esa ECOSPHERE

Forests, shrubs, and terrain: top-down and bottom-up controls on forest structure

Paul V. Bolstad,[1],† Katherine J. Elliott,[2] and Chelcy F. Miniat[2]

[1]Department of Forest Resources, University of Minnesota, 1530 Cleveland Avenue, St. Paul, Minnesota 55108 USA
[2]USDA Forest Service, Southern Research Station, Center for Forest Watershed Research, Coweeta Hydrologic Laboratory, 3160 Coweeta Lab Road, Otto, North Carolina 28763 USA

Citation: Bolstad, P. V., K. J. Elliott, and C. F. Miniat. 2018. Forests, shrubs, and terrain: top-down and bottom-up controls on forest structure. Ecosphere 9(4):e02185. 10.1002/ecs2.2185

Abstract. Overstory forest structure responds to terrain-related abiotic factors and to biotic interactions among overstory and understory plants. Unlike species abundance, tree height, biomass, and leaf area in many regions have been poorly quantified in relation to terrain-driven environmental gradients. In addition, the magnitude of understory influences on overstory structure has been poorly characterized for many forest systems. Our primary goal was to identify relationships between terrain (elevation, convexity, exposure), evergreen understory, and overstory structure (height, aboveground biomass, leaf area) in mature deciduous forests of the southern Appalachian Mountains. We used a combination of field point and plot measurements, LiDAR, and satellite image data to sample little-disturbed deciduous forest stands. Height, biomass, and gap frequency were significantly related to changes in elevation, exposure (aspect), and convexity (cove to ridge). Higher evergreen understory density was strongly correlated with decreases in forest height and biomass, with an impact observed across moisture, elevation, and exposure gradients. Canopies on ridges averaged half as tall at the highest evergreen understory densities when compared to those without evergreen shrubs (10 vs. 19 m), and overstory canopy height averaged 6 m shorter on sideslopes with high evergreen understory density compared to those with low evergreen understory density. Canopy height declined from low to high elevations, with larger relative decreases on ridges, but biomass increased from low to high elevations, due primarily to high biomass in coves at mid- to upper elevations. Biomass and canopy height declined from cove to ridge and north- to south-facing slopes. Responses in canopy height and aboveground biomass associated with changes in understory evergreen density were similar to impacts due to terrain. Gaps were more frequent on south-facing slopes. Previous studies at this site and others identify soil moisture and soil N competition as the most plausible mechanisms by which understory shrubs might influence overstory canopy structure, with low light limiting seedling recruitment as an additional mechanism. Our work suggests evergreen understory density, particularly on sideslope and ridge locations, substantially affects overstory canopy height and biomass.

Key words: evergreen understory; kalmia; LiDAR; rhododendron; southern Appalachian Mountains; terrain convexity.

Received 16 February 2018; accepted 27 February 2018. Corresponding Editor: Debra P. C. Peters.

† **E-mail:** pbolstad@umn.edu

INTRODUCTION

Forest structure is often the result of complex interactions between terrain-mediated differences in soils and microclimate, disturbance history, and the local suite of species. Forests in humid mountainous regions exhibit differences across space in soil moisture, air temperature, insolation, atmospheric humidity, and downslope water flow that affect plant species recruitment, productivity, and biomass accumulation (Foster 1988, Elliott et al. 1999, Tromp-van Meerveld and McDonnell 2006, Elliott and Swank 2008, Hwang et al. 2011). Terrain can also affect disturbance frequency and intensity, including drought mortality (Clinton et al. 1993), and wind damage (Elliott et al. 2002, Peterson 2007, Mitchell 2013), in turn affecting biotic structure and composition. The local suite of species is also determined in part by terrain (e.g., Barbour and Billings 2000, Barbour et al. 2007). Often affinities for a particular landscape location have been attributed to a spectrum of traits that suggest adaptation to moisture gradients from mesic coves to xeric ridges (Whittaker 1956, Bahari et al. 1985, Day and Monk 1988, Elliott et al. 1999, Denslow et al. 2010, Hawthorne and Miniat 2018) and, to a lesser extent, temperature gradients from low to high elevations (Morin et al. 2007, White and Millert 2008).

While general relationships between terrain and mature forest height, biomass, or other structural characteristics are widely acknowledged (e.g., McNab 1989, 1993, Burns and Honkala 1990), these relationships have been quantified in relatively few instances (Whittaker 1956, Bolstad et al. 1998*a*, Nagamatsu et al. 2003, Hansen et al. 2014). In general, stem diameter, tree basal area, and growth rates decrease from cove to ridge and from polar (north-facing in the Northern Hemisphere) to equatorial (south-facing) exposures, corresponding to changes in microclimate (Tajchman et al. 1988, 1997, Bolstad et al. 1998*b*). Authors have speculated that lower growth is due to drier soils from cove to ridges and higher vapor pressure deficits or drier soils from northeast to southwest exposures (Tajchman et al. 1988, Fekedulegn et al. 2003), and to shorter growing seasons and cooler temperatures at high elevations (Whittaker 1956, Meiners et al. 1984, Day and Monk 1988, Bolstad et al. 1998*b*, Fekedulegn et al. 2003). While general trends are assumed, height and biomass differences among landscape positions have rarely been quantified, in part due to difficulties in landscape-scale measurements of climate and forest structure across a broad range of conditions. Light detection and ranging (LiDAR)-based methods developed over the past decade may partially address the latter limitation (Dubayah and Drake 2000, Kane et al. 2010, Brubaker et al. 2014), by providing repeat, accurate, comprehensive canopy height and density measurements.

Forests of eastern North America have been influenced by changes in disturbance regimes, in turn affecting interactions among species that vary by key traits (Shugart 1984, Callaway and Walker 1997, Beckage et al. 2000, Nilsen et al. 2001, Wyckoff and Clark 2002, Abrams 2008). Variation in shade tolerance is central to common theories of canopy succession in eastern deciduous forests, with shade-tolerant species more successful in small-gap ascension (Shugart 1984, Bugmann 2001, Lienard et al. 2015). Without disturbance, shade-tolerant species may persist and reach sapling stages and reach the canopy via small canopy gaps. Fire exclusion and clearcutting have affected these interactions among tree species; fire exclusion facilitates expansion of shade-tolerant and fire-intolerant species (Abrams 1998, 2008, VanLear et al. 2002), and clearcutting facilitates shade intolerant, vigorous sprouters, and/or prolific seed producers that disperse widely and exhibit rapid early growth (Busing 1995, Elliott et al. 1997, Boring et al. 2014). Evergreen shrubs in the genera *Rhododendron* and *Kalmia* may dominate eastern North American forest understories and are often categorized as shade-tolerant and somewhat fire-intolerant, although there are surprisingly few field studies on fire response and regeneration dynamics of these taxa. They both appear to increase in density in canopy gaps created by disturbances (Plocher and Carvell 1987, Ford et al. 2012), although it is unclear whether due to seedling recruitment or resprouting/expansion of existing clones.

The impacts of *Rhododendron* and *Kalmia* on overstory structure have been poorly characterized in eastern deciduous forests (VanLear et al. 2002, Elliott and Swank 2008, Elliott and Vose 2012). In the southern Appalachians, *Rhododendron maximum* (L.) and *Kalmia latifolia* (L.) are widespread, form dense thickets, and appear to inhibit tree recruitment and early growth for a broad spectrum of tree species (Nilsen et al. 1999, Beckage et al. 2000, Beier et al. 2005). These evergreen shrubs may further compete for water or nutrients with established overstory trees, thereby reducing tree growth, or over longer time periods may alter canopy structure via reproductive suppression (Clinton and Vose 1996, Nilsen et al. 1999, 2001, Beier et al. 2005). Evergreen *Rhododendrons* are invasive elsewhere, causing significant declines in forest recruitment, density, and tree growth in western Europe and Asia (Dehnen-Schmutz et al. 2004, Maclean et al. 2017). The impacts of evergreen shrubs may be exacerbated due to historical changes in disturbance regimes in eastern North American forests, for example, widespread logging and fire exclusion (VanLear et al. 2002, Nowacki and Abrams 2008), although there appear to be no field studies that directly address *Rhododendron* fire tolerance. Increased evergreen understory may also have led to changes in leaf litter chemistry, decomposition rates, and other ecosystem properties (Monk et al. 1985, Wurzburger and Hendrick 2007, 2009). *Kalmia latifolia* impacts on tree regeneration are less well studied, but it is generally the most common evergreen understory species on xeric sites in the southern Appalachians, and it also appears to suppress overstory tree regeneration (Moser et al. 1996, Arthur et al. 1998, Waldrop and Brose 1999, Abella et al. 2003, Elliott et al. 2009, Hagan et al. 2015, Brose 2016).

While previous studies have identified general terrain responses in forest structure (Whittaker 1956, Day and Monk 1988, Bolstad et al. 2001), and mechanisms by which evergreen understory shrubs might affect tree recruitment or growth (Beckage et al. 2000, Nilsen et al. 2001, Wurzburger and Hendrick 2009), to our knowledge there are no studies on the relationships between terrain, overstory structure, and understory structure. Our primary goal was to quantify the relationships between forest structure (including evergreen shrubs) and terrain attributes that have been identified as proxies for changes in temperature, insolation, and available moisture in the southern Appalachian Mountains. Some southern Appalachian taxa are terrain generalists (e.g., *Acer rubrum* L., *Quercus montana* Wild.), others show strong preference for concave (cove) terrain positions (e.g., *Aesculus octandra* L. and *Liriodendron tulipifera* L.), or convex (ridge) positions (e.g., *Quercus coccinea* Muenchh, *Pinus rigida* L.). Still other species are restricted by elevation, for example, *Acer sacchaum* (Marsh.) at high elevation and *Quercus velutina* (Lam.) at low elevation. Using field plots, LiDAR, and optical remote-sensing data, we hypothesize that (1) overstory forest physical structure will change across terrain position, with shorter trees and less biomass on ridges, at higher elevations, and southern exposures, (2) evergreen understory shrub density, biomass, and leaf area will change across the landscape, with higher values on north-facing slopes, at higher elevations, and in coves, and (3) after controlling for terrain and elevation, evergreen understory density will be inversely correlated with overstory basal area, height, and biomass. We discuss our findings relative to previously documented, terrain-mediated climatic patterns in our study area, which are primarily local to regional gradients in insolation, temperature, precipitation, and to flow-mediated soil moisture.

