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Topography may mitigate drought effects on vegetation along a hillslope gradient

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Abstract

Topography may mitigate drought effects on vegetation along a hillslope gradient through redistribution of soil moisture. We examined the interaction of topography, climate, soil moisture, and transpiration in a low-elevation, mixed-hardwood forest in the southern Appalachian Mountains. The effects of meteorological variation (wet and dry years) and topographic position (upslope and cove) were tested on daily soil moisture amplitude and recession and plot and species-specific transpiration. Trees in the cove plot were 17% taller and had 45% greater sapwood area than those in the upslope plot. Lower rates of soil moisture recession following rainfall events were observed at the cove plot compared to the upper plot. Greater daily soil moisture amplitude and plot transpiration, even in dry years, suggest that lower slope positions may have been buffered against moderate drought. We also observed similar transpiration in *Quercus* spp., *Carya* spp., and *Liriodendron tulipifera* in the cove plot between dry and wet years. Plot transpiration was reduced by 51% in the dry year in the upslope plot only, and transpiration by individual species in the plot reflected this pattern, suggesting water stress in dry years may be exacerbated by topography. With drought predicted to increase for these systems, the different drought responses of species, in addition to topographic effects, may lead to complex shifts in species composition.

KEYWORDS

anisohydric, drought, isohydric, topography, transpiration

1 | INTRODUCTION

Increased hydrologic cycle variability with frequent and intensified droughts and floods is emerging as a critical impact of global change. Increases in temperature and intensity of both wet and dry extremes have been documented in the southern Appalachians and in the southeastern United States (Ford et al., 2011; Wu, Clark, & Vose, 2014) and are expected to increase with climate change (Carter et al., 2014). Severe droughts can have adverse effects on forest ecosystems and their functions, including widespread tree mortality (Hansen et al., 2001; Allen et al., 2010; Anderegg et al., 2013) and reduced water yield and productivity (Adams et al., 2012; Sun et al., 2015). Drought-induced tree mortality can occur through various mechanisms, such as carbon starvation, hydraulic failure, and reduced resistance to biotic agents (Breshears et al., 2009; Klein & Niu, 2014; McDowell et al., 2008). Water stress decreases forest productivity, while reduced precipitation decreases groundwater and streamflow.

Topography may mitigate or intensify drought effects on vegetation through a variety of processes. Spatial variation in soil moisture

increases along hillslope paths during dry periods, particularly in the upper soil layers (Helvey et al., 1972; Yeakley et al., 1998; Tromp-van Meerveld & McDonnell, 2006; Mitchell et al., 2012). This variation is also dependent on time since rainfall (Ivanov et al., 2010). A myriad of ecosystem processes in downslope positions may be affected by, or rely on, this spatial variation in soil moisture, including transpiration (Eberbach and Burrows, 2006; Mackay et al., 2002), tree growth (Adams et al., 2014; Berdanier & Clark, 2015; Elliott et al., 2015), and soil respiration (Riveros-Iregui & McGlynn, 2009; Pacific et al., 2011). Understanding the interaction of topography, soil moisture, and vegetation dynamic is important to identify vulnerable species and communities and the resulting impacts on ecosystem services in complex terrain.

Downslope areas are generally understood to have wetter soils than side slopes or ridges (Jencso et al., 2009; Pacific et al., 2011), and differences in forest community composition have long been attributed to topographically driven differences in environmental conditions (Monk & Day Jr, 1985; Elliott et al., 1999). However, interactions between topographically influenced soil conditions and climatic variability are poorly understood, as are implications for forest species

occupying these landscape positions. For example, variable mortality and growth responses to drought have been documented among different species and topographical positions. Mortality of aspen (*Populus tremuloides*) was lower in topographic convergent areas compared to topographic divergent areas in the southwestern United States (Tai et al., 2017). During a multiyear drought spanning 1984–1988 in the southern Appalachians, *Quercus* spp., particularly those in the red oak group, experienced proportionally more mortality than other species (Clinton et al., 1993). Moreover, mortality was 1.4 times higher in the ridge and midslopes than in lower slope positions (Clinton et al., 1993). Across two of the most extreme drought years in the last century (1986 and 2000), Elliott et al. (2015) found that species that often dominate mesic cove communities (*Liriodendron tulipifera* and *Acer rubrum*) had 33% lower growth rates than mixed oak (*Quercus* spp.) during the drought years, with a greater reduction in growth (23%) at upslope positions compared to cove positions.

Species along these hydrologic gradients also have contrasting water-use strategies, which may further interact with climate. *L. tulipifera* and *A. rubrum* that dominate cove, or downslope positions, are categorized as diffuse porous, isohydric species (Vose & Elliot, 2016). Isohydric species tightly regulate stomatal conductance to prevent leaf water potential declines with declining soil water potential. Species dominating drier upslope positions, such as *Quercus* spp., are ring-porous with anisohydric stomatal behavior (Vose & Elliot, 2016). Anisohydric species maintain relatively open stomata as vapor pressure and soil water deficits increase (Choat et al., 2012; Klein & Niu, 2014; McDowell et al., 2008). The vulnerability of isohydric and anisohydric species to drought may differ even under a similar level of water stress: tight regulation of gas exchange increases the risk of carbohydrate depletion, but maximizing gas exchange increases the risk of hydraulic disfunction at low water potentials (Mitchell et al., 2013). Thus, vegetation response to drought, which may be characterized by a period of low soil moisture and humidity, is influenced by its species-specific stomatal regulation.

The objective of our study was to examine the effect of topography on soil moisture and transpiration of low-elevation, southern Appalachian forest communities, including a mixed-oak upslope community and a mesic cove community, during two contrasting years (wet and dry). We hypothesized that the downslope (henceforth cove) plot would be less likely to experience soil water deficits than the upslope (henceforth upslope) plot during the dry year. A previous paper reported on the species-specific trends in sap flow and canopy conductance, but not soil moisture, across three measurement years (Ford et al., 2011). In this study, we compare transpiration and soil moisture from the wettest year (2004) and the driest year (2006) of the same measurement period and discuss the potential interactions among species, climate, and topography.

