

Forest tree growth response to hydroclimate variability in the southern Appalachians

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Abstract

Climate change will affect tree species growth and distribution; however, under the same climatic conditions species may differ in their response according to site conditions. We evaluated the climate-driven patterns of growth for six dominant deciduous tree species in the southern Appalachians. We categorized species into two functional groups based on their stomatal regulation and xylem architecture: isohydric, diffuse porous and anisohydric, ring porous. We hypothesized that within the same climatic regime: (i) species-specific differences in growth will be conditional on topographically mediated soil moisture availability; (ii) in extreme drought years, functional groups will have markedly different growth responses; and (iii) multiple hydroclimate variables will have direct and indirect effects on growth for each functional group. We used standardized tree-ring chronologies to examine growth of diffuse-porous (*Acer*, *Liriodendron*, and *Betula*) and ring-porous (*Quercus*) species vs. on-site climatic data from 1935 to 2003. *Quercus* species growing on upslope sites had higher basal area increment (BAI) than *Quercus* species growing on mesic, cove sites; whereas, *Acer* and *Liriodendron* had lower BAI on upslope compared to cove sites. Diffuse-porous species were more sensitive to climate than ring porous, especially during extreme drought years. Across functional groups, radial growth was more sensitive to precipitation distribution, such as small storms and dry spell length (DSL), rather than the total amount of precipitation. Based on structural equation modeling, diffuse-porous species on upslope sites were the most sensitive to multiple hydroclimate variables ($r^2 = 0.46$), while ring-porous species on upslope sites were the least sensitive ($r^2 = 0.32$). Spring precipitation, vapor pressure deficit, and summer storms had direct effects on summer AET/P, and summer AET/P, growing season small storms and DSL partially explained growth. Decreasing numbers of small storms and extending the days between rainfall events will result in significant growth reduction, even in regions with relatively high total annual rainfall.

Keywords: diffuse-porous, hydroclimate, productivity, radial growth, ring-porous, small storms, structural equation modeling, tree-rings

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Introduction

Novel climatic conditions due to climate change pose challenges for forest management and conservation. Particularly, temperature increases and precipitation shortages are expected to more strongly affect tree species growth and distribution in the near future (IPCC, 2014). Climatic changes will likely drive latitudinal and altitudinal shifts in species distribution worldwide (Hansen *et al.*, 2001; Allen *et al.*, 2010; Burrows *et al.*, 2014; Melillo *et al.*, 2014) in ways that could lead to novel species assemblages (Williams & Jackson, 2007). Some species are particularly more sensitive to climate or combinations of climatic variables than others (Clark *et al.*, 2012). Mountainous areas may offer short-dis-

tance escapes for some species facing climate change, which could also lead to the formation of novel species assemblages in these landscapes (Bertrand *et al.*, 2011; Dobrowski, 2011). Warming air and altered precipitation will likely result in changes in tree growth rates, mortality rates, competition, and species interactions all of which can modify the distribution of tree species (Konar *et al.*, 2010; Clark *et al.*, 2012, 2014a; Zolkos *et al.*, 2015). Even with stable or increased precipitation, temperature induced increases in evapotranspiration could lead to increased drought stress (Ford *et al.*, 2011a,b; Cook *et al.*, 2014).

The southeastern USA has experienced severe droughts causing tree mortality both in recent years and in the past (Hursh & Haasis, 1931; Elliott & Swank, 1994; Klos *et al.*, 2009; Pederson *et al.*, 2014). Because drought vulnerability varies by tree species and size, shifts in forest composition and structure can

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potentially result following drought events. While some have reported higher drought-related mortality in *Pinus* and mesophytic tree groups compared to *Quercus* (Klos *et al.*, 2009), others have reported the opposite with higher mortality in *Quercus* on slopes and ridges (Clinton *et al.*, 1993), suggesting that a general or predictive understanding of drought-related tree mortality will require both a mechanistic ecophysiological perspective as well as a long-term observational record. If future drought conditions are exacerbated due to warming, it stands to reason that these forests could become substantially less productive.

Tree-level sapflow data suggest wide variation in daily water use among species, and different sensitivities to water stress may depend, in-part, on xylem anatomy (Sperry *et al.*, 1994; Wheeler *et al.*, 2005; Taneda & Sperry, 2008; McCulloh *et al.*, 2010; Sperry, 2011). Under the same climatic regime, diffuse-porous species, such as *Betula lenta* L., *Nyssa sylvatica* Marsh., *Acer rubrum* L., and *Liriodendron tulipifera*, have much higher daily water use than ring-porous species, such as *Quercus montana* Willd. [*Q. prinus* L.] and *Q. rubra* L. (Ford *et al.*, 2011a). While *Quercus* and other species with ring-porous xylem anatomy have a potential for high water use based on xylem conduit diameter (Cochard & Tyree, 1990), field observations suggest that these species operate under a fraction of this potential, thus lending support for their low observed water use (Minniat *et al.*, 2015).

Under high humidity, or low vapor pressure deficit (D), with no other limitations to leaf physiology, plants have maximal rates of stomatal conductance and carbon assimilation. As soil water potential drops, and/or air humidity lessens (high D), plants respond by regulating stomatal conductance in different ways before catastrophic losses in hydraulic conductivity result (Sperry, 2011; Choat *et al.*, 2012; Meinzer *et al.*, 2013; Martínez-Vilalta *et al.*, 2014). Plants that have a high degree of apparent stomatal sensitivity to D and maintain leaf or xylem water potentials well above critical water potentials are classified as more isohydric; whereas, plants that allow actual leaf or xylem water potentials to fall throughout the day and approach critical water potentials are classified as anisohydric (Choat *et al.*, 2012; Sade *et al.*, 2012; Klein *et al.*, 2013). Plants in the latter group can maintain relatively high rates of stomatal conductance in high D or low soil moisture conditions, provided the critical water potential threshold in the plant hydraulic system is not crossed (Klein, 2014). Ring-porous species, particularly *Quercus* species, have lower leaf water potential thresholds for stomatal closure, exhibit more anisohydric as opposed to isohydric regulation of leaf water potential, and are more deeply rooted than diffuse-porous species

(Cavender-Bares & Bazzaz, 2000; Ewers *et al.*, 2007), and the sensitivity of stomatal conductance to D is lower in ring-porous species than in diffuse-porous species (Oren *et al.*, 1999; Oren & Pataki, 2001; Hölscher, 2004; Ford *et al.*, 2011a; Meinzer *et al.*, 2013).

While climate is an important factor of annual tree growth, which climatic variables are the most influential on radial growth may vary among species and site moisture conditions influenced by topography (Friedrichs *et al.*, 2009; Michelot *et al.*, 2012; Brzostek *et al.*, 2014; Clark *et al.*, 2014b; Martin-Benito & Pederson, 2015). In the Appalachian Mountains USA, the riparian or cove vs. upslope topographic positions are characterized by differences in solar radiation, cold air drainage, soil moisture (Yeakley *et al.*, 1998; Hwang *et al.*, 2014), summer and winter temperature regimes, and atmospheric drying potentials (Bolstad *et al.*, 1998). These distinct topographic positions buffer or modify climatic conditions and may provide suitable growing habitat or refugia, during some times of the year, for one functional group and not for the other. Few climate-growth studies have onsite, long-term climate data; instead, most studies use the nearest or regional NCDC NOAA climate data for their analyses (e.g. Fekedulegn *et al.*, 2003; Tardif *et al.*, 2006; Speer *et al.*, 2009; Copenheaver *et al.*, 2011; Harley *et al.*, 2011; Le Blanc & Terrell, 2011; Stambaugh *et al.*, 2011; Pederson *et al.*, 2012b). To our knowledge, no studies have examined the effects of hydroclimate variability, such as streamflow, actual evapotranspiration, number of storms, dry spell length, and D , on radial growth of deciduous trees.