Data and Methods

Study area

Analyses were based on measurements in subcatchments of the Coweeta Hydrologic Laboratory (CHL) in western North Carolina (Fig. 1), a third-order catchment in the southern Appalachian Mountains, that have been free from human disturbance for at least 80 yr, in a region of high temperate forest diversity, and that included tree species common across eastern U.S. deciduous forest types. Coweeta Hydrologic Laboratory is a 2184-ha research area located in the Nantahala Mountain Range within the Blue Ridge Physiographic Province, near the southern end of the Appalachian Mountain chain (latitude 35°03′ N, longitude 83°25′ W). Elevations range from 675 to 1592 m, and streams flow throughout the year, fed by approximately 1800 mm of annual precipitation. Mean annual temperature is 12.6°C. Most disturbance at CHL is prior to 1940 (Douglass and Hoover 1988). Between 1919 and 1923, selective but heavy cutting occurred on approximately one half of the forest. Chestnut blight (*Cryphonectria parasitica* (Murr.) Barr) was first noted in the early 1920s, and by 1940, the majority of previously dominant American chestnut (*Castanea dentata* (Marshall) Bork.) had died (Elliott and Swank 2008).

Data used

Primary data for this work included (1) a set of 282 rectangular (0.08 ha) permanent measurement plots (hereafter, field plots); (2) a 28 August

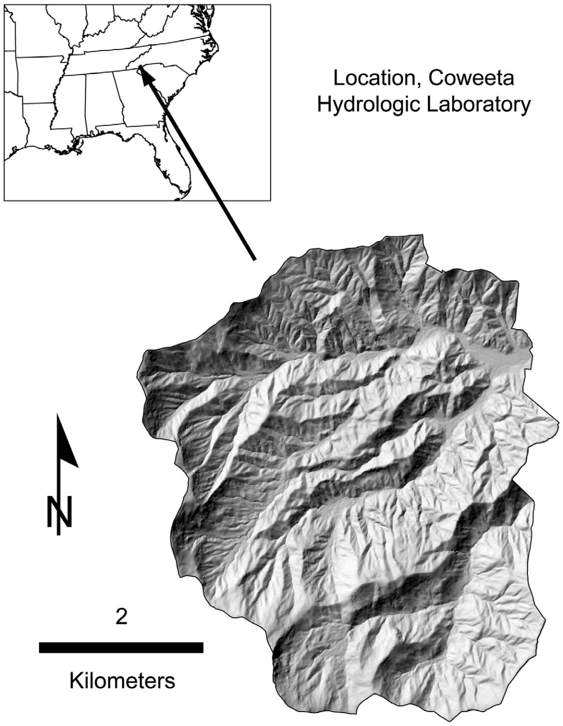

Fig. 1. Study area, the Coweeta Hydrologic Laboratory, in western North Carolina.

2009 leaf-on, LiDAR data collection; (3) a set of 165 randomly selected maximum tree height measurements across CHL (hereafter, field-height); (4) a 6.0-m resolution digital elevation model (DEM) derived from leaf-off LiDAR data collected in 2005 as part of statewide terrain mapping (NCFMP, www.ncfloodmaps.com); and (5) a fused 2.5-m resolution panchromatic, 5.0-m multispectral SPOT satellite image over CHL (SPOT). Unless specified otherwise, all data were collected within a five-year window, 2005–2010 inclusive, to minimize the impacts of disturbance events between various measurement dates.

Forest canopy heights from LiDAR data (hereafter, canopy heights) were estimated from 2009 leaf-on canopy returns less 2005 leaf-off terrain elevations. Herein, we use tree heights and canopy heights interchangeably and use maximum tree heights when referring to the maximum height of an individual tree. Canopy heights were based on first LiDAR returns, processed to sample the upper canopy and remove between and within-canopy gaps. Leaf-on data were collected with an Optech GEMINI ALTM instrument, with 1047-nanometer wavelength, a nominal beam divergence of 0.25 mrad, a 70 Hz maximum scan frequency, maximum scan angle of 21°, and average flying height of 600 m above terrain. First, second, third, and last returns were recorded, with a nominal elevation accuracy of 5–30 cm. Ground and canopy points were identified using the Terrasolid software, applying an iterative triangulation method (Chang et al. 2010). There was an average density of 8.46 returns/m^2.

Ground elevations and derived terrain surfaces were calculated from the 2005 leaf-off LiDAR data, processed to a 6.0-m cell resolution DEM. Details on data collection and processing are at www.ncfloodmaps.com. The 2005 leaf-off data were used for estimating ground elevations because surface-collected GPS (global positioning system, also referred to more generically as GNSS, or global navigation satellite system) showed the ground heights to have better than 12.0 cm relative vertical accuracy. Cell-centered statistics for a 1.8 m radius circle were calculated (radius chosen to achieve at least 20 canopy returns over most of the study area), including maximum, median, mean, and minimum heights, LiDAR return number, and proportion returned above a 0.5 m height (Næsset 2002). Total canopy closure was calculated as the number of first returns above 0.5 m height divided by the total number of first returns, overstory canopy closure as the number of first returns above a 5.0 m height divided by the total number of first returns, and mean overstory canopy height calculated as the average of all 1.8 m radius maximum first returns above a 5.0 m height. These LiDAR metrics were extracted for each of the 282 field-plot footprints and summed or averaged appropriately across each plot area.

Canopy gaps were identified from LiDAR heights. Canopy gap seed points were created from focal height differences (Bolstad 2012) and then expanded via a height-based region-growing algorithm (Secord and Zakhor 2007) to identify gaps. Gaps were defined as areas at least 15.0 m shorter than surrounding heights, larger than 50 m^2, and with a length/width ratio smaller than 8.0 to eliminate areas of crown shyness (Putz et al. 1984, Fish et al. 2006).

We validated the LiDAR-measured canopy heights by extracting maximum LiDAR heights for 165 individual trees and then comparing these against maximum tree heights measured with standard hypsometric methods (Avery and Burkhart 2015). Upper canopy trees were chosen at random within terrain position and species strata. Individual stem locations were measured with GNSS data with repeat-measure average error of <38 cm (Bolstad 2012).

We estimated aboveground biomass using species and diameter survey data from a network of 282 unmanaged reference plots measured in 2009–2010 (Vose and Elliott 2016). These long-term plots are 20 × 40 m rectangles arrayed on approximately N-S transects. Diameters of trees ≥2.5 cm diameter at breast height (dbh, 1.37 m) were measured to the nearest 0.1 cm, and component biomass and leaf area calculated using species-specific allometric relationships (Martin et al. 1998).

Terrain metrics were derived from the 2005 DEM data, including slope, aspect, and total, plan, and profile curvature calculated with a 150-m edge-dimension moving window (Bolstad 2012). An index of aspect-related southern exposure was calculated (Bolstad et al. 1998*a*), modified to integrate the April through October period to give an index with a maximum at an azimuth of 180° and a slope of 26.8°, minimum at an azimuth of 0° and slope of 26.8°, and linearly scaled to a range from 0 to 1000 for the upper and lower one percent tails observed for the study area.

Canopy spectral data were derived from SPOT-5 XS data collected 8 March 2007. Panchromatic 2.5-m resolution data were fused with 5-m green, red, and infrared bands using an intensity-hue-saturation algorithm to generate a pan-sharpened image at the 2.5-m resolution (Malpica 2007). The normalized difference vegetation index (NDVI) was calculated for the footprint of each field plot. High NDVI values were primarily due to reflectance from understory evergreen shrubs, *Rhododendron maximum* L. and *Kalmia latifolia* L., based on field-plot maps overlain with the SPOT image data. Overstory evergreen conifers of the genus *Pinus* and *Tsuga* comprise <2% of the basal area in the study area (Elliott et al. 1999), while understory evergreen shrubs are commonly found in patches spanning several hectares. An evergreen understory density index (hereafter, evergreen understory) was calculated by eliminating cells dominated by evergreen conifer trees from the NDVI raster.

A random sampling (approximately 44,000) of the 2009 LiDAR point heights was used to estimate basin-wide tree heights and canopy closure summary statistics. Samples were from areas with no direct human disturbance since the early 1930s. Areas with harvest, thinning, or within 15 m of roads were removed from sampling. Maximum LiDAR first returns in a 1.8 m radius circle were randomly sampled without replacement (from a population of 1.2 million) across the area from the 2009 leaf-on data, to better represent height (Brandtberg et al. 2003, Gaulton and Malthus 2010). Samples were limited to heights above 5.0 m, our defined boundary between shrub/sapling and overstory trees. Results were essentially unchanged with 3.0, 4.0, 6.0, or 7 m threshold heights, and while the evergreen understory shrubs occasionally reach heights of 10.0 m in our study area, they are infrequent above 5.0 m. Forest canopies in most cut or windthrow areas surpass a 5.0 m height in 6–8 yr.

Lastly, to evaluate relationships between canopy heights, evergreen understory, and environmental variables, we used a network of vapor pressure deficit (D) measurements, and soil moisture data collected from areas with and without evergreen shrubs at CHL. We evaluated the relationship between elevation and D from five climate stations located within CHL (Table 1) for the period 2012–2014. We calculated daily mean, maximum, and minimum D from hourly relative humidity and temperature measurements following Lowe (Lowe 1977); daily mean, maximum, and minimum D values were then averaged for the growing season (May 1–October 15). Soil moisture at 5.0–65 cm depth was collected near the lowest elevation climate station, at approximately 700 m elevation, within a mature, closed-canopy deciduous forest, both under 100% and 0% *Rhododendron* understory cover. Campbell Scientific CS615/CS616 water content reflectometers were sampled at half-hour intervals over an annual cycle.

Data analyses

All statistical tests reported here are based on permanent plot-level summaries (282 plots), field-measured maximum individual tree heights,

Table 1. Location, elevation, and aspect of the five climate stations within Coweeta Hydrologic Laboratory, western North Carolina.

	Climate station code numbers				
Variable	CS01	CS17	CS21	CS28	CS77
Latitude, longitude	35°03′37.48 83°25′48.36	35°02′43.33 83°26′14.63	35°03′59.63 83°26′09.12	35°02′47.60 83°27′54.05	35°01′49.27 83°27′37.60
Elevation (m)	685	887	817	1189	1398
Aspect	Valley floor	N-facing	S-facing	E-facing	NE-facing
Start date	8/1934	10/1969	7/1974	5/1985	4/1992

remote-sensing data extracted for plot or point footprints, or unbinned sample data (44,000 individual sample points), although sample points are binned in some figures for clarity. All statistical analyses were performed using R (R Development Core Team 2013), and significance in parameters was reported at $\alpha \leq 0.05$.

The relationship between LiDAR-estimated and field-measured individual tree heights was analyzed using linear regression (Myers et al. 2010). Field-based height measurements were intersected with LiDAR canopy height returns for 1.0-m^{-2} cells over the study area, and the containing tree crown identified visually. The maximum LiDAR return height was manually extracted from the containing crown and paired with each field-measured maximum tree height (n = 165).