2 | MATERIALS AND METHODS

2.1 | Study site

The study sites were located along the hillslope of watershed 18 (WS18), a northwest-facing, steeply sloping (average 53% slope),

12.5-ha catchment within the Coweeta Basin in the Nantahala Mountain Range of western North Carolina, USA (latitude 35°03 N, longitude 83°25 W). WS18 elevation ranges from 726 to 993 m. The climate is classified as marine, humid temperate (Swift et al., 1988). The long-term mean annual precipitation (P) at this elevation is 2,019 mm (79-year average, $SD \pm 326$ mm), while the mean growing season P from May to October is 886 mm (80-year average during May–October, $SD \pm 213$ mm). Soils fall into two main series: The Saunook series, a fine-loamy, mixed, mesic Humic Hapludult, is present at streamside positions (~50-cm depth) and Cowee–Evard complex soils, a fine-loamy, mixed-oxidic, mesic Typic Hapludult, is typically present on ridges (~70-cm depth; Knoepp and Swank, 1994).

WS18 is a mixed hardwood reference watershed and has been unmanaged since being selectively logged in the early 1900s. It is relatively undisturbed with the exceptions of the chestnut blight, which decimated *Castanea dentata* (American chestnut) trees in the southern Appalachians in the 1920s (Elliott & Swank, 2008; Kovner, 1955; Woods, 1957), and invasion of the hemlock woolly adelgid in the mid-2000s, which decimated the *Tsuga canadensis* (eastern hemlock) principally in the riparian areas (Ford et al., 2012; Brantley et al., 2013). Plant community composition in WS18 is closely associated with elevation, aspect, and soil moisture (Day & Monk, 1974).

Plot locations and sizes were selected to represent two common topographic positions, upslope and cove, and sample the major overstory species present. However, they do not represent the full range of conditions (e.g., soils, topography, and species composition). The upslope plot is located near the ridge, with a plot area of 1,295 m² and mean elevation of 806 m (Figure 1, Table 1). The cove plot is located approximately midway to the bottom of the watershed in a sheltered and moist position, with a plot area of 1,905 m² and mean elevation of 769 m. The upslope plot is dominated by *Quercus prinus* (chestnut oak) and *Carya* spp. (hickory) in the overstory, with *Kalmia latifolia* (mountain laurel) understory. The cove plot is dominated by *Quercus rubra* (northern red oak), *L. tulipifera* (tulip poplar), and *Carya* spp. in the overstory, with *Rhododendron maximum* (rhododendron) in the understory. Other species that are present in the sample plots include *Betula lenta* (sweet birch), *A. rubrum* (red maple), *Nyssa sylvatica* (black gum), and *Oxydendrum arboreum* (sourwood). Diameter at breast height and height were measured for all trees in the plots, with measurements from the end of 2006 growing season being used in this study. Leaf area of overstory trees with diameter at breast height > 5 cm and sapwood area of the sample trees were estimated using species- and site-specific allometric relationships (Martin et al., 1998).

2.2 | Environmental variables

An open-field climate station (CS17) was located midslope in an adjacent watershed (less than 200 m from the measured plots). CS17 measured precipitation (P , Belfort Instrument, Baltimore, MD, and USA) every 1 min and logged 15-min totals, air temperature and relative humidity (T_a and RH, model HMP45C, Campbell Scientific, Inc.), solar radiation (model 8-48, Epply Lab Inc., Newport, RI), and wind speed and direction (Met One 014A anemometer, Campbell Scientific) every 1 min and logged 15-min averages and totals. In the cove plot in WS18, a T_a and RH sensor (model CS500, Campbell Scientific, Inc.) was

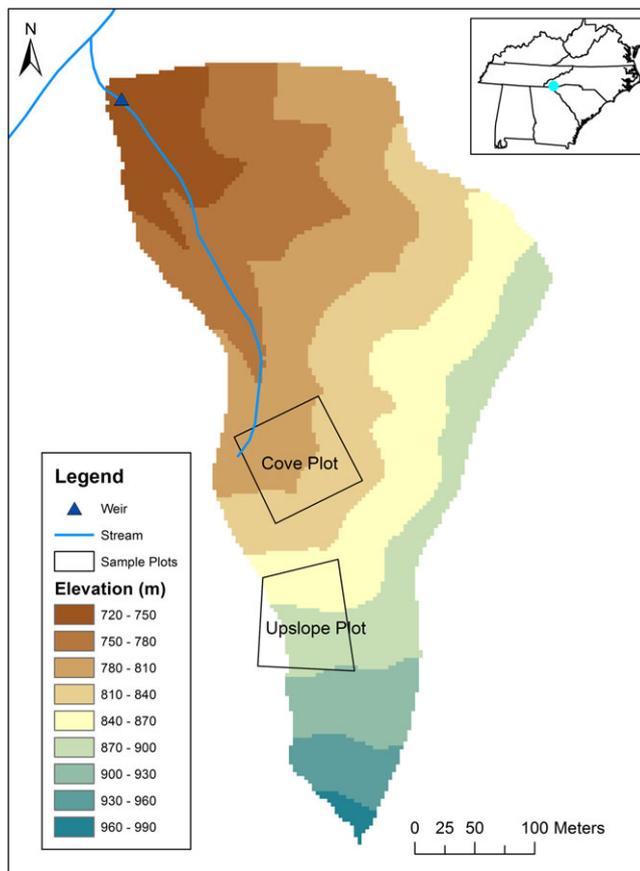


FIGURE 1 Locations and topography of WS18, upslope, and cove plots

TABLE 1 Characteristics of upslope and cove plots

	Upslope	Cove
Area (m ²)	1905	1294.6
Mean elevation (m)	806	769
Mean slope (°)	31	26
Upslope accumulation area (m ²)	9,657	34,734
LAI (m ² m ⁻²)	6.2	6.5
BA (m ² ha ⁻¹)	38.3	40.1
Density (stems ha ⁻¹)	646	471

Total peak leaf area index (LAI, projected), basal area (BA), and stem density of trees greater than 5 cm in diameter at 1.3 m above ground height at plot level.

mounted at two-thirds canopy height. We used T_a to calculate saturation vapor pressure (e_s) according to Lowe (1977). Actual vapor pressure (e_a) was calculated from fractional RH and e_s . Vapor pressure deficit (D , kPa) was calculated as the difference between e_s and e_a . Barometric air pressure was recorded hourly in the valley floor (Chart No. 5-1071, Belfort Instrument Co.).