The aims of our research were to detect the climate-driven patterns of tree growth of dominant deciduous tree species in the southern Appalachians. Water use is related both to xylem architecture (diffuse- vs. ring porous) and stomatal regulation classification (iso- vs. anisohydric) (Oren *et al.*, 1999; Hoffman *et al.*, 2011; Johnson *et al.*, 2011; Meinzer *et al.*, 2013; Klein, 2014; Martínez-Vilalta *et al.*, 2014). For our purposes, we reduced this complexity and draw generalizations among water use strategies and forest productivity by categorizing species into two main stomatal/xylem functional groups: isohydric, diffuse porous (hereafter, diffuse porous) and anisohydric, ring porous (hereafter, ring porous). We hypothesize that within the same climatic regime, (i) there will be species-specific differences in growth that will be conditional on topographically mediated soil moisture availability (e.g. mesic, coves or drier, upslope topographic positions); (ii) in extreme drought and wet years, ring-porous species will have markedly different growth responses than diffuse-porous species, again, conditional on topographic position; and (iii) there will be growth responses to multiple hydroclimate variables

and these variables will have direct and indirect effects on growth for each functional group; these responses will also be conditional on topographic position.

We evaluated the climatic controls on radial growth of species with diffuse-porous (*Acer rubrum*, *Betula lenta*, *Liriodendron tulipifera*) and ring-porous (*Quercus alba* L., *Q. montana*, and *Q. rubra*) xylem in cove vs. upslope topographic positions within the Coweeta Basin, southern Appalachians (CHL, Coweeta Hydrologic Laboratory). Our climate record, including precipitation and temperature, was obtained onsite at CHL (Laseter *et al.*, 2012). Because of the high resolution in the climate and stream discharge data at CHL, we were able to calculate other variables related to hydroclimate, such as number of storms by storm size (mm of rainfall per event), dry spell length, streamflow, actual evapotranspiration, and *D*.

Materials and methods

Study area

Our research site was the Coweeta Hydrologic Laboratory (CHL) located in the Nantahala Mountain Range of western North Carolina, USA, within the Blue Ridge Physiographic Province, in the southern Appalachians (latitude 35°03'N, longitude 83°25'W). The 2185 ha laboratory consists of two adjacent, east-facing, bowl-shaped basins; Coweeta Basin and Dryman Fork Basin. Elevations range 675–1592 m, and slopes are steep (30–100%). Soils are deep sandy loams (Thomas, 1996). Relief has a major influence on hydrology, climate, and vegetation (Bolstad *et al.*, 1998; Elliott *et al.*, 1999). Mean annual temperature is 12.6 °C, and seasonally ranges 3.3–21.6 °C. While annual rainfall is usually abundant in this region averaging ca. 1800 mm, dry years, such as the recorded droughts between 1985–1988 and 1998–2002, are increasingly common (Laseter *et al.*, 2012). From a multi-centennial perspective, these recent droughts were severe, although not as severe as droughts during the 18th and 19th centuries. In fact, the middle portion of the 20th century contained some of the strongest pluvials since 1665 (Pederson *et al.*, 2012b).

Field sampling

We sampled 22 forest stands across the elevation gradient and north- and south-facing exposures in CHL, in reference areas that had no human disturbance since 1923 or longer. Within each of these stands, we established transects extending from the stream edge to the ridge, a total of 54 transects. Collections were separated by topographic position; cove and riparian trees were those sampled within 20 m of the stream (classified as mesic, cove topographic condition), and upslope trees were those sampled more than 20 m from the stream edge (classified as dry, upslope topographic condition). Topographic moisture conditions have been verified in CHL (Yeakley *et al.*, 1998; Hwang *et al.*, 2014). In all stands, we collected tree-ring

cores from six species (*Acer rubrum* L., *Betula lenta* L., *Liriodendron tulipifera* L., *Quercus alba* L., *Quercus montana* Willd., and *Quercus rubra* L.) that were most abundant; of the 34 tree species present in CHL, these six comprise more than 50% of the total basal area (Elliott & Swank, 2008). We sampled 15–40 trees per stand for a total of 465 trees (Table S1) ranging in size from 10.0 to 110.6 cm dbh. Our sampling design allowed us to sample a large number of trees and tree sizes (Fig. S1) across CHL, and to avoid bias, such as sampling only large trees or sampling a small number of trees (see Nehrbass-Ahles *et al.*, 2014).

Tree-ring cores were extracted from all sampled trees at one meter from the ground parallel to topographic contours. Visual cross-dating was used to date, and identify missing rings, cracks, or damage (Fritts, 1976; Phillips, 1985; Yamaguchi, 1991; Stokes & Smiley, 1996). After dating, annual ring widths were measured to the nearest 0.001 mm using a linear-encoded stage, microscope, and software (Velmet Inc., Bloomfield, NY, Olympus America Inc., Center Valley, PA, J2X software, Holderness, NH), followed by statistical cross-dating (COFECHA, Holmes, 1983; Grissino-Mayer, 2001).

Chronology development

We estimated annual basal area increment ($BAI = \pi (R_t^2 - R_{t-1}^2)$) from ring widths, where *R* is xylem radius from two consecutive years (*t* and *t*–1), assuming that a circle's area approximated the stem cross-sectional area. Each tree's BAI series was calculated, and then, all trees were averaged into a BAI site/species chronology. The BAI chronology for each species only extended to the year where at least 10 trees represented the average BAI for that year. We removed years specific to growth reduction caused by fall cankerworm (*Alsophila pomelaria* Harris) defoliation (1974–1978, Butler *et al.*, 2014) (Fig. 1).

We grouped species into isohydric, diffuse-porous (*A. rubrum*, *B. lenta*, and *L. tulipifera*) or anisohydric, ring-porous (*Q. alba*, *Q. montana*, and *Q. rubra*) categories, and whether they were growing on cove sites or upslope sites, for a total of four tree-ring chronologies. All chronologies were standardized and detrended using standard methods (ARSTAN, Cook, 1985; Cook & Krusic, 2013). The purpose of standardization is to remove or reduce nonclimatic influences in ring-width series, such as the allometric growth trend or growth patterns resulting from changes in local competition. Changes in ring variance through time arise from various sources and require stabilization before final chronologies can be used to relate to past climate (see Peters *et al.*, 2015). Stabilization of ring width variance due to changes in the local mean was achieved through adaptive power transformation (Cook & Peters, 1981); replication-driven variance was reduced through either an rbar weighted or a hybrid rbar weighted and spline procedure (Cook & Krusic, 2013); and a two-third spline was used to remove abrupt changes in growth related to ecological interactions, such as local competition (Cook & Peters, 1981). R-bar, the mean correlation of all time-series in a sample collection, and the expressed population signal (EPS) were used to quantify chronology quality (Table S1) (Cook, 1985; Cook *et al.*, 1990; Bunn *et al.*, 2013).