We used multiple linear regression to relate plot data to 2009 canopy height, the 2005 terrain metrics (convexity, elevation, and exposure), and the SPOT image-derived evergreen understory density index. First, LiDAR-derived canopy heights were extracted for each of the 282 field-plot footprints and averaged for a mean plot canopy height. Plot height means were then related to terrain metrics and evergreen understory. We also fit linear regression models for the 44,000 point canopy heights against terrain metrics and evergreen understory. In addition, plot aboveground biomass was related to plot mean canopy heights, terrain metrics, and evergreen understory. We examined all possible two-variable interactions in the linear regression models and selected reduced models based on parameter significance (P < 0.10) in the full model, and on outlier, heteroscedascity, Akaike information criteria (AIC), and other influence tests (Zar 1999). We also evaluated separate models based on terrain convexity categories (i.e., landscape positions of cove, sideslope, and ridge). Difference in canopy gap frequency by elevation, landscape position, and aspect categories was tested using chi-square analysis (Corder and Foreman 2009). To estimate the impact of elevation, convexity, southern exposure, and evergreen understory density, we estimated Δ factors for each significant model by multiplying the estimated linear regression coefficient by the range or distal quantiles of the variable, for example, the height Δ for convexity for pooled plot data was obtained by multiplying the highest minus lowest convexity ($941.5 - 3.9 = 937.6$) by the convexity regression coefficient (-0.0035) for the multivariate model to yield a change in canopy height of -3.28 m. Implied changes by multiplying coefficients over quantile ranges (e.g., 5–95%, 10–90%) rather than extreme ranges are sometimes reported and showed equivalent rankings but reduced magnitude.

RESULTS

Canopy heights and aboveground biomass

Canopies were taller in coves compared to sideslopes and ridges (Fig. 2), heights decreased with increasing elevation, and were lower on south-facing (equatorial) vs. north-facing (polar) slopes, supporting our first hypothesis. Canopies were also shorter with higher evergreen understory densities (P < 0.10 in all and P < 0.01 in most cases, Table 2), supporting our third hypothesis. No two- or three-way interaction terms were significant among elevation, exposure, or evergreen understory. Heights on cove sites averaged about 25 m, almost 9 m taller than canopy heights on ridge sites, while sideslopes were intermediate, averaging 22 m. Within

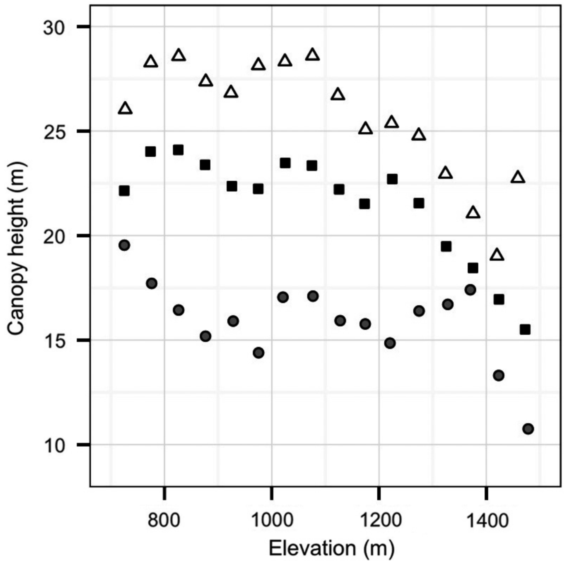

Fig. 2. LiDAR-estimated canopy height related to binned elevation point samples grouped by terrain convexity categories (landscape positions of cove [open triangles], sideslope [black squares], and ridge [gray circles]).

terrain position, canopy height changed nonlinearly with elevation, approximately constant over some interval of lower elevations, then declining more rapidly past threshold elevations of ~1100 m for coves, 1200 m for sideslopes, and 1400 m for ridges (Fig. 2). Canopy height changes for the lowest vs. highest elevation quartile were similar for all terrain positions, with an approximately 4.7 m decrease from 700 to 1450 m elevations. Declines were largest in relative terms on ridges (near 28% decrease in canopy height from low to high elevation sites), than sideslopes (19%), or coves (17%). Heights were on average shorter by 3.7 m (plot) to 5.2 m (points) at extreme southern vs. northern exposures, and 8.9–10.8 m shorter at extreme ridge vs. cove locations.

Separate models for each landscape category (cove, sideslope, or ridge positions) showed that for coves and sideslopes, canopy height was significantly related to elevation, exposure, and evergreen understory for both the field plots and sampled points (Table 3). On ridge sites, evergreen understory density index was a significant height determinant for both points and plots, while elevation and exposure were significant predictors of height for point but not plot locations (Table 3). Elevation and exposure show approximately equal effects on canopy height over our sampling, with a somewhat larger decline associated with evergreen understory density (Table 3).

Overstory canopy height declined up to 12.7 m across the range of evergreen understory amounts, with declines greatest at ridge locations and least in coves (Table 3). Heights declined as much from sparse to dense evergreen understory as they did across of the ranges of elevation, convexity, or exposure observed at our sites. Within each landscape position (cove, sideslope, ridge), canopy heights decreased significantly at higher evergreen understory densities (Table 3); binned sample point averages reveal that height declined more at ridges (9.2 and 13.6 m for extreme points and plots, respectively) and sideslopes (8.9 and 12.5 m) than coves (6.2 and 7.4 m). Binned plots show an approximately linear decline in height

Table 2. Multiple regression coefficients and *P*-values of canopy height and biomass using independent variables of elevation, exposure, convexity, and evergreen understory density index.

Category	Elevation (*P*)	Δ (m or kg/ha)	Exposure (*P*)	Δ (m or kg/ha)	Convexity (*P*)	Δ (m or kg/ha)	EUD (*P*)	Δ (m or kg/ha)	Model adjusted R^2†
Heights (m)									
Plots	−0.0039**	−2.96	−0.0035**	−3.28	−0.0095**	−8.94	−27.81**	−8.7	0.50
Points	−0.0066**	−6.18	−0.0032**	−5.20	−0.0109**	−10.8	−22.82**	−12.7	0.34
Biomass (kg/ha)									
Plots	93.3**	70,815	−63.7**	−67,929	−74.0**	−69,456	−236,032**	−74,160	0.36

Notes: Models are based on field-plot average LiDAR heights and the randomly sampled leaf-on LiDAR heights. Significance is based on a two-sided *t*-test on reduced sum-of-squares comparison for each factor when removed from the full linear model. The magnitude of the change, Δ, implied by the estimated coefficient is computed over the range observed for each independent variable. EUD is evergreen understory density. Parametric significance in this table is indicated as ** for $P < 0.01$.

† Full model.

Table 3. Multiple regression coefficients and P-values, by convexity categories (landscape positions of ridge, sideslope, and cove), for canopy height using independent variables of elevation, exposure, and evergreen understory density index.

Landscape position	N	Predictor variable coefficients ($P > \|t\|$)						Model adjusted R^2†
		Elevation	ΔH (m)	Exposure	ΔH (m)	EUDI	ΔH (m)	
Ridge								
Plots	21	−0.001 ns	−0.68	−0.003 ns	−1.8	−33.12**	−9.2	0.36
Points	3193	−0.0053**	−2.77	−0.0016**	−2.33	−27.5**	−13.6	0.20
Sideslope								
Plots	213	−0.007**	−4.2	−0.0045**	−4.6	−28.8**	−8.9	0.20
Points	33,863	−0.0080**		−0.0033**		−25.3**	−12.5	0.16
Cove								
Plots	48	−0.0056*	−3.6	−0.0041*	−4.1	−22.9**	−6.2	0.21
Points	7172	−0.0071**	−5.7	−0.0024**	−3.3	−16.9**	−7.4	0.10

Notes: Model estimates are based on field-plot average LiDAR heights and the randomly sampled, leaf-on LiDAR heights. Significance is based on a two-sided t-test on reduced sum-of-squares comparison for each factor. The magnitude of the change, ΔH, is calculated from the estimated slope coefficient from the fit model multiplied by the range observed for the corresponding independent variable. EUDI is evergreen understory density index. Parametric significance in this table is indicated as * for $P < 0.05$, ** for $P < 0.01$.

† Full model.

with increasing evergreen understory on ridge and sideslope locations (Fig. 3), with scant decline across evergreen understory densities at cove locations. There was no significant interaction between evergreen understory and elevation, neither for field plots nor for LiDAR point sample data ($P > 0.10$). Canopies were consistently shorter in the presence of higher evergreen understory both for north-facing and south-facing sideslopes (Table 4), with an average canopy height reduction of 6.4 m (south-facing) and 6.0 m (north-facing).

Aboveground biomass variation generally parallels that of canopy height. Biomass averaged 252,800 kg/ha, ranged from 73,600 to 606,100 kg/ha, and reached highest values in field plots with taller canopies, at mid- to upper elevations, and lower convexities (coves relative to ridges; Tables 2 and 3, Fig. 4a–c). The trend of increasing biomass with elevation was strongly influenced by cove and lower sideslope plots found between 1000 and 1300 m elevation, characteristically near the base of upper escarpments. Within landscape positions, biomass was significantly affected by elevation, exposure, and evergreen understory, but the magnitude and nature of relationships varied among terrain positions (Table 5). On sideslopes, exposure and evergreen understory had significant negative effects and elevation had a significant positive effect on biomass. However, only evergreen understory density was significantly related to a decline in biomass on ridges, while elevation and exposure had no significant effect; and none of these factors had a significant effect on biomass for coves (Table 5).

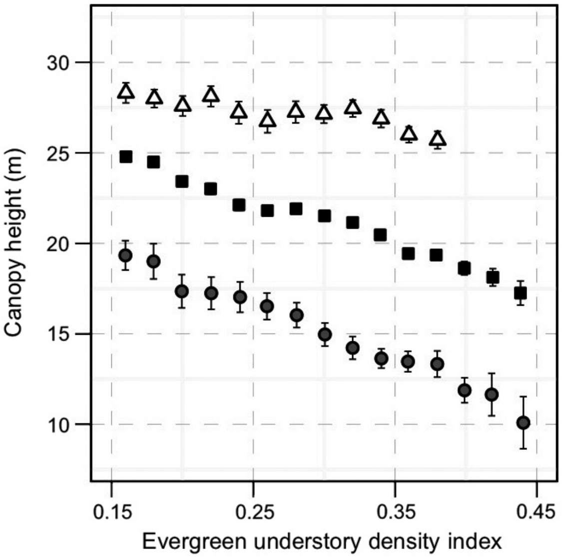

Fig. 3. Average canopy height related to evergreen understory density index for binned sets of the 44,000 leaf-on LiDAR samples (bars ± 1 SE of mean) grouped by terrain convexity categories (landscape positions of cove [open triangles], sideslope [black squares], and ridge [gray circles]).

Table 4. Average overstory canopy heights (trees >5 m) from LiDAR on sideslopes, categorized by exposure (north-facing, azimuth orientation <90° or >270°; south-facing, azimuth orientation >90° and <270°) and evergreen understory density index based on normalized difference vegetation index calculated from 2.5-m resolution satellite images.

	Mean plot canopy height, SE (m)	
Category	South-facing	North-facing
Low evergreen understory density	24.2 a (0.16)	26.4 b (0.19)
High evergreen understory density	17.8 c (0.12)	20.4 d (0.13)

Notes: Mean values for the 25th quartiles (low evergreen understory density) and 75th quartiles (high evergreen understory density). Standard errors are in parentheses, and different letters following means indicate differences significant in a two-sided *t*-test.

