar severity (Fig. 1b) and fairly moderate; droughts of this magnitude have occurred with an average frequency of approximately one per 10-15 years (Fig. 1a, @helcoski\_growing\_2019). Therefore, we excpect that most species are adapted, and individual trees acclimatized, to survive droughts of this nature. While the majority of trees experienced reduced growth, a substantial portion had increased growth (Fig. 1b), supporting the observation that these droughts did not induce extreme stress on the entire forest. It is likely for this reason, combined with the fact that many factors other than climate affect tree growth in closed-canopy forests, 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). Methodologically, the moderate nature of these droughts is an advantage because our analysis considers only trees that survived all of these droughts, and we lack information on the trees that were killed. These are likely to be relatively modest in number, and local forest monitoring data stretching back to the late 1980s confirms that the 1999 drought did not trigger major declines in tree abundance or biomass (*Anderson-Teixeira et al., in revision*). Thus, the droughts considered here are substantially weaker than those that have triggered massive tree die-off (e.g., [@allen\_global\_2010]), many of which have shaped our understanding about the role of tree size [@bennett\_larger\_2015; @stovall\_tree\_2019] and, to some extent, traits underlying drought response mechanisms (@greenwood\_tree\_2017; @anderegg\_meta-analysis\_2016). Nevertheless, our results are consistent with findings from more extreme droughts.

Our analysis indicates that height, as opposed to canopy position or root water access, is the primary factor through which tree size mediates drought response. Taller trees face inherent biophysical challenges in lifting water a greater distance against the effects of gravity and friction [@ryan\_hydraulic\_2006; @mcdowell\_darcys\_2015; @mcdowell\_relationships\_2011; @couvreur\_water\_2018]. Vertical gradients in stem and leaf traits, including smaller and thicker (higher LMA) leaves, more negative and lower hydraulic conductivity at greater heights [@couvreur\_water\_2018; @koike\_leaf\_2001; @mcdowell\_relationships\_2011], make it biophysically possible for trees to become tall [@couvreur\_water\_2018], yet height becomes a liability when drought incurs additional hydraulic challenges. Taller trees also face different microenvironments (Fig. 2a-b), in part because they are more likely to be in dominant canopy positions (Fig. 2d). Even under non-drought conditions, evaporative demand increases with tree height as taller trees are more closely coupled to the atmosphere (**REFS- Jarvis 1984?**; [@bretfeld\_plant\_2018]). Exposed canopy leaves reach higher temperatures ([*Smith & Nobel 1977*](https://doi.org/10.1093/jxb/28.1.169)), particularly during drought when solar radiation tends to be higher and less water is available for evaporative cooling of the leaves. Furthermore, daytime CO\_2\_ concentrations tend to decrease with height [@koike\_leaf\_2001], implying that water costs of CO uptake increase with height. Correlation between height and canopy position (Fig. 2d) makes it challenging to disentangle the relative importance of height *per se* from microenvironment. However, signficant decoupling between height and canopy position can be introduced by the configuration of neighboring trees (Fig. 2d) [@muller-landau\_testing\_2006], and we show that height is a far stronger predictor of drought response than crown position (Tables 1,4,5). Our analysis does have the limitation that canopy positions were recored in 2018 and undoubtedly changed for some trees since the 1960s, and we note that became an increasingly poor predictor moving from 1999 back to 1966 (Table 4). 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 *H1.2*. 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 suppressed, and their relatively low (after correcting for height effects) is real, which is consistent with analyses showing that suppressed and/or particularly crowded trees can suffer disproportionately during drought (**REFS- Alan?**). The observed height-sensitivity of , together with the apparent lack of importance of root water access (*H1.3*), agrees with the concept that physiological limitations to transpiration under drought shift from root water access to the plant-atmosphere intreface as forests age [@bretfeld\_plant\_2018], such that tall trees (dominants) 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 disentanging the roles of tree height and crown exposure.