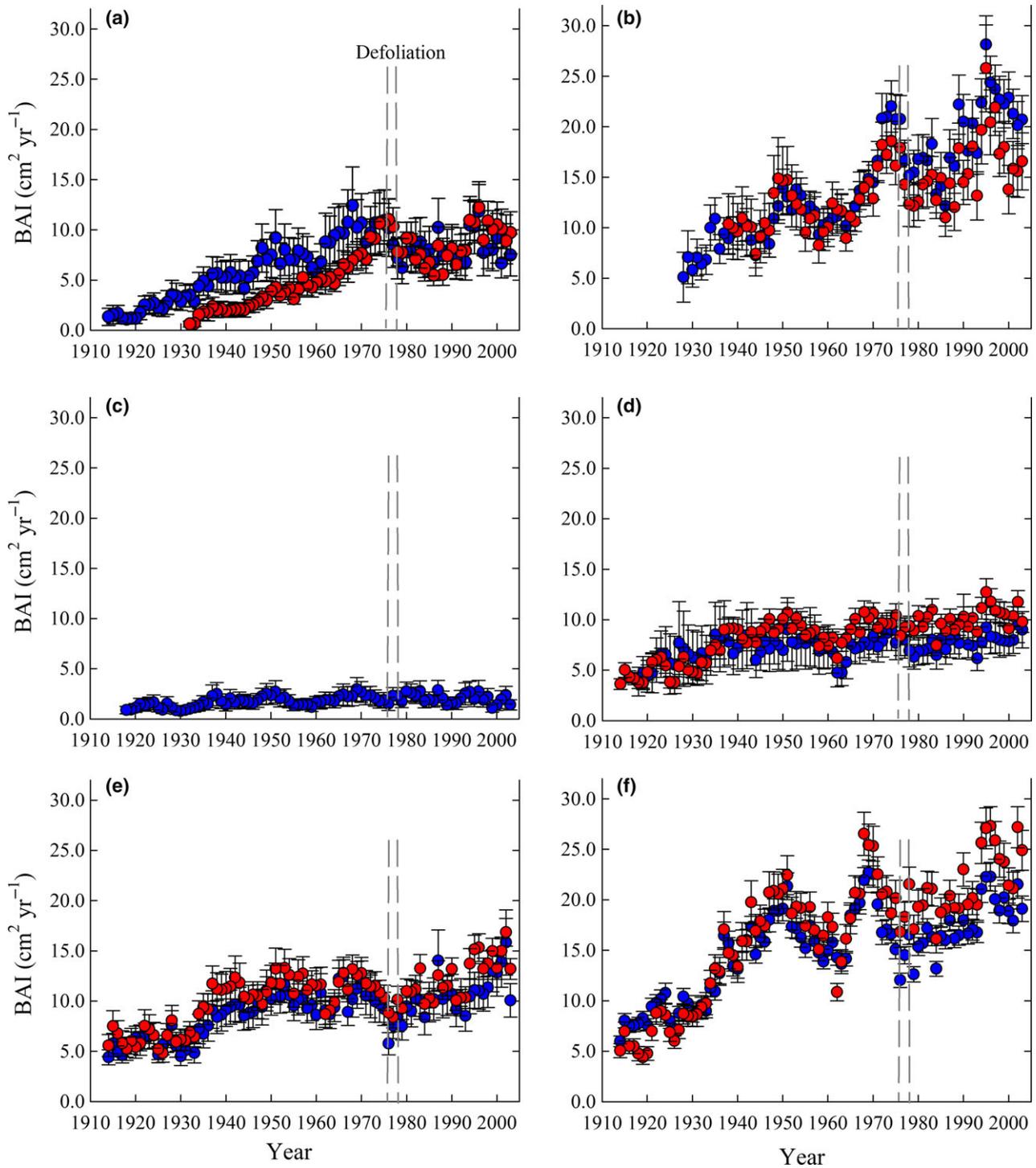


Fig. 1 Basal area increment (BAI, $\text{cm}^2 \text{yr}^{-1}$) for (a) *Acer rubrum*, (b) *Liriodendron tulipifera*, (c) *Betula lenta*, (d) *Quercus alba*, (e) *Quercus montana*, and (f) *Quercus rubra* growing on mesic, cove or drier, upslope topographic moisture conditions. The vertical dashed-lines bracket the years of insect defoliation and were excluded from statistical analyses.

Climate data

Daily air temperature, precipitation (*P*) amount and intensity, and relative humidity (since 1935) and solar radiation (since 1960) data recorded on-site at the main climate station (CS01)

were used (methods described in Laseter *et al.*, 2012). Daily minimum and maximum temperatures were recorded and then averaged to estimate a monthly minimum (T_{MIN}) and maximum (T_{MAX}) temperature. We calculated daily maximum

vapor pressure deficit from daily relative humidity and daily temperature measurements (Lowe, 1977), and daily maximum values were then averaged to provide monthly maximum D (D_{MAX}). Storm events are defined as precipitation ≥ 0.25 mm, and a small storm is total event precipitation ≤ 0.76 mm. Dry spell length (DSL) is the number of days between storm events of any size. We chose two reference watersheds located at mid-elevation (730–990 m) to represent the 22 sampled stands without human disturbance since 1923, a south-facing WS02 and a north-facing WS18. Streamflow (Q) from these two reference watersheds was measured using permanent weirs that record stream head every 5 min since 1935. We estimated actual evapotranspiration by mass balance where $AET = P - Q$ and Q is the average streamflow from the two watersheds; thus, $AET/P = 1 - Q/P$, which represents the fraction of P available for AET. At subannual timescales, antecedent soil moisture and storage (ΔS) are likely not negligible. Hydrologists at Coweeta (CHL) have used $P - Q$ to infer AET at subannual time scales (see Hwang *et al.*, 2014). CHL has tight bedrock (Swift *et al.*, 1988) and typically shallow soils (120–180 cm depth to saprolite, Hales *et al.*, 2009). Seasonally, $P - Q$ estimates are always positive and generally agree with watershed scale trends in modeled water use and sapflow (Ford *et al.*, 2011a) and remotely sensed trends in water use (Hwang *et al.*, 2014).

Palmer Drought Severity Index (PDSI) data were obtained from North Carolina Climate Division 01: Western Mountains from 1895 to 2012 from the National Climatic Data Center (<http://www.ncdc.noaa.gov>). PDSI is a regional drought index that spans positive numbers (wet) and negative numbers (droughty) and incorporates both the amount and time since precipitation (Palmer, 1965; Alley, 1984; Wells & Goddard, 2004). Seasons were defined as: winter (Dec, Jan, Feb), spring (Mar, Apr, May), summer (Jun, Jul, Aug), and fall (Sep, Oct, Nov); and dormant (Nov, Dec, Jan, Feb, Mar, Apr) and growing (May, Jun, Jul, Aug, Sep, Oct). A list of symbols and abbreviations are provided in Table 1.