Evergreen understory

Evergreen understory density, basal area, and leaf area showed strong correlations with canopy height and biomass, both overall and within terrain categories (Tables 2, 3, and 6), and complex relationships with terrain attributes. Evergreen understory basal area on the field plots averaged 1.32 m^2/ha and was inversely related to overstory tree height and overstory biomass in almost all models ($P < 0.01$, *F*-test in multivariate regression model). We observed higher shrub density and mass on ridge sites than coves (Fig. 5), and in areas corresponding to shorter, lower biomass overstories, supporting our second hypothesis. Understory density, basal area, and mass significantly increased as elevation increased, with highest values typically observed on plots at mid- to upper elevation ridges. Evergreen understory increased from cove to ridge, with basal area averaging 1.8 m^2/ha on ridge sites, defined as the top quartile of landform convexity; this evergreen basal area was more than twice that for cove sites comprising the bottom convexity quartile.

Evergreen understory density was also higher on south-facing sideslopes than north-facing sideslopes and coves ($P < 0.01$, *F*-test in multivariate regression model), but there was no exposure effect in models fit for ridge plots ($P > 0.1$, *F*-test). Shrub basal area for plots in the most south-facing quartile averaged 1.7 m^2/ha, while the north-facing quartile averaged 1.1 m^2/ha basal area.

Overstory canopy closure and leaf area index

Overstory canopy closure (and percent cover) was high, with 90% of the field plots having >80% of the returns from above 5.0 m. Canopy closures in a 5.0-m circle spanned the range from 18.0% to 99.2%. Mean canopy closures differed by landscape position, averaging 89.2%, 90.2%, and 71.8% on coves, sideslopes, and ridges, respectively, but these differences were not significant when pooled across landscape positions. Overstory canopy closure was related to evergreen understory measured by the point samples. There was a significant decrease in overstory canopy closure with increasing evergreen understory for ridges (Fig. 6, $P < 0.01$), but not for coves or sideslopes ($P > 0.10$). Canopy closure had a significant nonlinear component ($P < 0.01$ for quadratic term in a linear regression model), and variability increased with high evergreen densities. Overstory canopy closure was not related to elevation, exposure, or convexity for the pooled plot data nor for plots analyzed by landscape position.

Total leaf area index (LAI) increased with canopy height, higher elevations, lower convexity (in coves), and at higher evergreen understory densities (all $P < 0.05$). Except for canopy height, differences in leaf area were small over the range of conditions for each variable. For example, LAI averaged 5.06 m^2/m^2 on ridge plots and 5.31 m^2/m^2 on cove plots. Total LAI was not significantly related to exposure, suggesting that LAI was not lower on plots with southern exposure relative to northern exposure across all elevations, terrain convexities, and evergreen understory densities.

Within terrain class, LAI at ridge and sideslope positions were significantly related to canopy height, elevation, exposure, and understory evergreen density in various combinations ($P < 0.01$ for most), but no significant relationships were found in coves between LAI and terrain variables or evergreen density. LAI on ridges was most strongly related to canopy height, averaging 3.40 m^2/m^2 for average canopy heights <7.5 m (25th quartile height) and 6.57 m^2/m^2 for canopy

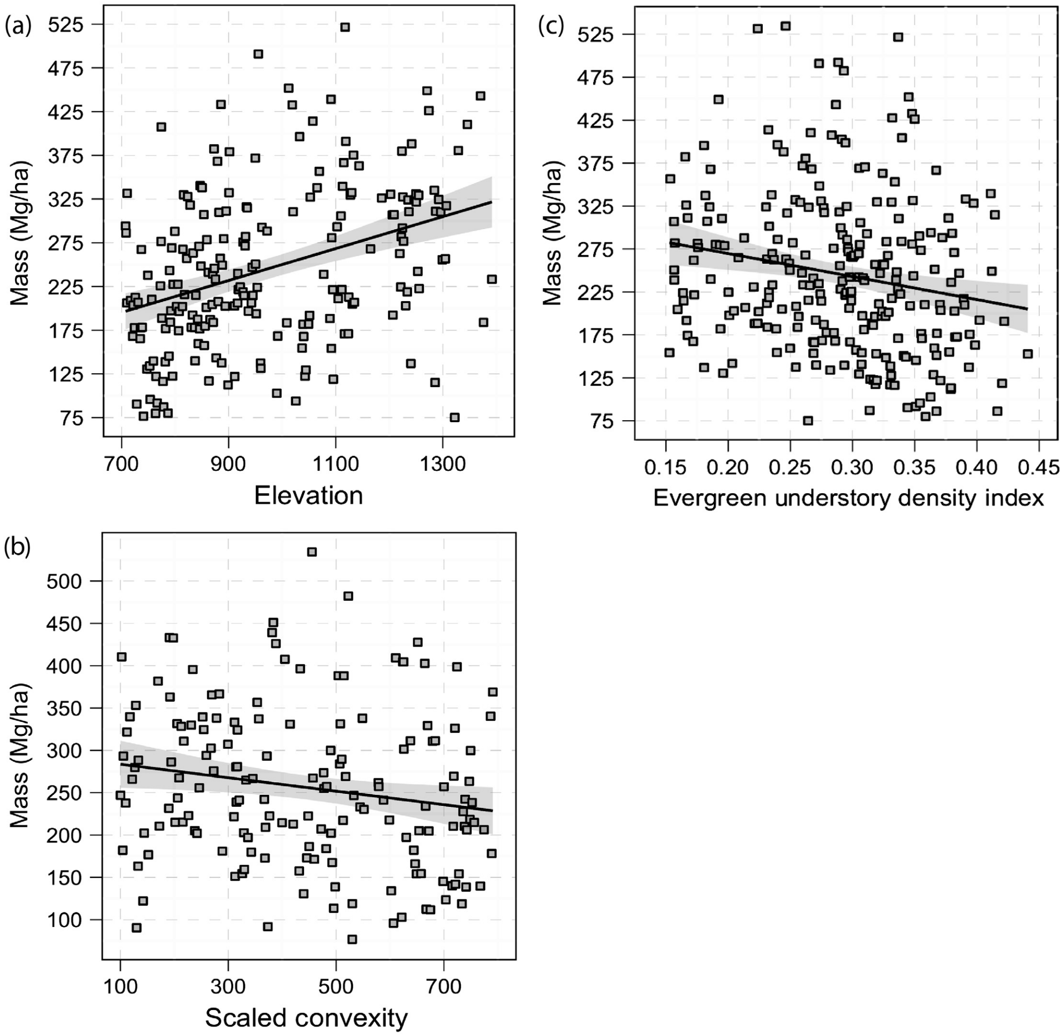

Fig. 4. Total aboveground biomass (Mg/ha) related to (a) elevation, (b) evergreen understory density index, and (c) scaled convexity (coves have low values, and ridges have high values). Stepwise multiple regression showed that biomass was significantly related to all three variables (Table 4; model adjusted $R^2 = 0.46$, $P < 0.05$).

heights taller than 12.2 m (75th quartile height). LAI on ridges also increased significantly with elevation, but only slightly, with an average plot LAI of 5.07 m^2/m^2 for ridges below 855 m (25th quartile) and of 5.39 m^2/m^2 for ridges above 1150 m (75th quartile).

Evergreen understory LAI increased with canopy height and scaled convexity (model adjusted $R^2 = 0.26$, $P < 0.05$), and increased with elevation, and from cove to ridge locations (Fig. 7). Evergreen understory LAI was an increasing proportion of total LAI across scaled convexity, ranging from an average of 2.9% in the deepest coves to 7.9% of total LAI on the sharpest ridges (Fig. 7a, b).

Gap density and size

Gaps were more frequent on south- than north-facing slopes (Table 7, $\chi^2 = 270.2$, $P < 0.01$), but were less frequent at higher elevations, in coves, or with higher evergreen understory densities (Table 7). Gap density increased from 1.61 gaps/ha to 2.17 ha^{-1} from north- to south-facing exposures. However, gap size was not

Table 5. Multiple regression coefficients and P-values, overstory biomass by terrain convexity categories (landscape positions of ridge, sideslope, and cove), for field-measured plots.

		Predictor variable coefficients ($P > \lvert t \rvert$)						
Landscape position	N	Elevation coefficient	ΔM (Mg/ha)	Exposure coefficient	ΔM (Mg/ha)	EUDI	ΔM (Mg/ha)	Adjusted R^2†
Ridge								
Plots	21	ns	–	ns	–	−102,800**	−28.7	0.50
Sideslope								
Plots	213	121.6*	72.4	−100.4*	−102.5	−312,453**	−98.1	0.19
Cove								
Plots	48	ns	–	ns	–	ns	–	0.09

Notes: Overstory biomass was the dependent variable with independent variables of elevation, exposure, and evergreen understory density index. Significance is based on a two-sided t-test on reduced sum-of-squares comparison for each factor. The magnitude of the change, ΔM, implied by the estimated regression coefficient, is computed over the range observed for each independent variable. EUDI is evergreen understory density index. Parametric significance in this table is indicated as * for $P < 0.05$, ** for $P < 0.01$.

† Full model.

Table 6. Multiple regression coefficients and P-values of evergreen understory basal area using independent variables of average canopy height, elevation, exposure, and convexity.

	Predictor variable coefficients ($P > \lvert t \rvert$)							
Category	Elevation (P)	Δ	Exposure (P)	Δ	Convexity (P)	Δ	Canopy height (P)	Δ
Shrub basal area (m^2/ha)	0.00593*	0.45 (m^2/ha)	0.00085**	0.91 (m^2/ha)	0.00046*	0.43 (m^2/ha)	−0.0503**	−1.34 (m^2/ha)
Shrub density (ha^{-1})	0.551**	405 (ha^{-1})	0.383**	405 (ha^{-1})	0.247**	231 (ha^{-1})	−17.1*	−235 (ha^{-1})
Shrub biomass (kg/ha)	ns	–	2.619**	2756 (kg/ha)	1.631**	1529 (kg/ha)	−105.1**	2837 (kg/ha)

Notes: Models are based on field-plot average measurements. Significance is based on a two-sided t-test on reduced sum-of-squares comparison for each factor when removed from the full linear model. The magnitude of the change, Δ, implied by the estimated coefficient is computed over the range observed for each independent variable. Results are generally similar when evergreen understory density index or leaf area are analyzed. Parametric significance in this table is indicated as * for $P < 0.05$, ** for $P < 0.01$.

significantly related to elevation, convexity, exposure, or evergreen understory indices or amounts.

Discussion

Our analysis revealed that trees were shorter and plots had less biomass on ridges (more convex terrain positions), on south-facing slopes, and in areas with a denser evergreen understory. Heights declined with elevation, but biomass increased to mid-elevations, most markedly in coves. Overstory LAI was lowest on ridges with high evergreen understory density. Gaps were more frequent on south-facing slopes. The strongest responses in canopy height and aboveground biomass were associated with changes in evergreen understory density, particularly at ridge and sideslope locations, with slightly smaller but still significant responses observed along terrain convexity, exposure, and elevation gradients.