2.3 | Soil moisture

Percent volumetric soil water content (θ , v/v %) was estimated using time domain reflectometry probes (models CS615 and CS616, Campbell Scientific, Inc.). Two 30 cm long probes were inserted vertically into the soil in each plot spanning 0- to 30-cm and 30- to 60-cm

soil depth at two locations ($n = 4$ per plot). Probes were queried every 1 min, and 15-min averages were logged (CR10X, Campbell Scientific, Inc.). Hourly soil moisture content (θ) was corrected with soil temperature measured at a depth of 5 and 20 cm for the 0- to 30-cm and 30- to 60-cm soil depth, respectively, according to calibration equations specified by the manufacturer. Daily mean θ_d at each plot was calculated by averaging the four measurements, representing an average over 0- to 60-cm soil depth.

We calculated the daily amplitude (θ_A) and recession slope ($\Delta\theta$) of soil moisture to describe soil water dynamics. Daily θ_A was defined as half of the difference between maximum and minimum θ , indicating drainage and vegetation water use. The range of plant-available soil water for Cowee-Evard complex (EvF) soils at the upslope plot is 10–25%, but the range for Saunook series (SbD) soils at the cove plot is 10–20% (Thomas, 1996). Daily $\Delta\theta$ was defined as the difference in θ recorded at midnight (24:00) and the measurement of the previous midnight, indicating the daily recession of soil moisture. Cumulative daily $\Delta\theta$ illustrates the change (loss or gain) in soil moisture over the growing season.

2.4 | Transpiration measurements

To estimate transpiration, we used constant heat dissipation probes (Granier, 1985) to monitor a subset of trees in the upslope and cove plots. Thirty-two trees in the upslope and cove plots were monitored for sap flux density throughout 2004 and 2006. Measurements from a *Carya* spp. sample tree in the cove plot were excluded from analysis due to inconsistent sap flux data.

Sap flux density (kg H₂O m⁻² sapwood s⁻¹) was determined by installing probes in the outer 2 or 3 cm of the functional xylem with two sets of probes installed circumferentially at least 90° apart. Probes were installed, shielded from thermal gradients, and wired to data loggers as described by Ford and Vose (2007), and a full description of measurements and scaling procedures is in this study (Ford, Hubbard et al., 2011). Briefly, however, sap flux measurements were scaled to whole-tree sap flow (F , kg H₂O s⁻¹) using radial profile measurements (Ford, Hubbard et al., 2011). Transpiration per unit projected leaf area (E_L , kg H₂O m⁻² s⁻¹) was estimated by dividing F by the projected leaf area estimated for each tree.

We estimated mean stomatal conductance (G_s , m s⁻¹) from E_L and D using the following general equation:

$$G_s = \frac{K_G(T) \cdot E_L}{D}, \quad (1)$$

where K_G is a function of temperature ($115.8 + 0.4236 T$; kPa m³ kg⁻¹) and accounts for the temperature effects on the psychrometric constant, latent heat of vaporization, and the specific heat and density of air (Phillips & Oren, 1998). We converted to molar units following Pearcy, Schulze and Zimmermann (1989). Several conditions must be met for Equation 1 to more accurately estimate G_s in hardwoods (Ewers & Oren, 2000). Specifically, (a) boundary layer conductance must be high so that atmospheric D approximates leaf-to-air D , (b) heterogeneity in canopy D must be low, and (c) stem sap flow must represent the magnitude and timing of leaf fluxes from the canopy. We excluded days when $D < 0.6$ kPa to minimize errors

due to (a) and (b). We used mean day-time E_L to minimize errors due to (c).

To estimate mean plot transpiration per unit leaf area (E_t , mm d^{-1}), we multiplied mean E_L for each species by the proportion of total leaf area index ($\text{m}^2 \text{m}^{-2}$) represented by that species. Sap flux gauged trees represented 74–79% of the species that occupy the overstory (Table 2). Unrepresented species were *A. rubrum*, *Acer pensylvanicum*, *B. lenta*, *O. arboreum*, and *N. sylvatica*. The E_L of unrepresented species was assigned a mean E_L of all species measured.

We present daytime growing season E_t estimates, defined here as days of year 128–280 during times 08:00–20:00, for years 2004 and 2006. We have excluded night time E_L as transpiration at night in this humid (average nighttime $D \sim 0.5$ kPa for 2004 and 2006) temperate forest is less than 3% of total daytime ecosystem evapotranspiration (Oishi and Miniati, unpublished data). Daytime E_t data from the upslope and cove plots were available for 94 days and 78 days, respectively, during the growing season of 2004, but they were available for 69 days and 70 days during the growing season of 2006. Approximately 4% and 15% of daily E_t from upslope and cove plots in 2004 were gap-filled based on linear relationships between hourly E_L and D at WS18 ($R^2 > .5$). Missing hourly E_L data in 2006 were not gap-filled due to missing D at WS18 and nonlinear relationship between E_L and D at CS17.

2.5 | Statistical analysis

To characterize the wet and dry years, we tested for differences in mean D during the growing season of 2004 and 2006 using a Student's t test. Difference in mean θ_d among years and sites was tested using a two-factor repeated-measure analysis of variance (ANOVA). To test the effects of climatic variation (year) and sites on mean daily plot E_t ,

we used a repeated-measure ANOVA with day of the year as the repeated effect. Finally, to test for differences in mean daily E_L for each dominant species, we used a repeated-measure ANOVA with sample tree as the repeated effect. Due to missing data, the comparison of E_t between plots and years was based on data from common days of the year across the groups.

We examined the changes in θ_A and cumulative $\Delta\theta$ in days following rainfall events. We log-transformed θ_A data to reduce heteroscedascity. We used mixed effects ANOVA models to test for the effects of site, number of days following rainfall events, and the site by time interaction in wet and dry years. A null mixed effect model with an intercept was formulated with rainfall event as the random (repeated) effect. The alternative models had site, number of days following rainfall event, or the interaction of both factors as the fixed effects, with rainfall event as the repeated effect. We performed a likelihood ratio test to compare the null and alternative models. All statistical tests were performed in R version 3.2.2 (The R Foundation for Statistical Computing, Vienna, Austria) at the $\alpha = .05$ level, and Tukey's post hoc honestly significant difference was used to separate levels of variables when needed.