Statistical analyses

To determine whether functional groups (i.e. diffuse porous and ring porous) responded differently under *extreme* precipitation conditions and between topographic positions, we used a repeated-measures analysis of variance (PROC MIXED, SAS v9.4, SAS Institute, Cary, NC, USA). We evaluated BAI of functional group by topographic position (cove vs. upslope) and by type of extreme year (wet or dry) on individual tree cores ($n = 424$) assuming that multiple years within each tree core would not be independent. In this case, the diffuse-porous group consisted of only *A. rubrum* and *L. tulipifera* because *B. lenta* only occurred on cove sites. We compared BAI in years with extremely high precipitation (1973 and 1995 had 44 cm (24%) and 33 cm (18%) above mean annual P , respectively) to BAI in a years with extremely low precipitation (1986 and 2000 had 56 cm (–31%) and 57 cm (–32%) below mean annual P , respectively). The 1985–1988 drought was the most severe on record, with a rainfall deficit of 181 cm over this 4 year period, containing the 2nd and 3rd driest years on record (Laseter *et al.*, 2012). Due to the numerous

Table 1 List of symbols and abbreviations used in this study

Symbol	Unit	Definition
D	kPa	Vapor pressure deficit
D_{MAX}	kPa	Mean maximum daily vapor pressure deficit, average of daily maximum values
T_{MIN}	°C	Mean minimum daily temperature
T_{MAX}	°C	Mean maximum daily temperature
P	mm	Precipitation
Q	mm	Streamflow
DSL	days	Number of days between rainfall events
AET	mm	Actual evapotranspiration, calculated by mass balance where $AET = P - Q$
Q/P	mm mm ⁻¹	Runoff ratio, ratio of Q -to- P
AET/P	mm mm ⁻¹	Ratio of AET-to- P , by mass balance $AET/P = 1 - Q/P$
BAI	cm ² yr ⁻¹	Basal area increment = $\pi (R_t^2 - R_{t-1}^2)$, where R is xylem radius from two consecutive years (t and $t-1$)
ANPP	kg ha ⁻¹ yr ⁻¹	Annual net primary productivity
PDSI		Palmer Drought Severity Index (Palmer, 1965)
SEM		Structural equation modeling (Kline, 2005)
CHL		Coweeta Hydrologic Laboratory
Win		Winter (December, January, February)
Spr		Spring (March, April, May)
Sum		Summer (June, July, August)
Grow		Growing season (May, June, July, August, September, October)
p		Previous year's, used in climate subscripts as lower case ' P '

factors affecting growth, we interpreted differences as statistically significant at the $\alpha = 0.1$ level.

We evaluated the importance of small storms on future growth using data from the long-term permanent plot network in CHL. We selected 6 plots (20- × 40-m) located in mesic, coves and 6 plots located on dry, upslope topographic positions. We assigned growth increment values to all trees in these twelve plots depending on whether they were ring porous or diffuse porous. These plots do not fit into the sampling regime of the 22 stands, other than they covered the same geographic area and they had similar characteristics as the sampled stands, that is, coves and upslopes with similar species composition and in reference areas. We used the most recent survey (2010) to calculate 'current' aboveground biomass using allometric equations developed by Martin *et al.* (1998) for trees in CHL. Then, we calculated annual growth by applying the radial increment for a year (1958) with low number of storms and the radial increment for a year (1994) with a high number of storms (Fig. S1C) to all trees in each plot. Annual

net primary production was calculated as: ANPP ($\text{kg ha}^{-1} \text{yr}^{-1}$) = year 2 (current aboveground biomass + 1 year of biomass increment) – year 1 (current aboveground biomass). All values were calculated by plot and then averaged with \pm standard errors.

Standardized ring-width chronology (hereafter, radial growth) and seasonal climate relationships were examined for each chronology (functional group by topographic position) with Pearson's correlations. Although we did find significant correlations for specific months (data not shown), we wanted to limit potential complications from multiple comparisons that could require a Bonferroni correction. Thus, to simplify our findings here, we focused on seasons and the growing season. Findings from other ongoing studies at Coweeta, particularly atmospheric deposition (J.D. Knoepp, unpublished data), show that small storms of the size in our study are important; we also evaluated other sizes of storms and found that small storms (≤ 0.76 mm) and total number of storms (all sizes) were most highly related to radial growth (Table S2).

We used structural equation modeling (SEM) to address the effects of multiple climate variables on radial growth; we constructed a conceptual model and tested it using SEM (Grace *et al.*, 2010). SEM is an advanced multivariate statistical process used to construct theoretical concepts, test hypotheses, account for measurement errors, and consider both direct and indirect effects of variables on one another (Malaeb *et al.*, 2000; Kline, 2005). We developed one model for each chronology with years being replicates ($n = 62$). Climate variables were selected from those significantly correlated ($P < 0.05$) with radial growth. We used SEM with manifest (observed) variables to test an *a priori* conceptual model. Our purpose in using SEM was to gain insight into the relative importance of various climate variables that may influence radial growth by partitioning covariance among variables along pathways. Path models are most effective when the variable structure is parsimonious using a small number of correlated predictor variables that have notable effects on each response variable, and predictor variable intercorrelations are not so high ($r \geq 0.8$) that variables are basically redundant (Kline, 2005). To reduce problems of collinearity among variables, we inspected the correlation matrix among all climate variables (Table S3). We also plotted variable pairs to identify linear or nonlinear relationships and determine whether any variable required transformation. Only a single variable from the same family of variables was included in the analysis (Quinn & Keough, 2002). For example, if both number of growing season storms and number of spring storms were significantly correlated with radial growth, only the one with the highest correlation coefficient was included in the model. All analyses were performed on the variance covariance matrix using PROC CALIS (SAS v9.4; SAS Institute). Indices of goodness of fit were used to select the models that best fit the data (Hatcher, 1994; Kline, 2005).

Results

As expected, some climate variables were correlated with one another (Table S2, Fig. S2a–i). Precipitation,

both total amount and the number of storms, was negatively correlated to solar radiation in spring and summer and negatively related to DSL (Table S3). While P amount was higher in the spring (479 ± 16.8 mm) than the summer (409 ± 16.5 mm), there were fewer storms (35 ± 0.7 storms in spring; 44 ± 1.0 storms in summer), yet average DSL was comparable (3.4 ± 0.06 days in spring, 3.2 ± 0.07 days in summer) (Fig. S1a,b,e). The number of small storms and D_{MAX} was positively correlated in the spring ($r = 0.333$, $P = 0.007$) and growing season ($r = 0.251$, $P = 0.039$) (Table S3). Numbers of small storms and D_{MAX} were positively correlated in the spring ($r = 0.333$, $P = 0.007$) and growing season days ($r = 0.251$, $P = 0.039$) (Table S3). This positive relationship initially might be counterintuitive, because even small rain events increase air humidity and lower D . However, comparing timing of D_{MAX} and timing of small storms in the growing season during daylight hours shows that D_{MAX} and small storms occur at different times during the day. Small storms either occurred very early in the day (0600–0800) or very late in the day (1700–1800), whereas D_{MAX} most frequently occurred prior to late day small storms, between 1300 and 1600 h, after which D was reduced (Fig. S3a). D_{MAX} was considerably lower on days with a small storm (1.52 ± 0.09 kPa) than on days without rainfall (2.12 ± 0.02 kPa) (Fig. S3a,b). Maximum solar radiation occurred most frequently between 1200 and 1300 h on days with and without storms (Fig. S3a,b).

Topographic position was an important determinant of BAI growth, but this depended on species (Fig. 1). Across all years and trees, *Quercus rubra*, *Q. alba*, and *Q. montana* growing on upslope sites had higher BAI than their corresponding conspecifics growing on cove sites ($F_{1,1304} = 5.16$, $P = 0.023$), averaging 14%, 22% and 47% greater BAI on upslopes compared to coves, respectively. On the other hand, in numerous years, *L. tulipifera* (time*topography, $F_{63,2048} = 1.49$, $P = 0.001$) and *Acer rubrum* (time*topography, $F_{33,840} = 1.44$, $P = 0.052$) had lower BAI on upslope sites than cove sites, averaging 13% and 31% lower BAI on upslopes compared to coves, respectively. *L. tulipifera* and *Q. rubra* had greater BAI than all other species ($F_{1,1295} = 288$, $P < 0.001$); across all landscape positions and years, these two species had 1.9 times higher BAI than the other species. Overall, *B. lenta* had the lowest BAI, approximately 15% of all others (Fig. 1).