These terrain-related patterns of heights and density likely reflect biological and climatic controls on forest structure and biomass accumulation, rather than direct human disturbance history. Our sites have been unmanaged for the past 80 yr, with no large-scale, stand-replacing disturbance events since the loss of American chestnut in the 1930s (Elliott and Swank 2008). Hemlock woolly adelgid has killed almost all canopy hemlock trees starting in 2002, but these initially comprised approximately 1% of the canopy trees across our site, sporadically abundant along riparian corridors (Elliott et al. 1999, Narayanaraj et al. 2010). Previous work indicates

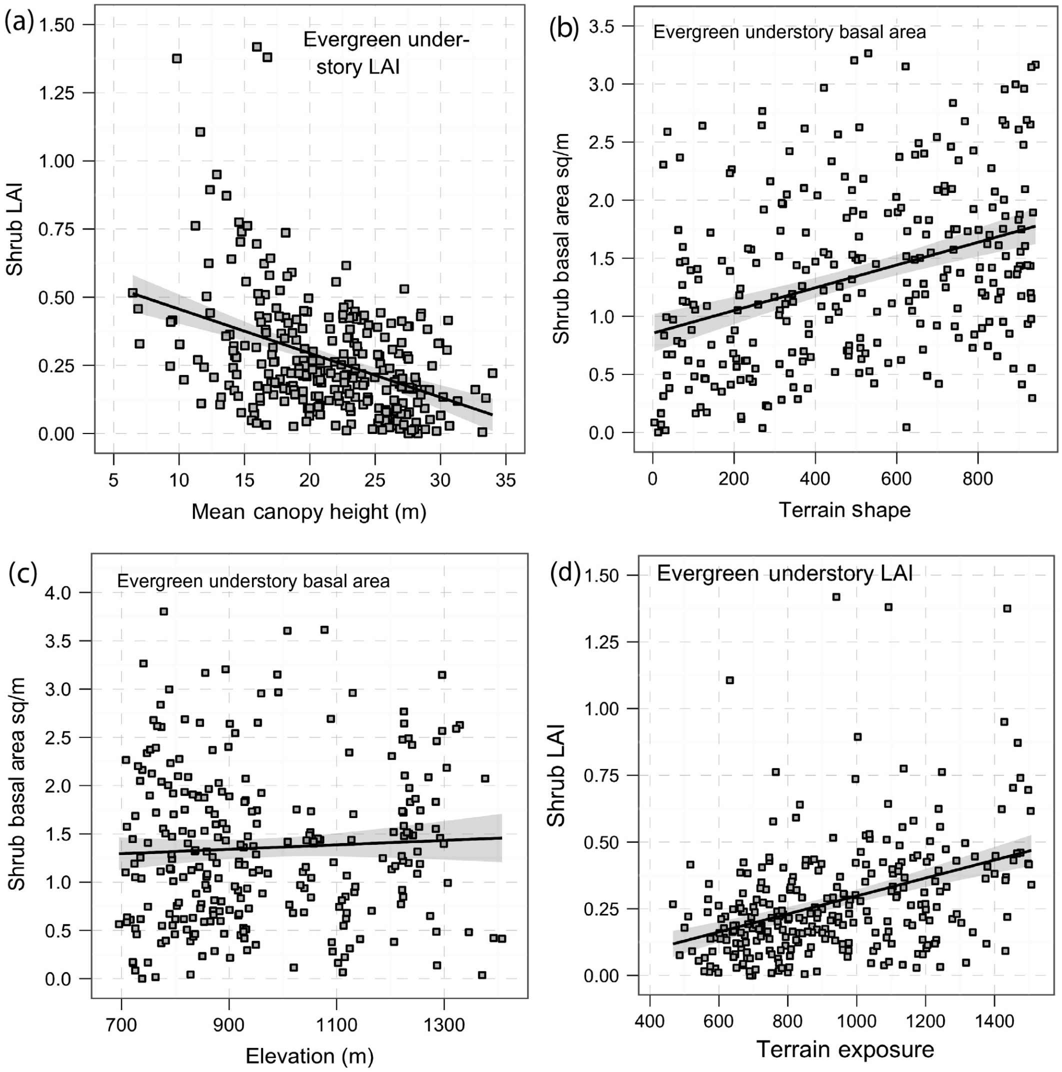

Fig. 5. Evergreen understory basal area vs. (a) height, (b) terrain shape (convexity), (c) elevation, and (d) exposure. Each point represents average values measured for a 0.08-ha sample plot.

the overstory canopy predates sub-canopy evergreen shrubs at our site (Elliott and Vose 2011, Brose 2016). Canopy closure typically occurs within 10 yr after disturbance, and competition-induced mortality occurs over the next 40 yr (Elliott et al. 1997, Boring et al. 2014). Height growth decelerates after ca. 60 yr, depending on site quality and species (Burns and Honkala 1990). Thus, sufficient time has passed so that height, LAI, and gap frequency would depend more on bioclimatic, site fertility, local biotic interaction, and localized natural disturbances rather than variation in logging intensity or *Castanea* density from more than 80 yr ago.

In contrast to height, LAI, and gap frequency, biomass perhaps shows some impact from past logging, as harvests were likely more frequent and complete at lower elevation coves and adjacent sideslopes, with idiosyncratic patterns at mid- to upper elevations and away from road networks (De Viso 1986, Lewis 1989). Biomass can show longer legacy effects from past disturbances (Lorimer 1980, Elliott et al. 1999, Brose and Waldrop 2010), so patterns across terrain may be confounded by human intervention history. Harvesting in the region was less frequent and less intensive on ridge locations (Elliott and Swank 2008), so biomass patterns there may better reflect natural biological or climatic driven processes, but we do not have specific information for our study site prior to 1930.

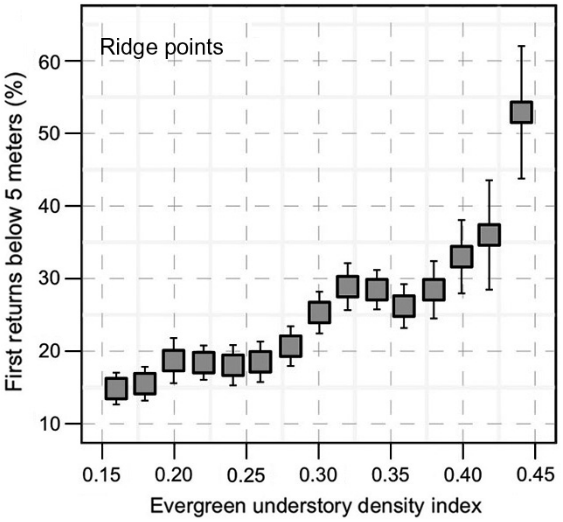

Fig. 6. Percent of first canopy returns from under 5 m related to evergreen understory density index using ridge points only, showing decreasing overstory canopy density on ridges with increasing shrub presence.

Terrain effects on forest characteristics

Canopy height and aboveground biomass were strongly correlated, and both were strongly related to terrain convexity, elevation, and exposure. Canopy heights decreased from coves to ridges and lower to higher elevations, while biomass was substantially lower on ridges vs. coves and sideslopes, and biomass increased with

Table 7. Gap area, size, and density by aspect.

Variable	North (± 45° from North)	East or West (>45° from N and S)	South (± 45° from S)
Area in study bounds (ha)	276.5	431.5	317.8
Gap area (% of total area)	1.91	2.47	2.97
Average gap size (m^2)	117.7	130.6	136.0
Gap density (gaps/ha)	1.61	1.89	2.17

Note: Gaps were significantly more frequent on south- vs. north-facing slopes ($\chi^2 = 270.2$, $P < 0.01$), but differences in area and size were non-significant ($P > 0.10$).

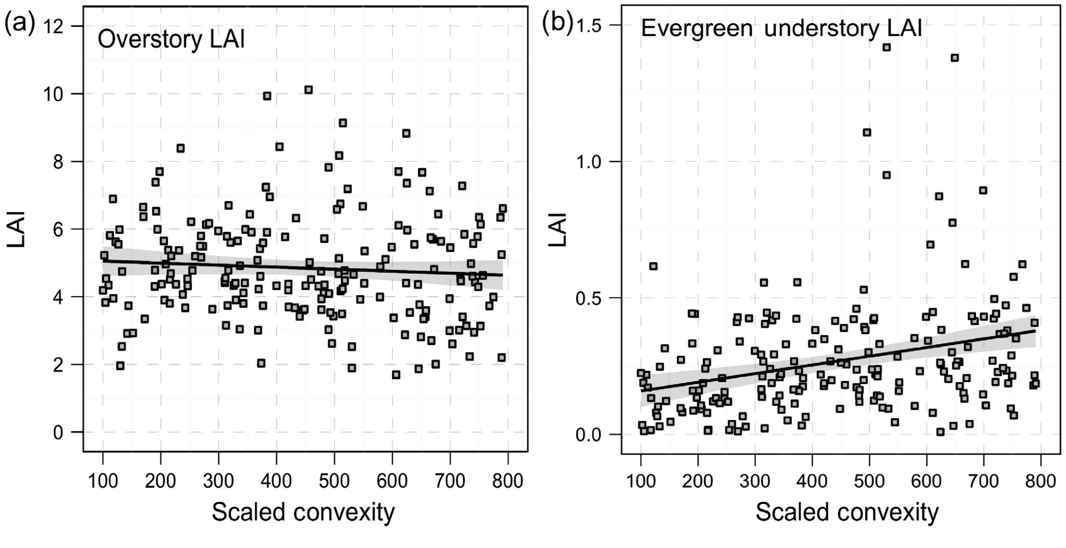

Fig. 7. Leaf area index (LAI) of (a) overstory plus evergreen understory and (b) evergreen understory only, *Rhododendron maximum* and *Kalmia latifolia*, related to scaled convexity, showing decreasing overstory leaf area and increasing understory leaf area when moving from coves to ridges.

elevation, largely due to high biomass in upper elevation coves. Canopies were shorter on south- compared to north-facing slopes, and height reduction due to exposure was less than that observed from coves to adjacent ridges.

Controls on maximum canopy height and height growth rates are complex and can range from resources, such as soil moisture, soil nutrients, and light quality, to genetic and evolutionary factors among or within species, such as hydraulic limitations (Ryan and Yoder 1997, Becker et al. 2000, Schafer et al. 2000, Koch and Fredeen 2005, Ryan et al. 2006). Temperature and growing season length decrease as elevation increases (Swift et al. 1988, Hwang et al. 2011) and could cause shorter canopies under equal stand ages. Canopy height may be limited hydraulically by resistances associated with the xylem conduits, gravity, and high vapor pressure deficits (*D*; Koch and Fredeen 2005). Hydraulic limitation and lower soil moisture are perhaps the most plausible explanations for cove to ridge decreases in canopy height, and decreased heights at southern vs. northern exposures, observed across all elevations. Higher summer temperatures, more frequent high *D*, and increased water stress have been observed at sideslope vs. cove locations in our study basin (Hawthorne and Miniat 2018). Lower soil moisture and radial growth have been observed on ridge and south-facing sites in the southern Appalachians, consistent with a water limitation hypothesis (Werling and Tajchman 1984, Tajchman et al. 1997).