3 | RESULTS AND DISCUSSION

3.1 | Stand and species characteristics

Species composition, as well as tree architecture, varied between the upslope and cove communities (Table 2). Sample trees were 17% taller in the cove plot ($F_{1,30} = 5.87$, $p < .05$), had 45% greater sapwood area ($F_{1,30} = 4.52$, $p < .05$), and had greater leaf area supported for any unit sapwood area ($F_{1,30} = 27.79$, $p < .01$) compared to the upslope plot.

TABLE 2 Characteristics of tree species monitored for sap flux density in each plot

Characteristics	Site	Dominant species				Other species
		<i>Quercus prinus</i>	<i>Quercus rubra</i>	<i>Carya spp.</i>	<i>Liriodendron tulipifera</i>	
Plot level:						
LAI ($\text{m}^2 \text{m}^{-2}$)	Upslope	3.5	0.6	0.5	0.01	1.6
	Cove	0.3	1.9	1.5	1.4	1.4
BA ($\text{m}^2 \text{ha}^{-1}$)	Upslope	22.2	3.5	3.0	0.03	9.6
	Cove	1.6	11.6	9.8	10.1	7.0
Density (stems ha^{-1})	Upslope	131	10	26	5	474
	Cove	8	31	85	124	223
Sample trees:						
N	Upslope	11	2	3	0	
	Cove	1	3	6	6	
DBH (cm)	Upslope	52.2 (1.95)	59 (19.5)	35.6 (5.02)	N/A	
	Cove	51.1	62.9 (1.74)	42.2 (1.36)	46.1 (1.25)	
Height (m)	Upslope	28.2 (0.59) b	29.6 (5.37) b	27.2 (2.24) b	N/A	
	Cove	28.5 a	31.5 (0.46) a	30.3 (0.54) a	36.9 (0.61) a	
A_{sw} (cm^2)	Upslope	395.5 (21.5) b	327.5 (168.4) b	441.3 (113.7) b	N/A	
	Cove	357.4 a	317.0 (15.7) a	571.2 (38.1) a	743.0 (37.0) a	
A_L (m^2)	Upslope	386.5 (25.6)	565.3 (318)	174.6 (44.8)	N/A	
	Cove	317.9	514.1 (29.7)	225.9 (15.0)	224.4 (11.8)	
$A_L : A_{sw}$	Upslope	0.88 (0.02) b	1.54 (0.18) a	0.40 (0.00) c	N/A	
	Cove	0.89 b	1.62 (0.01) a	0.40 (0.00) c	0.30 (0.00) c	

Plot peak leaf area index (LAI, projected), basal area (BA), and stem density of trees greater than 5 cm in diameter at 1.3 m above ground height. Means (standard error) of diameter at breast height (DBH), height, sapwood (A_{sw}), and leaf area (A_L) measurements of sample trees. All measurements and estimates are from 2006 growing season. Different letters denote statistically significant difference among species or topographic positions.

The upslope and cove plots had similar total basal and leaf areas, so any difference in plot E_t is likely due to species composition. Individual species also supported significantly different amounts of leaf area for each unit of sapwood area ($F_{3, 28} = 101.0$, $p < .01$), but variation in diameter and leaf area between species were not significant. The ranking among species was related to xylem anatomy: the two ring-porous sapwood species (*Quercus* spp.) supported significantly more leaf area per unit sapwood area than species with smaller conduits, which included semi-ring-porous (*Carya* spp.) and diffuse porous (*L. tulipifera*) sapwood species.

Greater sapwood area and tree height have been observed in downslope positions compared to upslope positions in mixed deciduous-conifer forest (Tromp-van Meerveld and McDonnell, 2006), mixed eucalyptus (Mitchell et al., 2012), and Japanese cedar forest (Kumagai et al., 2008). Vegetation density, measured with normalized difference vegetation index, can increase with topographical wetness index in the southern Appalachian, for example, in convergent and downslope positions compared to divergent and upslope positions (Hwang et al., 2012). Soil nutrient content and cycling rates also confirm this, as cove positions in these low elevation watersheds have higher nitrogen (N) mineralization rates and soil moisture than upslope positions (Knoepp et al. 1998, 2002). Thus, greater availability of soil moisture and nutrients at downslope positions may result in greater productivity.

3.2 | Climatic variation

Total annual P in 2004 and 2006 was 2,159 and 1,691 mm, respectively, 7% higher and 16% lower than the long-term average (79-year average 2,019 mm, $SD \pm 326$ mm). Growing season P (1,073 and 528 mm, Figure 2a) in 2004 and 2006 was 21% higher and 40% lower than the long-term average (80-year average during May–October was 886 mm, $SD \pm 213$ mm). The mean of daily maximum D was significantly lower in 2004 than in 2006 (1.5 and 2.3 kPa, $p < .01$).

Severity and frequency of drought, as well as a more extreme P distribution, have been increasing in the Coweeta Basin over the last 75 years (Laseter et al., 2012). The dry year of 2006 was the beginning of a multiyear below-average precipitation that ended in 2009. From a multicentennial perspective, the recent droughts have not been as severe as droughts during the 18th and 19th centuries (McEwan et al., 2011). Decreased P tends to occur with increased D that results in relatively higher transpiration compared to other hydrologic fluxes during drought, but very humid years result in lower D , lower transpiration, and a greater proportion of interception (Oishi et al., 2010).

Although lower precipitation and higher D characterized the relatively dry year of 2006 compared to the relatively wet year of 2004, soil moisture was only significantly lower at the upper topographic position in the drier year (Figure 2c, site effect $F_{1, 456} = 2,566$, $p < .01$; year effect $F_{1, 456} = 225$, $p < .01$; site by year interaction $F_{1, 456} = 126$, $p < .01$). Daily mean soil moisture content (θ_d) in the cove plot was similar in the dry and wet years (31% and 32% in 2006 and 2004, respectively) as well as greater than θ_d in the upper plot, but θ_d of the upper plot was markedly lower in the dry year compared to the wet year (19% and 24%, respectively).