The development of tree-ring chronologies for all dominant tree species at our site [@helcoski\_growing\_2019] made it possible to compare historical drought responses across 12 species and their associated traits at a single site for the first time (**verify- Neil, Alan**). 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–with both appearing in the top overall model and two of the three top models for each drought (Table 5)–is consistent with studies demonstrating that these are physiolgoically meaningful traits linked to species distribution along moisture gradients [@medeiros\_extensive\_2019] (**MORE REFS–KAT/NOBBY/LAWREN**). Importantly, this finding indicates that and , which can be measured relatively easily [@bartlett\_rapid\_2012; @scoffoni\_leaf\_2014], 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 diverse tropical forests, where linking hydraulic traits to drought responses would be invaluable for forecasting how little-known species and whole forests will respond to future droughts (**REFS?–KAT/NOBBY/LAWREN**).

Our analysis of hydraulic traits focused on species-level comparisons and did not characterize the role of variation with height. As noted above, leaves found higher on a tree tend to have more hydraulically conservative traits, and therefore we would expect that average leaf characteristics of an individual tree would scale with its crown height, with taller individuals having on average more drought-resistant traits. If vertical trends for and , which have not been characterized (***LAWREN, IS THIS TRUE?****), follow the general pattern of increasing leaf drought resistance with height, our analysis would be biased in a conservative direction when assessing* H2.3\* (Table 1)–*i.e.*, accounting traits on an individual level should result in a stronger negative effect of . Further characterization of leaf hydraulic traits in relation to height and crown exposure would be valuable for enhancing our understanding of the interactive effects of tree height and traits on drought responses.

Although the physiological mechanisms discussed above lead to generally consistent directions of growth responses to tree height and hydaulic traits across droughts, indicating the universality of the underlying mechanisms, the relative importance of the drivers varied widely across droughts, indicating an interaction with drought characteristics (Tables 4-5). Although there were not signficant differences in among the drought years, tended to be somewhat lower in 1966 (Fig. 1, Table 4). Height and dominant canopy position had the stronger negative effects in this drought than in the others (Tables 4-5), which could potentially be linked to the fact that this was the longest-lasting drought and and that height becomes a stronger predictor of mortality as the severity of the drought increases [@stovall\_tree\_2019]. In 1977, which was the weakest drought in terms of PDSI (Fig. S2, Table S3), ring-porous species had lower , contrasting with their higher in the other two droughts and perhaps indicating that ring-porosity provides less of an advantage in terms of drought adaptation under less extreme droughts, consistent with @elliott\_forest\_2015. In the 1999 drought, which was the most intense in terms of growing season PDSI and the second-longest in duration, xylem architecture was the most useful predictor, with diffuse-porous species suffering most. Thus, responses differed with the nature of each drought. Of course, site characteristics also define the nature of droughts, and comparisons of size and trait effects across sites, as well as across more droughts at a single site, would be of great value to elucidating the mechanisms through which drought characteristics interact with driver variables to shape tree growth responses.

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 suffering disproportionately in forests around the world [@bennett\_larger\_2015; @stovall\_tree\_2019], and we here show 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. Considering just height and crown position, this would suggest that 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. Pioneer species at our site (*Liriodendron tulipifera*, *Quercus spp.*, *Fraxinus americana*) have 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 getting at the very signficant question of whether and how drought tolerance changes as forests age. 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

Thanks to all researchers who helped to collect the data used here, in particular Jennifer C. McGarvey, Jonathan R. Thomspon, and Victoria Meakem for original collection and processing of cores. Thanks also to Camila Medeiros for guidance on hydraulic and functional trait measurements and to Edward Brzostek’s lab for collaboration on leaf sampling. \*\* others??\*\* This study was funded by the Smithsonian’s Forest Global Earth Observatory (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.* (**Neil, this is copied from Ryan’s paper. accurate here?** **coauthors, other funding?**)

### 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. **coauthors, please check/edit**