Past observations suggest that *D* alone is not the primary variable causing differences in canopy height across the broad elevation gradient in our study area, as height under this hypothesis should decrease with increasing *D* in all conditions. Inter- and intraspecific differences modulate climate-driven adjustments in leaf area, with altered leaf area at drier sites during dry periods and years (Grier and Running 1977, Schafer et al. 2000, Oren and Pataki 2001, Reich and Bolstad 2001, Leuzinger et al. 2005, Carnicer et al. 2011). Reduced carbon assimilation can occur on dry days, and leaf fall and early senescence may accompany dry periods, thereby reducing growth. While vegetation structure conformed to this prediction from north- to south-facing slopes, it did not with elevation; heights at our site decrease with decreasing *D* along elevation gradients (Bolstad et al. 1998*b*, Hwang et al. 2014; Fig. 8). We do not see an increase in canopy height with elevation at any terrain position as would be expected under a singular *D* limitation hypothesis. If *D* alone was the dominant hydraulic limit on height growth across all elevations, we would not expect the relatively large difference in canopy height that we observed across short-distance terrain convexity gradients that have similar above canopy *D*, nor would we expect height declining as *D* declines with increasing elevation. Reduced heights with elevation may be a temperature response, as growing season length and average temperature decrease upslope, and a combined soil moisture/*D* response when moving from cove to ridges.

Soil moisture availability is lower on ridges compared to coves and may interact with *D* or be a dominant control for the almost 70% taller mature forests on cove sites than nearby ridge sites (Helvey et al. 1972, McNab 1993, Yeakley et al. 1998). This moisture difference is more pronounced at low compared to high elevations, suggesting that soil moisture availability relative to demand may be more important than absolute soil moisture availability. Although precipitation inputs are approximately equal across landscape positions at the same elevation (Swift et al. 1988), cove and more north-facing sideslopes have

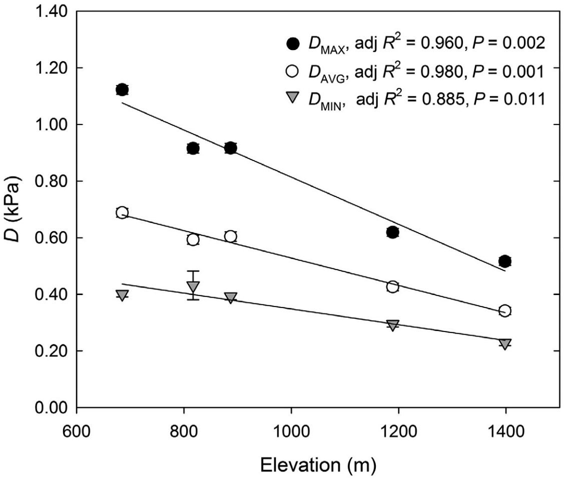

Fig. 8. Average, maximum, and minimum vapor pressure deficit (*D*) related to elevation for five climate stations within the Coweeta Basin, see Table 1.

more stable soil moisture profiles, deeper soils (Hicks and Chabot 1985), receive downslope subsidies through subsurface water flow, and have lower soil evaporation rates (Desta et al. 2004). As the growing season progresses, recharge, transpiration, and growth may be limited in ridge locations due to accumulating soil moisture deficits (Ford et al. 2011, Thomsen et al. 2013, Hawthorne and Miniat 2018). Soil moisture limitations, even in this relatively mesic region, agree with a broader set of studies relating height growth to soil moisture (Carmean 1972, Chen et al. 2002), and soil moisture stress is a significant cause of mortality at our site in drought years (Clinton et al. 1993, Kloeppel et al. 2003). Differences in evaporative demand between coves and ridges decrease with elevation, as the range of mean *D* declines (Fig. 8) and soil moisture deficits decrease (Helvey et al. 1972). Height differences among landscape positions decline from low to high elevations at our study site, from an approximate 10 m height span at an 800 m elevation to an approximately 4 m span at 1350 m elevation. While atmospheric moisture stress undoubtedly occurs at higher elevations, daily and seasonal accumulated water demand is lower. Our observed cove-to-ridge decrease in height and biomass is consistent with a number of studies that show a strong influence of topographic convergence and associated soil properties on landscape soil moisture availability (Kirkby 1988, Rodriguez-Iturbe et al. 1995, Western et al. 1999, Fernandez-Illescas et al. 2001), and potential growth responses to terrain shape (McNab 1989, 1993, Kabrick et al. 2014).

Canopy height differences across landscape position may in part be due to soil nutrient pools and processes (Albaugh et al. 1998, Boggs et al. 2005). Nitrogen mineralization rates have been observed to vary along topographical gradients in the southern Appalachians, with greater rates in coves relative to ridges, and at higher elevations in some studies (Garten and van Miegroet 1994, Knoepp and Swank 1998). In low-elevation watersheds, N mineralization rates have been reported almost three times greater in coves compared to sideslopes (Knoepp et al. 2008). Foliar litter quality (and species composition) is responsible for elevated N mineralization rates in coves compared to sideslopes, more so than moisture and temperature regimes of different landscape positions (Knoepp and Vose 2007).

At our site, others have found that nitrogen availability also varies with elevation (Knoepp et al. 2008). Greater nitrogen deposition at high elevation is driven by ~30% greater precipitation, resulting in N deposition increasing from 9.5 to 12.4 $\mathrm{kg \cdot ha^{-1} \cdot yr^{-1}}$ from low to high elevations across our study gradient (Knoepp et al. 2008). In addition, higher litterfall N, greater rates of soil N transformations, higher soil solution N, and greater stream N exports were found at high elevation than low elevation at our study site (Knoepp et al. 2008).

Wind is unlikely to be the primary cause of reduced heights from cove to ridge positions. While wind can alter height directly through sculpting and indirectly through windthrow (Mitchell 2013), neither of these are likely strong contributors to cove-to-ridge decreases in height in our study. Peak winds show weak directionality at the site, and while likely higher on ridges, we have no measures, and damage and windthrow appear at least as common in cove and sideslope positions. Average and peak wind speed increase with elevation, and so may be responsible for some of the decrease with heights. We do not have a sufficiently dense microclimatic network to test these effects.

We cannot de-convolve the changes in species from cove to ridge, maximum height limits, and our observations. Coves species such as *Liriodendron tulipifera* have taller maximum observed heights than common ridge species, for example, *Oxydendrum arboreum* or *Quercus coccinea*. While the two most common species at our site, *Acer rubrum* and *Quercus montana*, are common across nearly the complete range of elevations and terrain positions, most of the overstory species segregate by terrain position and elevation (Bolstad et al. 1998*a*, Elliott et al. 1999), according to traits identified with competitive advantages at those sites.

Evergreen understory and overstory forest characteristics

Evergreen understory density, chiefly *Rhododendron* and *Kalmia* species, shows as large a correlation with changes in canopy height and biomass as terrain variables. Forests with dense evergreen understory had lower LAI, were on average 6.2–13.6 m shorter, and had 74.1 Mg/ha less biomass. These relationships were strongest for ridge locations, but were also significant for sideslopes, with only slight and mostly non-significant effects of evergreen understory on canopy heights and biomass on coves. Canopies on ridges were only half as tall when high evergreen understory was present when compared to those without evergreen shrubs (10 vs. 19 m), and overstory canopy height was 6 m shorter with high evergreen understory compared to low evergreen understory on sideslopes (Table 3). This reduction was approximately three times greater than the height difference of south- vs. north-facing slopes (2 m; Table 4), suggesting that the average impact of evergreen understory is at least as large as differences in exposure.

We note that contrary to one of our hypotheses, evergreen understory density was higher on south-facing slopes. This may be due to the mix of evergreen species, with the more drought tolerant *Kalmia* able to exploit more xeric, south-facing sites at lower elevations, and both *Rhododendron* and *Kalmia* at upper elevations. These ericaceous shrubs may be responding to higher light environments. South-facing slopes in our study basin receive more insolation, warm up more quickly in the spring, and may support earlier growing season initiation and a longer period prior to overstory leaf out.

Our work, taken with previous findings, strongly suggests evergreen ericaceous shrubs may substantially affect forest structure across landscapes. Much work in forest ecology has focused on competitive interactions between overstory species, chiefly for light, but also as affected by water and nutrients (Shugart 1984, Bugmann 2001, Purves and Pacala 2008, Lienard et al. 2015). Our analysis suggests that understory shrubs may be effectively competing with overstory species and altering overstory structure, specifically height growth. Previous work has shown potential mechanisms via light, soil, and nutrient impacts detrimental to tree seedlings under *Rhododendron* and *Kalmia* (Monk et al. 1985, Nilsen et al. 1999, 2001, Beier et al. 2005), and preferential N access via chemical complexing in decomposition (Wurzburger and Hendrick 2007, 2009), but to date no studies have quantified potential resource limitations on overstory height or biomass due to these evergreen species. We show consistent reductions in overstory height or biomass that persist across terrain positions, when *Rhododendron* and *Kalmia* species are present. *Rhododendron* species have been noted as an important invasive exotic that affect overstory composition in the British Isles and mainland Europe (Dehnen-Schmutz et al. 2004, Eşen et al. 2004, Erfmeier and Bruelheide 2010), although impacts on forest height and biomass are not reported. Rhododendron has been reported to initiate best in clear-felled forest (Plocher and Carvell 1987), and *Kalmia* is actively controlled elsewhere in North America to improve forest growth (Swift et al. 1993, Mallik 2003, Thiffault and Jobidon 2006).

One might argue that evergreen understory has simply responded to less dense overstory, spreading in response to overstory drought mortality, ice damage, or other canopy-altering events. Previous studies suggest otherwise, as the evergreen species do not appear to have expanded their extent at our site in the past 80 yr (Elliott and Vose 2012). *Rhododendron* has increased in density in riparian areas after hemlock mortality (Ford et al. 2012). Conditions that lead to significant areal expansion of *Rhododendron* and *Kalmia* are poorly characterized in the southern Appalachians, but the species appear slow to spread there, with a predominantly clonal, long-life span, low seed recruitment strategy under overstory canopies; ramet origins in one study were tied to clear-felling disturbances and not expansion under intact canopies (Plocher and Carvell 1987).