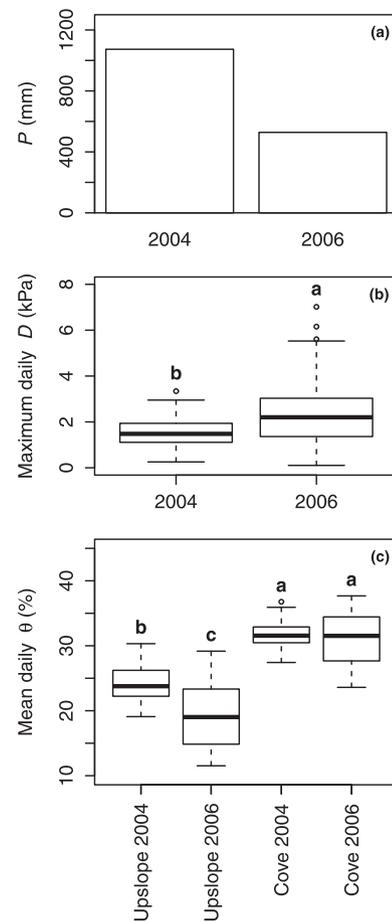


FIGURE 2 Precipitation (P , a), daily maximum vapor pressure deficit (D , b), and daily mean soil moisture (θ , c) during the growing season of 2004 and 2006. Center line in the boxplot indicates median, but the lower and upper extremes indicate the first and third quartile, respectively. Whiskers indicate points within 1.5 times of the interquartile range above or below the median. Letters denote statistically significant difference ($p < .05$) between years or among years and topographic positions

3.3 | Climate and topography effects on soil moisture

Both upslope and cove plots had similar patterns of θ_d variation during the growing season (Figure 3). However, soils in the cove plot were consistently wetter (greater magnitude of θ_d) compared to the upslope plot, particularly during the drier year of 2006, despite similar inputs of precipitation and slightly greater transpiration rates.

The daily drawdown of soil moisture, or θ_A , was related to both topographic position and the days since rainfall event (Figure 4a,b). In the wet year, both plots had a similar magnitude of diel change in soil moisture as well as a similar rate of decline in θ_A in the days following a rainfall event (site effect NS; time effect $\chi^2(6) = 54.9$, $p < .01$, site by time interaction NS; Figure 4a). In the dry year, the diel change in soil moisture was lower for the upslope plot compared to the cove plot (site effect $\chi^2(1) = 4.14$, $p < .05$; Figure 4b) and θ_A declined after the rainfall event to a greater extent in the upslope plot compared to the cove plot (time effect $\chi^2(6) = 34.9$, $p < .01$; site by time interaction NS; Figure 4b). Mean θ_A declined more rapidly in 2006 than in 2004.

Cumulative daily recession of soil moisture during the growing season ($\Delta\theta$) was affected by topographic position and timing of

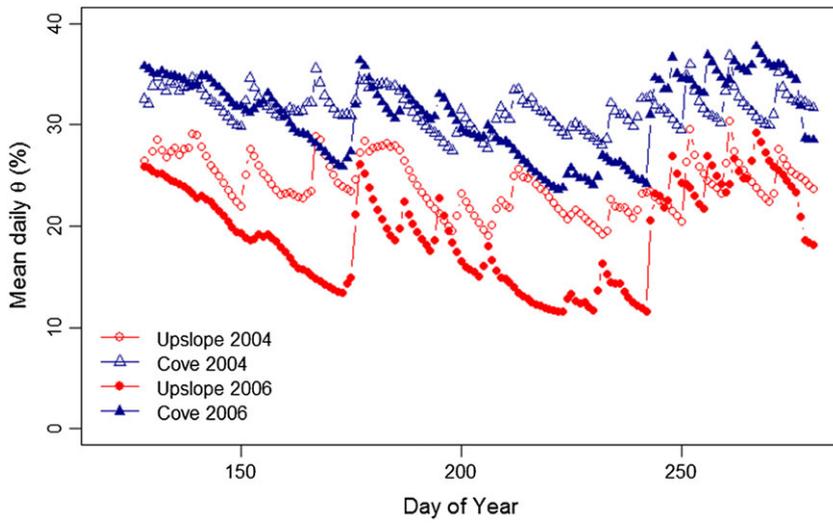


FIGURE 3 Mean daily soil moisture (θ_d) at the upslope and cove plots during 2004 and 2006