All trees grew less in drought years compared to extremely wet years, but the percent increase in BAI growth from a drought to a wet year depended on the xylem functional group (significant year, topography, and year*xylem interaction) (Fig. 2). Under extreme wet conditions compared to the extreme drought conditions, such as the 1985–1988 drought, the diffuse-por-

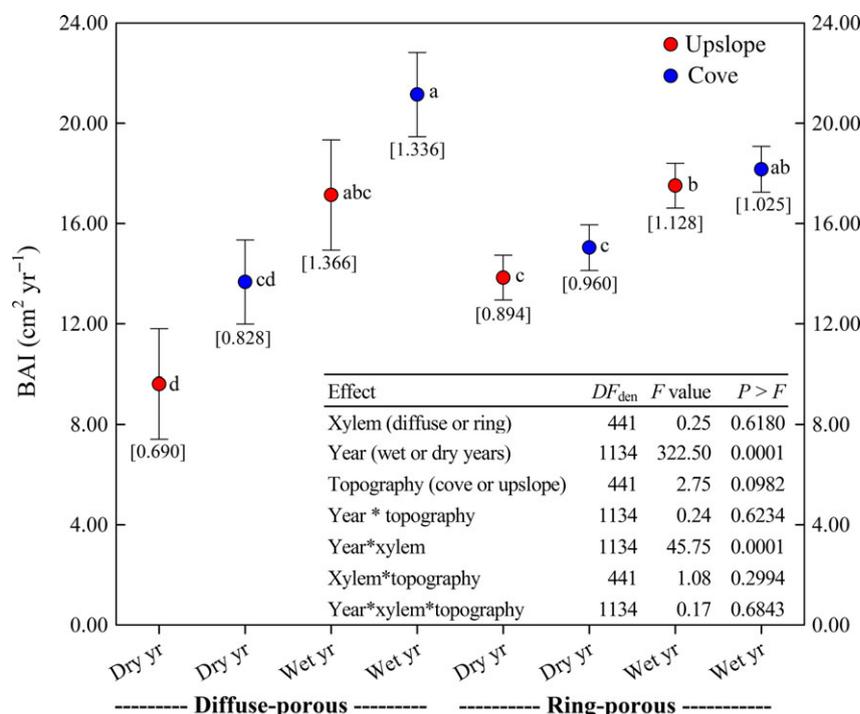


Fig. 2 Mean (\pm SE bars) basal area increment (BAI, $\text{cm}^2 \text{yr}^{-1}$) for dry years (1986, 2000) and wet years (1973, 1995) of diffuse-porous (*Acer rubrum*, *Liriodendron tulipifera*) and ring-porous (*Quercus alba*, *Q. montana*, *Q. rubra*) functional groups growing on cove or upslope topographic moisture conditions. Letters (a–c) denote significant differences. Values in brackets are the standardized tree-ring values for the dry years and wet years from the ARSTAN chronologies of each group. Inset is the repeated-measures analysis of variance table for xylem type (diffuse- or ring porous), year (wet or dry), topography (cove or upslope), and their interaction terms (PROC MIXED, SAS v9.4); denominator degrees of freedom (DF_{den}) is provided in the table and numerator DF is equal to 1 for all effects.

ous group had 78% higher BAI, whereas BAI for the ring-porous group was only 16% higher. Under drought, on upslope sites, the diffuse-porous group grew significantly less (23% less) than the ring porous (Fig. 2).

We found differences between diffuse-porous and ring-porous species in their radial growth responses to hydrologic climate variables. The strength of these responses depended on whether they were growing on cove or upslope sites (Fig. 3). Diffuse-porous species on cove and upslope sites responded positively to summer precipitation (Fig. 3a), but only diffuse-porous species on upslope sites responded to PDSI (Fig. 3a). While most groups responded positively to number of storms (Fig. 3a), all groups responded strongly and significantly to the number of small storms in the current and previous year's summer and growing season (Fig. 3a). All groups responded negatively to DSL (Fig. 3b), with radial growth of diffuse-porous species on upslope sites being the most negatively affected by DSL. Only diffuse-porous species' radial growth in upslope sites was negatively related to summer D_{MAX} (Fig. 3b). T_{MAX} did not influence radial growth of any group (not shown).

Radial growth of diffuse-porous species on cove and upslope sites was positively correlated with higher minimum winter temperatures (T_{MIN}) (Fig. 3b). Diffuse-porous species on cove sites responded positively to growing season solar radiation ($r = 0.332$, $P = 0.041$), but not on upslope sites ($r = 0.181$, $P = 0.276$). Radial growth of ring-porous species on upslope sites responded positively to solar radiation in the spring ($r = 0.394$, $P = 0.016$, 38 years of record) and summer ($r = 0.360$, $P = 0.026$). In contrast, ring-porous species on cove sites only responded positively to spring solar radiation ($r = 0.336$, $P = 0.042$). Only in spring did ring-porous species have a negative trend with P (Fig. 3a). This is also the season when low solar radiation corresponded with high P . Growth of diffuse-porous species on cove and upslope sites was positively related to previous summer AET/ P and negatively related to winter AET/ P . Growth of ring-porous species on cove and upslope sites was positively related to previous and current growing season AET/ P (Fig. 3b).

The results from our SEM analysis show the direct and indirect effects of multiple climate and hydrologic variables on tree radial growth (Fig. 4a,b). For the dif-