One might posit overstory height and biomass patters are a response to some complex environmental factors (Parker et al. 1989, Vose et al. 1995), with opportunistic spread or development of evergreen understory to areas where canopies are sparse for some other reason. Environmental factors such as soil moisture, nutrients, or atmospheric D may limit overstory canopy density, allow more light penetration, and hence support greater understory canopy development. This is unlikely, given that evergreen understory species are slow to spread in our site (Elliott and Vose 2012), post-date existing canopy trees, that dense evergreen understory and bare patches were found across all combinations of elevation, convexities, and exposure, on similar soils, and that canopy height and biomass depression was observed across most of these combinations. It would require that some unknown factor causes a limitation that preferentially affects the overstory and not the understory species, for example, greater nutrient use efficiency in evergreen vs. deciduous habits (Osnas et al. 2013), higher *D* only in the upper canopy, and lower water stress in the understory (Gallego et al. 1994, Rambo and North 2008). However, we conclude this is unlikely because the reductions in overstory LAI, biomass, and canopy density were found across moisture, temperature, and nutrient gradients. We observed an evergreen effect on northern and southern exposures (temperature and moisture), sideslopes at high vs. low elevations, and ridges vs. sideslopes vs. coves all at the same elevation (temperature, moisture, and nutrients), suggesting that evergreen understory is affecting overstory structure. Our evidence is observational, and definitive proof can best be provided by long-term, controlled, manipulative studies; however, our observations, combined with previous studies, strongly suggest understory impacts on overstory forest structure.

There are several mechanisms by which evergreen understory shrubs might influence overstory height, biomass, and density. Previous work has documented tree reproduction inhibition (Clinton et al. 1994, Clinton and Vose 1996, Beckage et al. 2000, Beier et al. 2005), lower surface light levels (Clinton et al. 1994), and moisture and nutrient limitation (Nilsen et al. 2001, Wurzburger and Hendrick 2007, 2009) under *Rhododendron*. Thus, trees may face a recruitment bottleneck such that the shorter heights and lower biomass may be a result of canopy mortality without replacement, or delayed recruitment and altered tree demographies relative to shrub-free sites. While plausible, this would require that the understory pre-date the overstory, or that there has been significant gap formation and mortality at the sites since stand initiation. Age measurements of *Rhododendron* and nearest neighbor trees at Coweeta revealed the mature forest trees were established prior to or at the same time as *Rhododendron* (Elliott and Vose 2012), and that existing *Rhododendron* ramets are unlikely to have inhibited initial overstory recruitment since the last landscape-scale disturbance. They found that evergreen *Rhododendron* aged 6–120 yr, while co-occurring overstory dominant trees averaged 113 yr old, with many trees >150 yr old. Most trees are older than the evergreen shrubs and pre-date chestnut decline, existing as saplings that opportunistically benefited from the chestnut blight. Mortality episodes have been noted since the 1930s, due both to drought and invasive exotics (Clinton et al. 1993, Narayanaraj et al. 2010), although these have been limited in scale and distribution. Stands are of an age to be entering a forest gap formation and replacement phase, so recruitment limitations post-initiation may due to evergreen shrubs may be the cause of some changes in overstory structure, but is likely not an overriding one.

Understories may alter overstories through altered soil nutrient pools. Soils under *Rhododendron* exhibit lower pH and cation concentrations (Boettcher and Kalisz 1990), and lower available N, with an altered soil N cycle relative to forests without *Rhododendron* (Wurzburger and Hendrick 2007). *Rhododendron* litter is associated with polyphenol-organic N complexes that were available to *Rhododendron* but not to deciduous broadleaved seedlings (Wurzburger and Hendrick 2009). Leaf N is tightly related to maximum photosynthesis and net leaf productivity over a range of species (Reich et al. 1998), and there is a strong relationship between total canopy LAI and canopy nitrogen content (Yin et al. 2003). Preferential soil N availability for the understory may sequester N resources, thereby reducing overstory growth and LAI, increasing access to light, and supporting higher understory LAI, as observed at the ridge sites (Figs. 6, 7). This explanation is consistent with our observation of approximately equal height growth reductions on north- and south-facing sideslopes, despite differences in temperature, soil moisture, and other environmental conditions. This N uptake hypothesis may explain the muted effects of evergreen understory density in cove locations, where there were generally slight responses in height growth, biomass, leaf area, and canopy closure, and where *Rhododendron* often reaches high densities. Higher soil N in coves may offset immobilization by *Rhododendron*, leaving sufficient supply for full canopy growth in coves. If true, we would expect overstory leaf N concentrations and/or total canopy N to be lower in the presence of a *Rhododendron* or *Kalmia* understory, and the difference to increase from cove to ridge.

We know of no published work on comparisons across understory densities and terrain gradients to test this proposed mechanism.

Increased water use and drier soils may be another mechanism by which evergreen understory species reduce overstory tree height, biomass, and canopy properties (Tyree 2003, Pallardy 2008). Although scant work exists, Grano (1970) reported sustained overstory response in mature *Pinus taeda*/*P. echinata* stands after understory removal on dry sites in Arkansas, with significant increases in biomass accumulation for more than a decade. Conversely, no response was observed on a broader set of studies on wetter sites in the northeastern United States (Kelty et al. 1987). Evergreen shrubs begin transpiration earlier in the season, and while transpiration rates per leaf-unit are lower than co-occurring trees due to more humid and shaded understory microclimate (Brantley et al. 2013), net water use could be a significant portion of total stand water use due to high understory leaf area and an extended transpiration season on drier sites. Other work has shown evergreen understory species segregate along topographical gradients (Lipscomb and Nilsen 1990), with drought-tolerance matched to available soil moisture. Long-term soil moisture measurements in a cove location at our site with and without an understory canopy show consistently lower soil moisture under *Rhododendron* shrub canopies, ranging 2.3–4.5% depending on sample year and season (Fig. 9). This difference is likely magnified at ridge locations in drier soils and could explain the strongest impacts of understory evergreens on ridge locations, most notably at lower elevations, but would not explain the reduced height growth due to evergreen understory on both wet and dry sites. Nitrogen and water limitation may interact, with N sequestration under evergreen shrubs leading to lower fine root growth and water harvesting potential by overstory trees, feeding back to sparser canopies and lower overstory production.

Integrated work would best identify if these overstory/understory associations are causal, and if so, the mechanisms by which understory evergreen shrubs alter overstory canopy structure. Our work shows that evergreen understory is related to widespread, consistent changes in overstory structure and, when combined with previous work, suggests mechanisms. Unambiguously quantifying the causes of the correlation will require further work. N competition and N sequestration hypotheses could be tested via sampling overstory leaf N concentration and total mass for stands with and without dense understory evergreen shrubs, by long-term N additions and measurement of growth response, by understory evergreen removal, or by N tracer studies. This sampling could be combined with soil moisture, evaporation, and transpiration measurements to estimate moisture consumption by components and identify the frequency and extent of moisture limitations on growth. Complimentary measurements across landscape positions may identify the breadth of identified mechanisms.

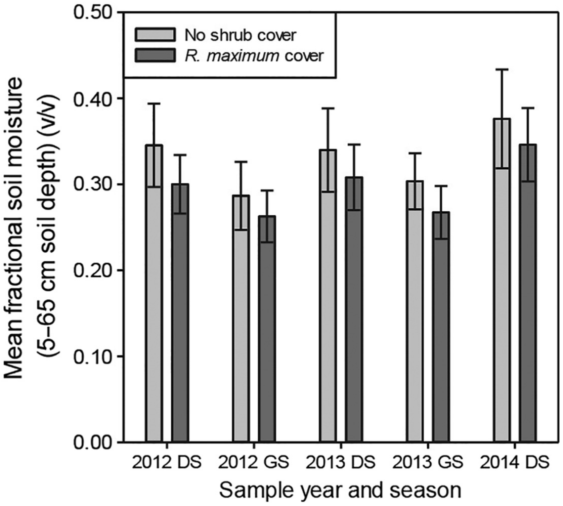

Fig. 9. Soil moisture data averaged across four depths (5, 20, 35, and 65 cm) per location with (n = 4) and without (n = 4) rhododendron evergreen shrub cover from TDR sensors (CS615, Campbell Scientific, Logan, Utah, USA). Measurements were made continuously during dormant (DS) and growing (GS) seasons for three years. Only data are shown when all sensors were logging across all depths and locations for comparison (C. F. Miniat and P. V. Bolstad, *unpublished data*). While differences are consistent and in the expected direction, they are not statistically significant.

CONCLUSIONS

Our analysis demonstrates strong relationship between canopy height and biomass and terrain shape, elevation, and exposure. We also found strong relationships between overstory structure and evergreen understory density, with reduced tree height, biomass, leaf area, and canopy closure in stands with high evergreen understory. This suggests understory structure and composition, and particularly evergreen understory density, have a significant effect on overstory forest structure, and that the influences vary by terrain conditions.

ACKNOWLEDGMENTS

This research was funded by USDA Forest Service, Southern Research Station, Coweeta Hydrologic Laboratory, the Coweeta LTER Project funded by National Science Foundation grants DEB-9632854, DEB-0218001, and DEB-1440485 and the McIntire-Stennis Program, the Minnesota Agriculture Experiment Station, and the University of Minnesota. We thank Patsy Clinton for her work in coordinating the survey of the permanent field plots. We thank two anonymous reviewers for help in improving the manuscript. The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

LITERATURE CITED

Abella, S. R., V. B. Shelburne, and N. W. MacDonald. 2003. Multifactor classification of forest landscape ecosystems of Jocassee Gorges, southern Appalachian Mountains, South Carolina. Canadian Journal of Forest Research 33:1933–1946.

Abrams, M. D. 1998. The red maple paradox. BioScience 48:355–364.

Abrams, M. D. 2008. The demise of fire and “Mesophication” of forests in the eastern United States. BioScience 58:123–138.

Albaugh, T. J., H. L. Allen, P. M. Dougherty, L. W. Kress, and J. S. King. 1998. Leaf area and above- and belowground growth response of loblolly pine to nutrient and water addition. Forest Science 44:317–328.

Arthur, M. A., R. D. Paratley, and B. A. Blankenship. 1998. Single and repeat fires affect survivorship and regeneration of woody and herbaceous species in an oak-pine forest. Journal of the Torrey Botanical Society 125:225–236.

Avery, T. E., and H. E. Burkhart. 2015. Forest measurements. Fifth edition. McGraw Hill, Boston, Massachusetts, USA.

Bahari, Z. A., S. G. Pallardy, and W. C. Parker. 1985. Photosynthesis, water relations, and drought adaptation in six woody species of oak-hickory forests in central Missouri. Forest Science 31:557–569.

Barbour, M. G., and W. D. Billings. 2000. North American terrestrial vegetation. Second edition. Cambridge University Press, Cambridge, UK.

Barbour, M., T. Keeler-Wolf, and A. A. Schoenherr. 2007. Terrestrial vegetation of California. Third edition. University of California Press, Berkeley, California, USA.

Beckage, B., J. S. Clark, B. D. Clinton, and B. L. Haines. 2000. A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understories. Canadian Journal of Forest Research 30:1617–1631.