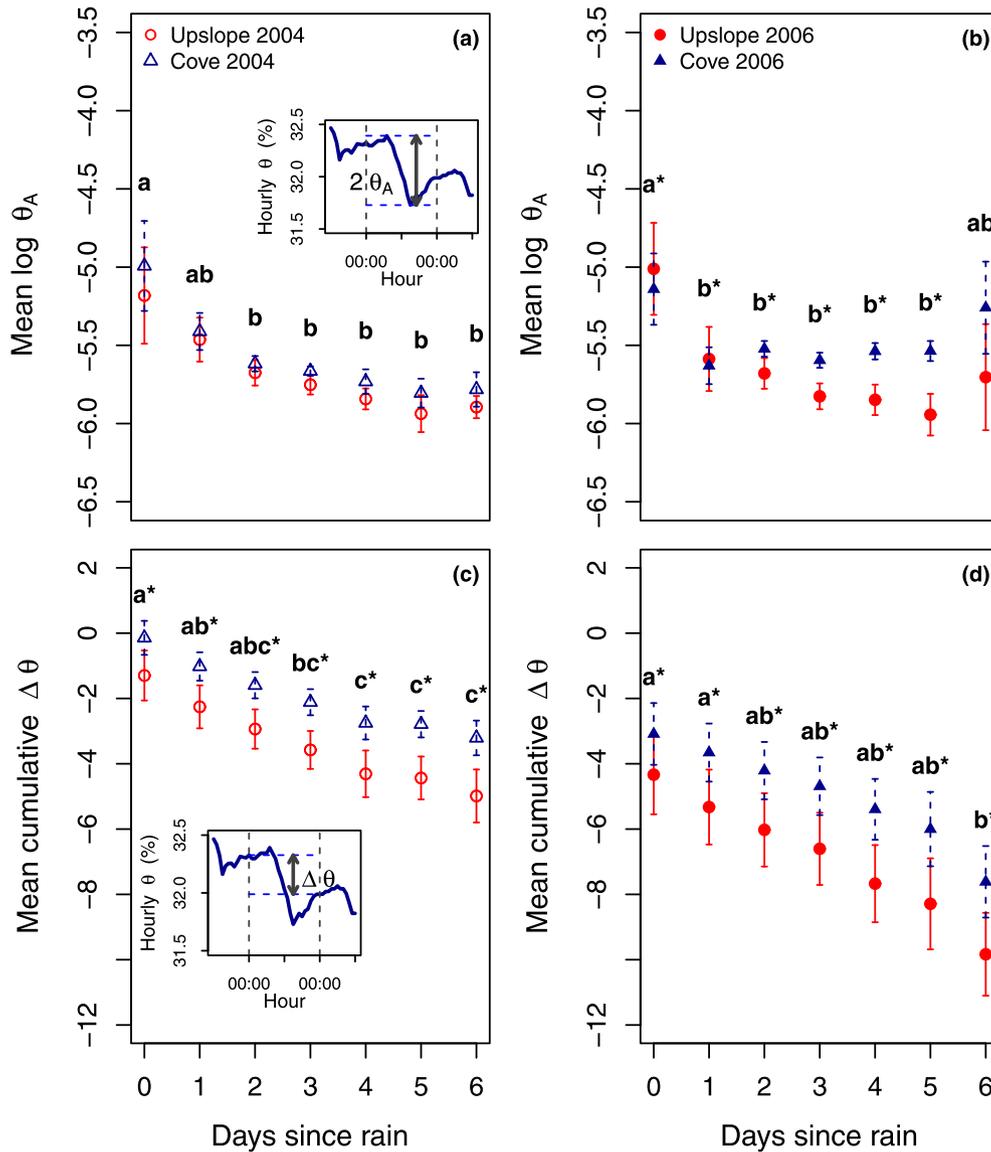


FIGURE 4 Mean logarithm of daily soil moisture amplitude (θ_A) following rain events in (a) 2004 and (b) 2006, and mean cumulative recession of soil moisture ($\Delta \theta$) during the same periods (c and d). Bars represent standard error. Different letters represent statistically significant difference ($p < .05$) among days since rain, asterisks denote significant difference between topographical positions, and colored letters denote interaction between days since rain and topographical positions. The inset plots show the estimation of daily θ_A (half of the difference between maximum and minimum θ) and $\Delta \theta$ (difference in θ measurements at 00:00)

precipitation input (Figure 4c,d). In the wet year, $\Delta\theta$ was lower for the upslope plot compared to the cove plot, indicating lower recharge and greater loss of soil moisture. $\Delta\theta$ in the days following rainfall event also declined significantly (site effect $\chi^2(1) = 42.2$, $p < .01$; time effect $\chi^2(6) = 220.5$, $p < .01$, site by time interaction NS; Figure 4c). In the dry year, a similar pattern in $\Delta\theta$ was observed (site effect $\chi^2(1) = 64.8$, $p < .01$; time effect $\chi^2(6) = 165.3$, $p < .01$; site by time interaction NS; Figure 4d). Between years, lower values at the start of the rainfall event were observed in 2006 compared to 2004.

Following rainfall events, the rate of soil moisture recession was greater in upslope positions regardless of precipitation input. Notwithstanding differences in soil texture, this manifests as lower θ_d compared to downslope positions. This variation in soil moisture distribution with topographic gradients has been observed in other studies (Helvey et al., 1972; Pacific et al., 2011; Tromp-van Meerveld and McDonnell, 2006; Yeakley et al., 1998). In southern Appalachians watersheds, hillslope soil moisture gradients were observed in the root zone (0–90 cm) during drier periods, indicating that topography exerted a more dominant control than soil properties in those periods (Yeakley et al., 1998).

Although the mechanism that maintained soil moisture at the cove plot during the dry year is unknown, several potential processes could be important. One possible explanation is that deep-rooted plants hydraulically lifted water from deeper soil layers, which replenished moisture in upper soil layers at the cove plot during dry conditions (Horton & Hart, 1998). Alternatively, θ_d may have been maintained by lateral drainage from shallow, unsaturated soils, which has been shown to sustain baseflow in steep forested slopes, with narrow incised channels (Hewlett & Hibbert, 1963). Finally, water table at the cove plot is likely to be shallower (closer to the surface) than at the upslope plot as groundwater moves from topographic divergent to topographic convergent areas (Western et al., 2001, Dingman, 2002).

3.4 | Climate and topography effects on transpiration

Variation in daily E_t was influenced by soil moisture availability, P , and maximum daily D (Figure 5). For most of the relatively wet 2004 growing season, E_t at both the upper and cove plots was similar, reflecting the similarities in soil moisture availability and dynamics. In the drier year, E_t was lower at the upslope plot than the cove plot. On average,