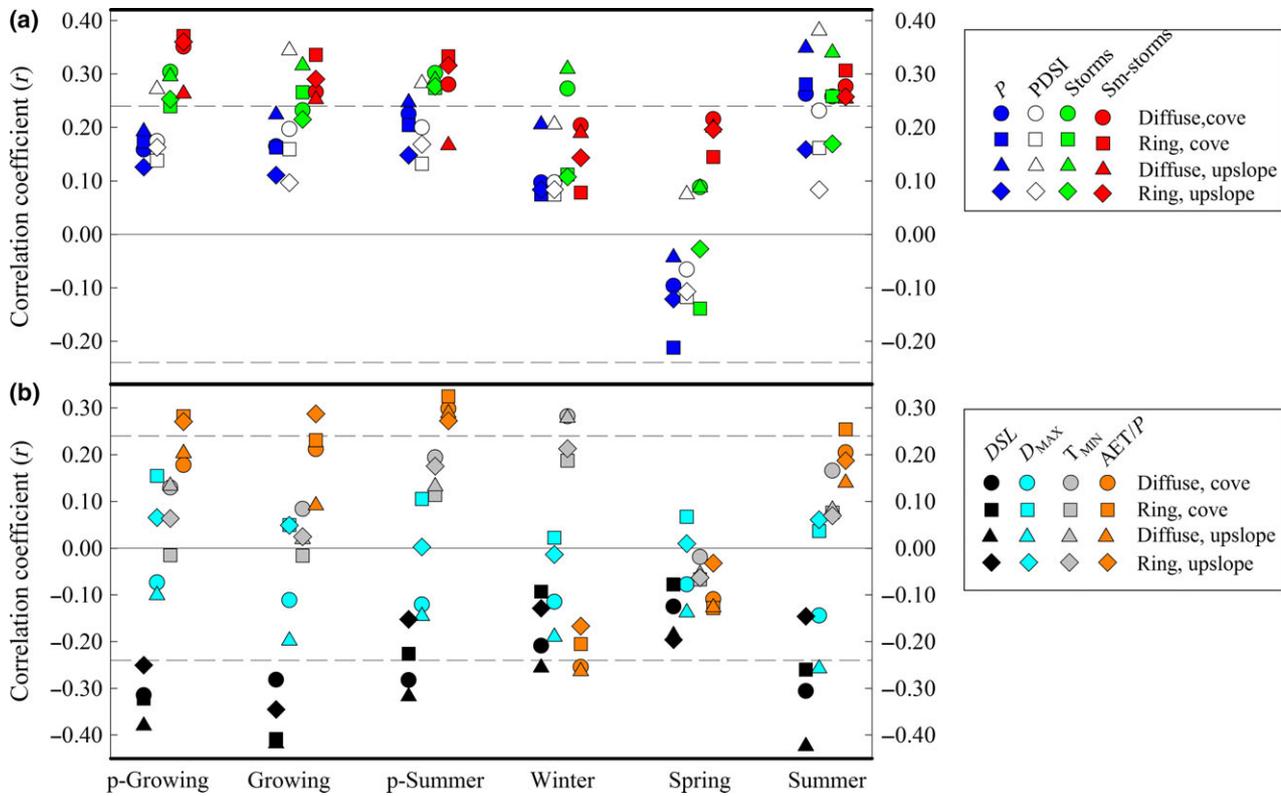


Fig. 3 Pearson correlations between standardized ring widths and seasonal climate for the diffuse-porous and ring-porous species growing on cove or upslope topographic moisture conditions: (a) precipitation, P ; Palmer Drought Severity Index, PDSI; number of storms of all size classes; and number of small storms (≤ 0.76 mm) and (b) dry spell length, DSL; mean maximum daily vapor pressure deficit, D_{MAX} ; minimum temperature, T_{MIN} ; and actual evapotranspiration-to-precipitation ratio, AET/P . Climate seasons are winter (Dec, Jan, Feb), spring (Mar, Apr, May), summer (Jun, Jul, Aug), and growing (May, Jun, Jul, Aug, Sep, Oct); lower case 'P' denotes previous year's climate season. Correlations significant at $\alpha = 0.05$ are indicated by horizontal dashed lines. All correlations used 62 years of record.

diffuse-porous species growing on cove sites, radial growth was significantly related to several climate variables, and indices of goodness of fit to the model were high (Table S4). Spring P , winter T_{MIN} , spring D_{MAX} , and number of storms in the summer had direct effects on summer AET/P , and indirect effects on radial growth mediated through summer AET/P . Summer AET/P , winter T_{MIN} , previous summer AET/P , previous and current growing season small storms, and growing season DSL and D_{MAX} had direct effects on radial growth (Fig. 4a). These direct and indirect effects explained 35% of the variation in AET/P_{Sum} and 43% of the variation in radial growth of diffuse-porous species growing on cove sites. Similar good-fit models were found for the other three chronologies using these climate variables. The models explained 46% of the variation in radial growth for diffuse-porous species growing on upslope sites (Fig. 4a), 41% for ring-porous species growing on cove sites (Fig. 4b), and 32% for ring-porous species growing on upslope sites (Fig. 4b, Table S4).

Discussion

We hypothesized that growth of six southern Appalachian deciduous trees would depend on whether the species were growing in cove or upslope topographic positions within the same climatic regime; functional groups of these species (i.e. diffuse porous or ring porous) would differ in their growth response and responses would be exacerbated under extreme drought; and multiple hydroclimate variables would explain growth of each functional group better than a single climate variable. *Quercus rubra* and *Liriodendron tulipifera* had much higher BAI than the other four deciduous species; however, *Q. rubra* grew more on upslope sites than cove sites, whereas it was the inverse for *L. tulipifera*. These differences can be partially explained by their contrasting stomatal regulation and xylem anatomy. Functional groups varied in their radial growth response to some climate variables based on their topographic moisture position, while other responses were similar across topography. Diffuse-por-

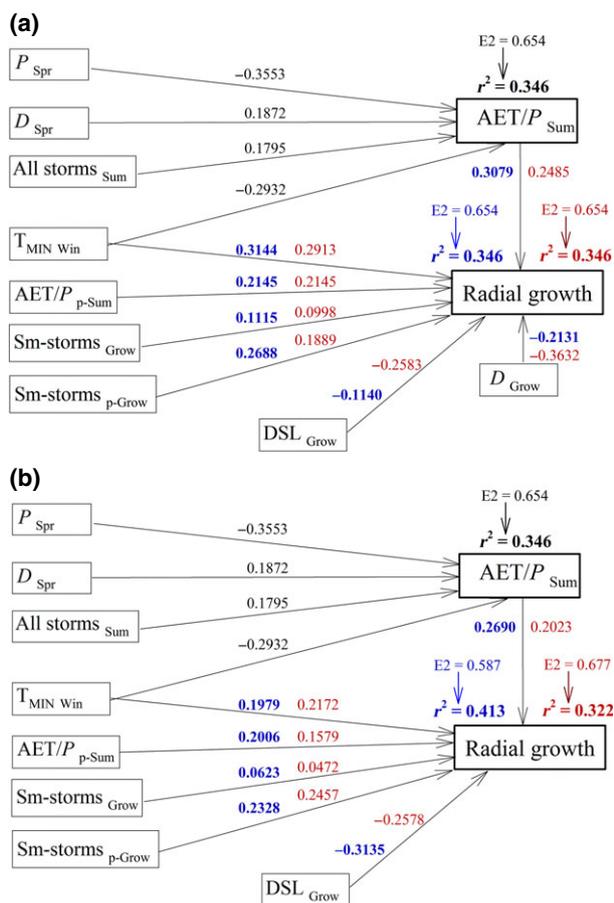


Fig. 4 Final structural equation models (SEM) with standardized path coefficients for actual evapotranspiration-to-precipitation ratio (AET/P) in the summer and annual radial growth (standardized tree-ring widths) for: (a) diffuse-porous species growing on cove and upslope sites and (b) ring-porous species growing on cove and upslope sites. Blue colored coefficients denote cove sites and red colored coefficients denote upslope site, shared coefficients are in black. Climate variables used in the models were small storms ≤ 0.76 mm of rainfall per event; D_{MAX} , mean maximum daily vapor pressure deficit; T_{MIN} , minimum temperature; P , precipitation; all storms, storm events of all sizes; DSL, dry spell length (number of days between rainfall events). The subscript for each climate variable are the seasons (Grow = growing season; Sum = summer; Win = winter; Spr = spring), and the lower case 'P' in the subscript denotes previous year's climate season. Straight lines denote direction of path coefficients. Correlations among climate variables are provided in Table S3. Goodness-of-fit statistics are provided in Table S3.

ous species were more sensitive to hydroclimate than ring-porous species, and this sensitivity was even more striking during extreme drought conditions. We found direct and indirect effects of hydroclimate variables on radial growth of both functional groups, which demonstrates that the interactions among hydroclimate vari-

ables were more predictive than a single climate variable.