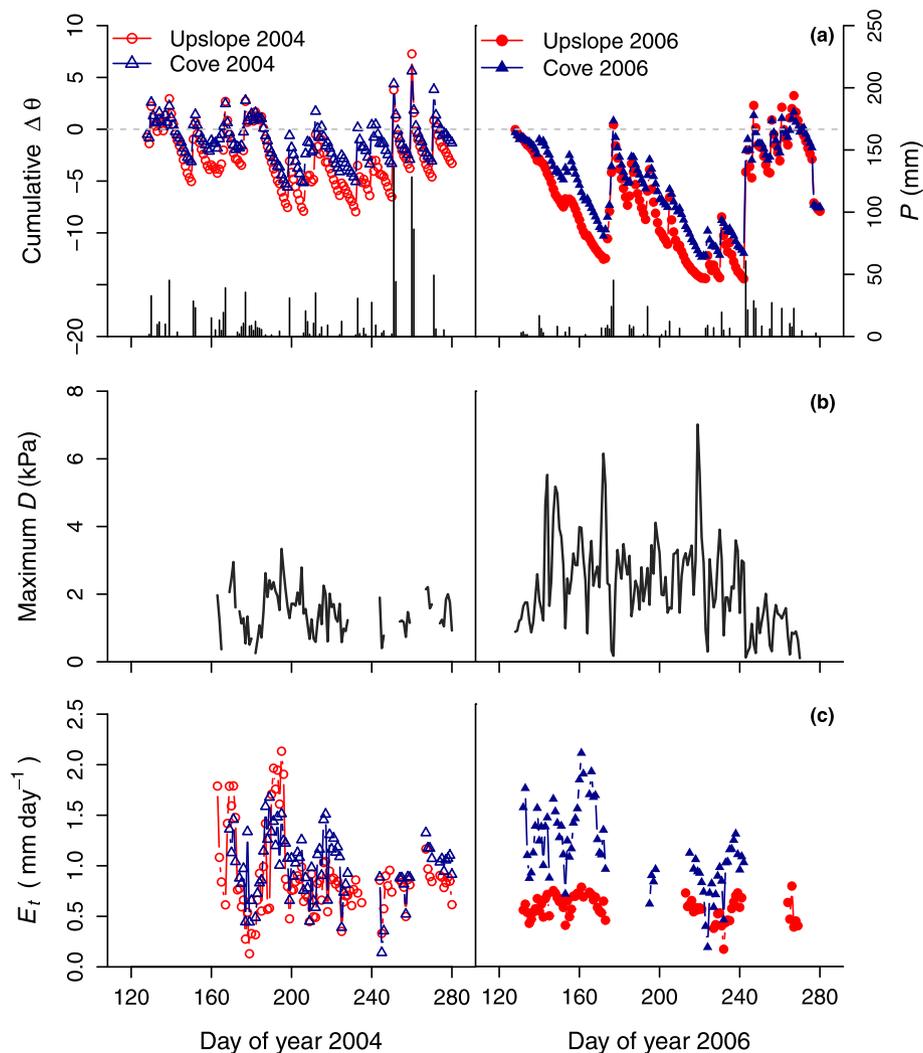


FIGURE 5 Time series of (a) cumulative daily recession of soil moisture ($\Delta\theta$) and precipitation (P), (b) maximum daily vapor pressure deficit (D), and (c) daily plot transpiration (E_t) at the upslope and cove plots during 2004 and 2006

mean daily E_t was 33% lower in the dry year compared to the wet year, and the difference was more pronounced in the upslope plot than in the cove plot, with the former being reduced by 51% and the latter by 15% (site effect $F_{1, 33} = 13.24$, $p < .01$; year effect $F_{1, 33} = 29.98$, $p < .01$; site by year interaction $F_{1, 33} = 8.70$, $p < .01$; Figure 6).

Greater E_t in downslope vegetation communities than in upslope communities has also been observed in other forests (Kumagai et al., 2008; Mitchell et al., 2012; Tromp-van Meerveld & McDonnell, 2006). The difference in E_t was attributed to differences in soil type and depth as well as stand structure (Kumagai et al., 2008; Mitchell et al., 2012; Tromp-van Meerveld & McDonnell, 2006). Another potential contributing factor is increased foliar nutrient from greater rates of N mineralization, which have been observed in the lower slope positions (coves) than ridges in the southern Appalachians (Garten et al., 1994; Knoepp & Swank, 1998). Yet N mineralization rates were more affected by foliar litter quality (and species composition) than moisture and temperature regimes of different topographic positions (Knoepp & Vose, 2007). The interaction between topoclimate, species composition, soil water, and nutrients may contribute to the vegetation pattern along the hillslope (Hwang et al., 2012; Tromp-van Meerveld & McDonnell, 2006).

There was a large variation in species-based E_L responses to climatic variation and topographic position (Figure 7). Mean E_L of *Q. prinus* (QUPR) decreased by 41% from wet to dry year but was insensitive to topographic position (site effect NS; year effect $F_{1, 10} = 27.11$, $p < .01$; site by year NS). E_L of *Q. rubra* (QURU) was sensitive to the interaction of climatic variation and topography, with 50% decrease in mean E_L from wet to dry year at the upslope plot and 2% increase at the cove plot (site effect NS; year effect NS; site by year $F_{1, 3} = 9.29$, $p = .056$). E_L of *Carya* spp. (CASP) was sensitive to topographic position during the wet year, with 56% lower mean E_L at the cove plot, but mean E_L decreased by 26% at the upslope plot and increased by 9% at the cove plot from wet to dry year (site effect $F_{1, 6} = 21.4$, $p < .01$; year effect NS; site by year $F_{1, 6} = 10.01$, $p < .05$). E_L of *L. tulipifera* (LITU) was insensitive to climatic variation (year effect NS), although we could

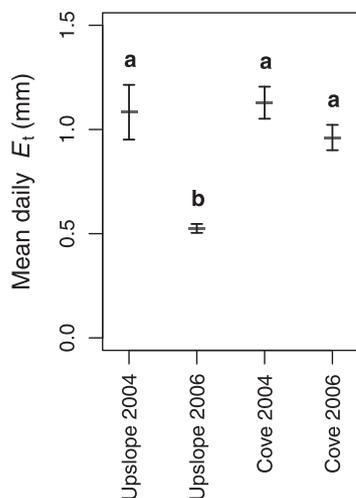


FIGURE 6 Mean plot E_t between years and topographic positions. Bars represent standard error. Different letters represent statistically significant difference ($p < .05$) between years and topographic positions

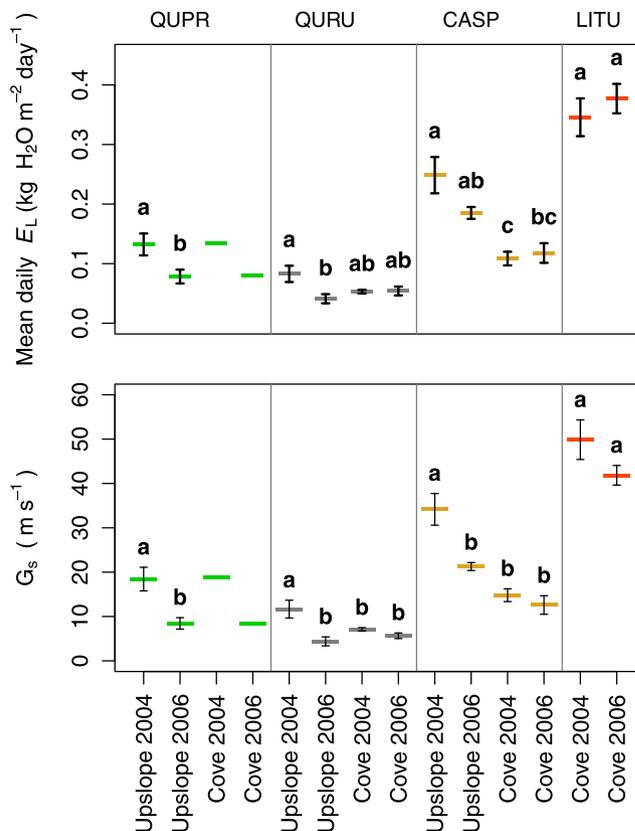


FIGURE 7 Mean daily E_L and G_s across species, years, and topographic positions. QUPR is *Quercus prinus*, QURU is *Quercus rubra*, CASP is *Carya* spp., and LITU is *Liriodendron tulipifera*. Different letters represent statistically significant difference ($p < .05$) between years and topographic positions within the same species. Bars represent standard error

not test for the effect of topography as this species did not occur in the upslope plot. E_L responses of *Quercus* spp. to climatic variation and position were reflected in E_t of the upslope plot, as they dominated the upslope plot. Meanwhile, E_L responses of *Carya* spp. and *L. tulipifera* that codominated the cove plot may explain the similarity between mean E_t of the cove plot between wet and dry years.

Responses of species G_s to climatic variation and topographical position were similar to E_L variation, with amplified effects of climatic variation and topographic position (Figure 7). G_s of *Q. rubra* was sensitive to climatic variation and its interaction with topography (site effect NS; year effect $F_{1, 3} = 27.7$, $p < .05$; site by year $F_{1, 3} = 15.7$, $p < .05$). The effects of climatic variation and topography were significant on G_s of *Carya* spp. (site effect $F_{1, 6} = 27.03$, $p < .01$; year effect $F_{1, 6} = 19.72$, $p < .01$; site by year $F_{1, 6} = 13.64$, $p < .01$).

In our study, E_L and G_s responses of individual species to drought varied based on their stomatal regulation strategy and xylem anatomy (Ford, Hubbard et al., 2011; Elliott et al., 2015; Roman et al., 2015). *L. tulipifera* is preferentially distributed in cove habitats and has high transpiration rates. It is also likely more sensitive to drought than *Quercus* spp. Among four common southern Appalachian tree species, Wurzbarger and Miniatt (2014) found that *L. tulipifera* had the greatest decline in growth and leaf physiology when exposed to moderate drought conditions. The lack of drought response in E_L of *L. tulipifera*

in the dry year (Figure 4) may be due to similar mean θ_d at the cove plot between wet and dry year (Figure 2), although the small decrease in mean G_s indicates its sensitivity to increased D . Consistent with our results is the finding that *L. tulipifera* had lower growth rate at upslope positions compared to downslope positions (Elliott et al., 2015).

The climate effect was significant for *Q. rubra* and *Carya* spp. in the upslope plot only (Figure 7). E_L of *Q. prinus* decreased at both topographic positions, although there was only one sample tree at the cove plot. *Quercus* spp. have a stomatal regulation strategy (anisohydry) that allows potentially higher carbon gain during drying air and soil conditions. However, it is at the risk of mortality if critical water potential thresholds are crossed. This strategy may explain the apparent contradictory patterns in the literature: *Quercus* spp. have greater mortality in upslope communities than in downslope communities during severe drought (Berdanier & Clark, 2015; Clinton et al., 1993) while showing higher growth rates in these upslope communities compared to isohydric species under conditions in which they can survive drought (Ford, Hubbard et al., 2011; Elliott et al., 2015; Roman et al., 2015).

3.5 | Implications of climate and topography interaction

Species composition and topography interacted with climate to differentially expose, or buffer from exposure, trees in up and downslope positions from drought. In dry years, wetter soils in the coves provided some buffer to drought effects to downslope communities, but drier soils exacerbated water stress in upslope communities. However, isohydric and anisohydric species that made up the downslope communities may not benefit equally from this. Wetter soils in cove plots may reduce the vulnerability of anisohydric species to hydraulic failure, when E_t exceeds critical xylem water potential and xylem cavitation occurs. Meanwhile, isohydric species would still be vulnerable if dry conditions are also characterized by low humidity, which would initiate stomatal closure to limit gas exchange and result in carbon starvation in the long term.

Drought-induced declines of isohydric species can potentially increase the fractional composition of anisohydric species in deciduous hardwood forests (McEwan et al., 2011; Roman et al., 2015). This could shift current trends of increasing mesophytic species in eastern North America toward those that may resemble forests of the mid 1900s, dominated by oak and hickory species (Caldwell et al., 2016; McEwan et al., 2011; Zolkos et al., 2015). A greater proportion of anisohydric species will likely reduce plot E_t and magnify the topography by species interaction, resulting in even wetter conditions in downslope positions in dry years. Yet manipulative studies along hillslopes to test this hypothesis are needed and may become increasingly relevant as pressure to manage forests for multiple ecosystem services in the face of climate change increases.

4 | CONCLUSION

We found that trees in cove positions are taller and have more sapwood area and leaf area supported per sapwood area than trees in upslope positions. Although both topographic positions were exposed

to the atmospheric dryness characteristic of low precipitation years, the upslope position had drier soils than downslope position. With ample precipitation, the upslope communities can transpire as much as the cove communities, despite lower soil water resources. With reduced precipitation, E_t was reduced in the upslope communities to a greater extent than in the downslope communities. We demonstrate that local conditions along a hillslope gradient can be decoupled from regional climate in southern Appalachian forests, potentially creating a refuge for some vegetation communities. Both isohydric and anisohydric species in cove positions may be buffered from very low soil moisture during drought; however, isohydric species may benefit less than anisohydric species if the drought is also characterized by low humidity.

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