Radial growth related to drought proxies

In our study, ring-porous species (i.e. *Q. rubra*, *Q. alba*, and *Q. montana*) did not respond to PDSI, a regional drought proxy; only diffuse-porous species on upslope sites showed a relationship with previous and current year PDSI. Other studies have examined climate-growth relationships for *Quercus* using various drought proxies (e.g. Harley *et al.*, 2011; Le Blanc & Terrell, 2011), and results vary depending on several factors, including the age of the trees and the latitudinal differences in climate (i.e. northern, central, or southern Appalachians). For example, Speer *et al.* (2009) calculated climate-growth models for five species of *Quercus*. In their models, all *Quercus* had a positive response to PDSI in summer (June, July) of the current year; however, *Q. montana* growth had a negative relationship with previous May PDSI. Clark *et al.* (2012) reported that *L. tulipifera* 'tracked' summer drought (based on PDSI), whereas *Quercus* species were less sensitive to summer drought. These relative sensitivities between *L. tulipifera* and *Quercus* species generally hold true in other regions of the eastern US (Pederson *et al.*, 2013; Brzostek *et al.*, 2014; Maxwell *et al.*, 2014; Martin-Benito & Pederson, 2015). Because we only evaluated the most dominant ring-porous genus, *Quercus*, our findings should be cautiously interpreted for other, less dominant ring-porous species (e.g. *Oxydendrum arboretum*, *Robinia pseudoacacia*) found in the southern Appalachians.

Topography influences radial growth

Although we did find significant correlations between climate and radial growth of functional groups depending on their topographic moisture position for some climate variables, topographic position provided no advantage or disadvantage to ring-porous species in extreme dry years. Interestingly, radial growth was greater for ring porous than diffuse-porous species on upslope sites in extreme dry years. On the other hand, diffuse-porous species growing in cove positions had significantly higher growth in wet years than dry years. That diffuse-porous species, such as *Liriodendron tulipifera*, are sensitive to drought in humid regions is similar to findings by Pederson *et al.* (2012a). Here, our findings suggest that even in the wetter southeastern USA, a substantial increase in growth might be expected on wetter sites during wetter years.

Radial growth of ring-porous species on upslope sites was positively correlated with summer solar radiation,

whereas this same group on cove sites was not. In contrast, radial growth of diffuse-porous species growing on upslope sites was not significantly correlated with solar radiation, while it was positively related on cove sites. This pattern could have arisen if ring-porous species growing in mesic coves acclimated to lower light during their ontogeny (Anderson & Tomlinson, 1998; Cavender-Bares & Bazzaz, 2000) and developed leaves acclimated to shade (sun vs. shade leaves, Wang & Bauerle, 2006). It is conceivable that trees in mesic coves could develop shade leaves as concave areas have less exposure and receive lower radiation input than upslope areas, regardless of cloud cover (Hwang *et al.*, 2011, 2014). These ontogenetic and morphologic adaptations might explain why radial growth of ring-porous species on cove sites was not significantly correlated with summer solar radiation, whereas radial growth on upslope sites was related to summer solar radiation.

Precipitation distribution influences radial growth more than amount

Seasonally, high amounts of precipitation in the spring can occasionally be negatively correlated with growth. For example, Le Blanc & Terrell (2011) found that < 10% of their *Quercus* sites showed a negative radial growth response to spring *P*, while the remaining sites showed no response. A study of six *Q. rubra* sites in the southern Appalachians indicated that changes in radial growth were related to seasonal covariance of temperature and precipitation (Crawford, 2012); higher spring precipitation delays soil warming and tree physiological activity. We found a strong positive radial growth response of the ring-porous group to spring solar radiation and negative trends to spring *P*, which suggests that *Quercus* experiences energy limitation when spring *P* is particularly high.

Across xylem anatomy groups, species, and topographic positions, radial growth was more sensitive to how precipitation was distributed rather than the total amount of precipitation. The distribution of rainfall (i.e. number of storms and DSL) in the current and previous growing seasons was more significant than the total amount of rainfall for both functional groups growing on cove and upslope sites. This suggests that small storms can provide sufficient relief from moisture stress and potentially increase carbon assimilation. It is important to note that the amount of water in the small storms (≤ 0.76 mm) would not be enough to infiltrate the canopy, as canopy interception for hardwood forests in the growing season is *ca.* 2.0 mm for forests with fully developed canopy (S.T. Brantley, unpublished data), and an additional 0.5–1.0 mm of rainfall could be intercepted by the forest floor and evaporate before

infiltration to the mineral soil (Helvey & Patric, 1965; J.D. Brantley, unpublished data). Rather, we speculate that the mechanism is one of small storms reducing *D*, and in turn, allowing higher stomatal conductance and thus high carbon assimilation rates. When other environmental variables are not limiting (e.g. solar radiation), high rates of stomatal conductance occur at low *D* that decline exponentially with increasing *D* (Ford *et al.*, 2011a; Boggs *et al.*, 2015). Even small decreases in *D* could lead to increases in growth, as stomatal conductance is greatest during humid conditions in the daytime. During these relatively humid conditions is also when solar radiation peaked, again potentially conferring high CO₂ uptake and carbon fixation rates.

To our knowledge, no other studies have examined the influences of number of storms and storm size on radial growth, but our results suggest that if precipitation distributions change in the future (e.g. intensification, *sensu* Huntington, 2006), growth loss may be substantial. For example, we estimated annual net primary production (ANPP) of diffuse-porous and ring-porous species growing on cove and upslope sites within CHL. We applied the radial growth increment for each functional group based on a year with a low number of small storms vs. a year with a high number of small storms to the current biomass of cove and upslope plots (Table 2). The ANPP for the low number vs. high number of storms would be 4489 and 6307 kg ha⁻¹ yr⁻¹, respectively. This estimate represents a 29% loss in growth on upslope sites if the number of small storms is reduced. The same calculations for cove plots resulted in an ANPP of 7240 kg ha⁻¹ yr⁻¹ for low number of small storms and 9632 kg ha⁻¹ yr⁻¹ for high number of small storms, a potential 25% loss in growth on cove sites if number of small storms continues to decrease. These estimates are simplified, as it is not likely that only the number of small storms will change in the future, but they do highlight the relative importance of small storms in the region.

Effects of AET/P on radial growth

Current and previous growing season AET/*P* were positively related to radial growth of ring-porous species, and previous summer AET/*P* was positively related to radial growth of both functional groups growing on cove and upslope sites, but the relationships were stronger for upslope sites. This relationship between radial growth and AET/*P* demonstrates the direct linkage between physiological and hydrologic processes, that is, trees of both functional groups were transpiring and assimilating carbon, and subsequently AET increased. This hydrologic variable is likely also

Table 2 Average aboveground biomass and aboveground net primary production (ANPP) for six cove and six upslope plots within Coweeta Hydrologic Laboratory

	Cove plots		Upslope plots	
	Biomass (kg ha ⁻¹)	ANPP (kg ha ⁻¹ yr ⁻¹)	Biomass (kg ha ⁻¹)	ANPP (kg ha ⁻¹ yr ⁻¹)
Current	377 390 (75 765)		180 004 (27 026)	
Low number of storms	384 630 (77 065)	7240 (1340)	184 311 (27 407)	4489 (350)
High number of storms	387 022 (77 579)	9632 (1878)	186 311 (27 407)	6307 (467)
Low vs. High	Δ ANPP = -2392 ± 552 kg ha ⁻¹ yr ⁻¹ potential 25% loss in ANPP		Δ ANPP = -1818 ± 131 kg ha ⁻¹ yr ⁻¹ potential 29% loss in ANPP	

related to the *availability* of the precipitation to be used in evapotranspiration. In other words, precipitation that is held in the soil which does not immediately contribute to streamflow could contribute to higher evapotranspiration and thus growth; quantitatively, this is seen as a negative correlation between AET/*P* and the fraction of *P* that ends up as *Q* (Table S3). Ring-porous species were sensitive to AET/*P* through the growing season with a stronger response in the summer. Diffuse-porous species were most sensitive to previous summer AET/*P* indicating that when conditions in the previous year are favorable these trees may store more carbon. Drier, upslope sites appear to be especially vulnerable to prior summer hydroclimatic conditions.

The strong radial growth response of both functional groups to previous year growing season conditions emphasizes the importance of previous-year climate for physiological processes, such as carbohydrate storage, for growth the next year. Other studies have shown that radial growth is related to both the previous and current year climate (e.g. Cook *et al.*, 2001; Ford & Brooks, 2003; García-Suárez *et al.*, 2009; Harley *et al.*, 2011). In our study, radial growth of both functional groups responded to previous and current growing season number of storms, number of small storms, DSL, and AET/*P*.

Forest growth in a warmer more hydrologically variable climate

Radial growth was sensitive to diverse and interacting climate variables, and future growth for southern Appalachian forests would be best predicted while considering all interacting variables (see Pederson *et al.*, 2015). We used SEMs to estimate causal effects through path analysis and were able to construct good-fit models for multiple climate variables by their direct effects on AET/*P* and their direct and indirect effects on radial growth responses. Our results showed that multiple climate variables predicted growth of our functional groups more than a single climate variable. Spring pre-

cipitation, spring D_{MAX} , and summer storms explained a large proportion of the variation in summer AET/*P*, and summer AET/*P*, growing season small storms and DSL partially explained radial growth. Diffuse-porous species growing on upslope sites were the most sensitive to climate ($r^2 = 0.46$), while ring-porous species growing on these same site types were the least sensitive ($r^2 = 0.32$). Previous and current growing season small storms were important variables in all four SEM models (combined coefficients for small storms ranged from 0.2887 to 0.3803). *D* is an important climate factor affecting tree growth as it directly influences photosynthesis and transpiration (Meinzer *et al.*, 2013) and the rate of evapotranspiration (Meinzer *et al.*, 2013).

In our SEM models, growing season D_{MAX} had a direct effect and spring D_{MAX} had an indirect effect mediated through summer AET/*P* on diffuse-porous species; whereas, we only found an indirect effect of spring D_{MAX} on ring-porous species. In contrast to our results, Voelker *et al.* (2014) found that *Quercus macrocarpa* Michx. was responsive to growing season D_{MAX} ; however, they explained that radial growth was more strongly related to D_{MAX} at the center and western edge (drier regions) of the species range compared with the northern and wettest regions. In general, the sensitivity of stomatal conductance to *D* is lower in ring-porous species than in diffuse-porous species (Oren *et al.*, 1999; Oren & Pataki, 2001; Hölscher, 2004; Ford *et al.*, 2011a; Meinzer *et al.*, 2013).

Winter temperature affected radial growth of diffuse-porous species on cove and upslope sites (Fig. 2b). Specifically, we found that less harsh winter temperatures (higher winter T_{MIN}) promoted greater growth of diffuse-porous species. These findings are in line with Martin-Benito & Pederson (2015) who showed that *L. tulipifera* is among the most sensitive species to winter temperatures from the southern Appalachian region up to eastern New York State. In our study, ring-porous species did not respond to winter T_{MIN} , possibly because these species rely on a combination of photoperiod and temperature to break

dormancy, while diffuse-porous species do not have a photoperiod requirement (Caffarra & Donnelly, 2010; Korner & Basler, 2010). Bud burst is typically earlier in diffuse-porous than ring-porous species (Wang *et al.*, 1992), perhaps later bud burst provides a safety margin for ring-porous species that are susceptible to embolism triggered by freezing events. With warmer winter temperatures leaf out may occur earlier than the current timing of spring leaf-out, which begins the first week of April (around day 100) in low-elevation positions (Hwang *et al.*, 2014). Bud burst and leaf development can be advanced if spring solar radiation and temperature are above a threshold level (Hwang *et al.*, 2014). However, variability in weather during this critical time can be more harmful to plants than a consistently cold spring (Gu *et al.*, 2008). If a warm period is followed by a late spring freeze, as seen in 2007, then newly formed leaves and shoots will be killed, and xylem vessels could embolize. A warming trend of 0.5 °C per decade beginning in the 1970s has been documented at our site and in the region, with minimum temperatures increasing at a greater rate than maximum temperature (Laseter *et al.*, 2012).

We found that hydroclimate variability influences growth of eastern deciduous trees, as seen in the relationships between number of small storms and DSL in the growing season and AET/*P* ratio in the summer and growth in our SEM models. Climate warming has already increased AET and subsequently reduced *Q* at our site. These changes are only expected to increase in the future (Cook *et al.*, 2014; Creed *et al.*, 2014). Even in regions with relatively high total annual rainfall (1800 mm), such as the southern Appalachians, decreasing numbers of small storms and extending the days between rainfall events can trigger stomatal closure for some species depending on whether they are diffuse porous or ring porous resulting in significant growth reduction.

Increasing variability in the precipitation distribution and the resulting impacts on forest productivity and carbon sequestration in these humid deciduous forests has received far less attention in the literature than the impacts of shifts in the mean precipitation regimes (Wullschleger & Hanson, 2003). Our results show that aboveground growth can be altered by as much as 25–29% in average precipitation years with only varying the distributions of that rainfall. In these humid, heavily forested regions with high precipitation, because the complex topography and orographic origins of precipitation challenge GCMs to replicate historic patterns of precipitation, there is much uncertainty in how the future precipitation regimes will

change in a warmer, higher-CO₂ world (IPCC, 2014; Farrior *et al.*, 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 Descriptive statistics of tree ring residual chronologies by functional group (diffuse-porous and ring-porous) and topographic moisture condition (cove or upslope): number of sampled trees used in the chronologies; mean ring width (SD), series inter-correlation, r_{bar} , between tree expressed population signal (EPS), and subsample signal strength (SSS).

Table S2 Pearson's correlations between storm size and radial growth (standardized tree-ring width) of diffuse-porous and ring-porous groups growing on cove and upslope sites.

Table S3 Pearson correlations among climate variables for the spring (Mar, Apr, May), summer (Jun, Jul, Aug), and growing season (May, Jun, Jul, Aug, Sep, Oct).

Table S4 Structural equation models with standardized path coefficients and goodness-of-fit statistics for radial growth (standardized tree-ring width) of diffuse-porous species growing on mesic, cove or drier, upslope sites and ring-porous species growing on cove or upslope sites.

Fig. S1 Diameter size class distribution of all sampled trees.

Fig. S2 Measured climate variables for a 76-year record (1936–2012): (a) precipitation; (b) number of storms of all sizes; (c) number of small storms (≤ 0.76 mm rainfall per event); (d) mean maximum vapor pressure deficit (D_{MAX} , average of daily maximum values); (e) dry spell length (DSL, number of days between rainfall events); (f) mean maximum temperature (T_{MAX}); (g) mean minimum temperature (T_{MIN}); (h) solar radiation; and (i) streamflow (Q). Climate seasons are spring (Mar, Apr, May) and summer (Jun, Jul, Aug).

Fig. S3 (a) Frequency histogram of the timing of D_{MAX} (black), the timing of small storms (grey), and the timing of maximum solar radiation ($Solar_{MAX}$, white) during days in which only one small storm occurred, daylight hours, and growing season days. (b) Frequency histogram of the timing of D_{MAX} (black) and the timing of $Solar_{MAX}$ (white) during days in which there were no storms, daylight hours, and growing season days.