Becker, P., F. C. Meinzer, and S. D. Wullschleger. 2000. Hydraulic limitation of tree height: a critique. Functional Ecology 14:4–11.

Beier, C. M., J. L. Horton, J. F. Walker, B. D. Clinton, and E. T. Nilsen. 2005. Carbon limitation leads to suppression of first year oak seedlings beneath evergreen understory shrubs in southern Appalachian hardwood forests. Plant Ecology 176:131–142.

Boettcher, S. E., and P. J. Kalisz. 1990. Single-tree influence on soil properties in the mountains of eastern Kentucky. Ecology 71:1365–1372.

Boggs, J. L., S. G. McNulty, M. J. Gavazzi, and J. M. Myers. 2005. Tree growth, foliar chemistry, and nitrogen cycling across a nitrogen deposition gradient in southern Appalachian deciduous forests. Canadian Journal of Forest Research 35:1901–1913.

Bolstad, P. V. 2012. GIS fundamentals: a first text on Geographic Information Systems. Fourth edition. Eider Press, White Bear Lake, Minnesota, USA.

Bolstad, P. V., W. Swank, and J. Vose. 1998*a*. Predicting southern Appalachian overstory vegetation with digital terrain data. Landscape Ecology 13:271–283.

Bolstad, P. V., L. Swift, F. Collins, and J. Régnière. 1998*b*. Measured and predicted air temperatures at basin to regional scales in the southern Appalachian Mountains. Agricultural and Forest Meteorology 91:161–176.

Bolstad, P. V., J. M. Vose, and S. G. McNulty. 2001. Forest productivity, leaf area, and terrain in southern Appalachian deciduous forests. Forest Science 47:419–427.

Boring, L. R., K. J. Elliott, and W. T. Swank. 2014. Successional forest dynamics: 30 years following clearcutting. Pages 11–35 *in* W. T. Swank and J. R. Webster, editors. Long-term response of a forest watershed ecosystem: clearcutting in the southern Appalachians (The Long-term Ecological Research Network Series). Oxford University Press, Oxfordshire, UK.

Brandtberg, T., T. A. Warner, R. E. Landenberger, and J. B. McGraw. 2003. Detection and analysis of individual leaf-off tree crowns in small footprint, high sampling density lidar data from the eastern deciduous forest in North America. Remote Sensing of Environment 85:290–303.

Brantley, S., C. R. Ford, and J. M. Vose. 2013. Future species composition will affect forest water use after loss of eastern hemlock from southern Appalachian forests. Ecological Applications 23:777–790.

Brose, P. H. 2016. Origin, development, and impact of mountain laurel thickets on the mixed-oak forests of the central Appalachian Mountains, USA. Forest Ecology and Management 374:33–41.

Brose, P. H., and T. A. Waldrop. 2010. A dendrochronological analysis of a disturbance–succession model for oak–pine forests of the Appalachian Mountains, USA. Canadian Journal of Forest Research 40:1373–1385.

Brubaker, K. M., S. E. Johnson, J. Brinks, and L. P. Leites. 2014. Estimating canopy height of deciduous forests at a regional scale with leaf-off, low point density LiDAR. Canadian Journal of Remote Sensing 40:123–134.

Bugmann, H. 2001. A review of forest gap models. Climatic Change 51:259–305.

Burns, R. M., and B. H. Honkala. 1990. Silvics of North America: 2. Hardwoods. Agriculture Handbook 654. USDA Forest Service, Washington, D.C., USA.

Busing, R. T. 1995. Disturbance and the population dynamics of *Liriodendron tulipifera* – Simulations with a spatial model of forest succession. Journal of Ecology 83:45–53.

Callaway, R. M., and L. R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78:1958–1965.

Carmean, W. H. 1972. Site index curves for upland oaks in the Central States. Forest Science 18:109–120.

Carnicer, J., M. Coll, M. Ninyerola, X. Pons, G. Sanchez, and J. Penuelas. 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. Proceedings of the National Academy of Sciences 108:1474–1478.

Chang, L. D., K. C. Slatton, and C. Krekeler. 2010. Bare-earth extraction from airborne LiDAR data based on segmentation modeling and iterative surface corrections. Journal of Applied Remote Sensing 4:41884. https://doi.org/10.1117/1.3491194

Chen, H. Y. H., P. V. Krestov, K. Klinka, and L.-D. Chang. 2002. Trembling aspen site index in relation to environmental measures of site quality at two spatial scales. Journal of Applied Remote Sensing 32:112–119.

Clinton, B. D., L. R. Boring, and W. T. Swank. 1993. Canopy gap characteristics and drought influences in oak forests of the Coweeta Basin. Ecology 74:1551–1558.

Clinton, B. D., L. R. Boring, and W. T. Swank. 1994. Regeneration patterns in canopy gaps of mixed-oak forests of the southern Appalachians: influences of topographic position and evergreen understory. American Midland Naturalist 132:308–319.

Clinton, B. D., and J. M. Vose. 1996. Effects of *Rhododendron maximum* L. on *Acer rubrum* L. seedling establishment. Castanea 61:38–45.

Corder, G. W., and D. I. Foreman. 2009. Nonparametric statistics for non-statisticians: a step-by-step approach. John Wiley & Sons Inc, Hoboken, New Jersey, USA.

Day, F. P., and C. D. Monk. 1988. Forest communities and patterns. Pages 141–150 *in* W. T. Swank and D. A. Crossley Jr., editors. Forest hydrology and ecology at Coweeta. Springer-Verlag, New York, New York, USA.

De Viso, M. S. 1986. The deforestation of western North Carolina: 1900 to 1920. Pioneer America Society Transactions 9:89–94.

Dehnen-Schmutz, K., C. M. Perrings, and M. Williamson. 2004. Controlling *Rhododendron ponticum* in the British Isles: an economic analysis. Journal of Environmental Management 70:323–332.

Denslow, M. W., M. W. Palmer, and Z. E. Murrell. 2010. Patterns of native and exotic vascular plant richness along an elevational gradient from sea level to the summit of the Appalachian Mountains, USA. Journal of the Torrey Botanical Society 137:67–80.

Desta, F., J. J. Colbert, J. S. Rentch, and K. W. Gottschalk. 2004. Aspect induced differences in vegetation, soil, and microclimatic characteristics of an Appalachian watershed. Castanea 69:92–108.

Douglass, J. E., and M. D. Hoover. 1988. History of Coweeta. Pages 17–31 *in* W. T. Swank and D. A. Crossley Jr., editors. Forest hydrology and ecology at Coweeta. Springer-Verlag, New York, New York, USA.

Dubayah, R. O., and J. B. Drake. 2000. Lidar remote sensing for forestry. Journal of Forestry 98:44–46.

Elliott, K. J., L. R. Boring, W. T. Swank, and B. R. Haines. 1997. Successional changes in diversity and composition in a clearcut watershed in Coweeta Basin, North Carolina. Forest Ecology and Management 92:67–85.

Elliott, K. J., S. L. Hitchcock, and L. Krueger. 2002. Vegetation response to large scale disturbance in a southern Appalachian forest: Hurricane Opal and salvage logging. Journal of the Torrey Botanical Society 129:48–59.

Elliott, K. J., and W. T. Swank. 2008. Long-term changes in forest composition and diversity following early logging (1919–1923) and the decline of American chestnut (*Castanea dentata*). Plant Ecology 197:155–172.

Elliott, K. J., and J. M. Vose. 2011. The contribution of the Coweeta Hydrologic Laboratory to developing an understanding of long-term (1934–2008) changes in managed and unmanaged forests. Forest Ecology and Management 261:900–910.

Elliott, K. J., and J. M. Vose. 2012. Age and distribution of an evergreen clonal shrub in the Coweeta Basin: *Rhododendron maximum* L. Journal of the Torrey Botanical Society 139:149–166.

Elliott, K. J., J. M. Vose, and R. L. Hendrick. 2009. Long-term effects of high intensity prescribed fire on vegetation dynamics in the Wine Spring Creek watershed, western North Carolina, USA. Fire Ecology 5:66–85.

Elliott, K. J., J. M. Vose, W. T. Swank, and P. V. Bolstad. 1999. Long-term patterns in vegetation-site relationships in a southern Appalachian Forest. Journal of the Torrey Botanical Society 126:320–334.

Erfmeier, A., and H. Bruelheide. 2010. Invasibility or invasiveness? Effects of habitat, genotype, and their interaction on invasive *Rhododendron ponticum* populations. Biological Invasions 12:657–676.

Eşen, D., S. M. Zedaker, J. L. Kirwan, and P. Mou. 2004. Soil and site factors influencing purple-flowered rhododendron (*Rhododendron ponticum* L.) and eastern beech forests (*Fagus orientalis* Lipsky) in Turkey. Forest Ecology and Management 203:229–240.

Fekedulegn, D., R. R. Hicks, and J. J. Colbert. 2003. Influence of topographic aspect, precipitation and drought on radial growth of four major tree species in an Appalachian watershed. Forest Ecology and Management 177:409–425.

Fernandez-Illescas, C. P., A. Porporato, F. Laio, and I. Rodriguez-Iturbe. 2001. The ecohydrological role of soil texture in a water-limited ecosystem. Water Resources Research 37:2863–2872.

Fish, H., V. J. Lieffers, U. Silins, and R. J. Hall. 2006. Crown shyness in lodgepole pine stands of varying stand height, density, and site index in the upper foothills of Alberta. Canadian Journal of Forest Research 36:2104–2111.

Ford, C. R., K. J. Elliott, B. D. Clinton, B. D. Kloeppel, and J. M. Vose. 2012. Forest dynamics following eastern hemlock mortality in the southern Appalachians. Oikos 4:523–536.

Ford, C. R., S. H. Laseter, W. T. Swank, and J. M. Vose. 2011. Can forest management be used to sustain water-based ecosystem services in the face of climate change? Ecological Applications 21:2049–2067.

Foster, D. R. 1988. Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah Forest, south-western New Hampshire, U.S.A. Journal of Ecology 76:105–134.

Gallego, H. A., M. Rico, G. Moreno, and I. Santa Regina. 1994. Leaf water potential and stomatal conductance in *Quercus pyrenaica* Wild. forests: vertical gradients and response to environmental factors. Tree Physiology 14:1039–1047.

Garten, C. T., and H. van Miegroet. 1994. Relationships between soil nitrogen dynamics and natural ^{15}N abundance in plant foliage from Great Smoky Mountains National Park. Canadian Journal of Forest Research 24:1636–1645.

Gaulton, R., and T. J. Malthus. 2010. LiDAR mapping of canopy gaps in continuous cover forests: a comparison of canopy height model and point cloud based techniques. International Journal of Remote Sensing 31:1193–1211.

Grano, C. X. 1970. Small hardwoods reduce growth of pine overstory. SO RP-55. USDA Forest Service, Southern Research Station, New Orleans, Louisiana, USA.

Grier, C. G., and S. W. Running. 1977. Leaf area of mature northwestern coniferous forests: relation to site water balance. Ecology 58:893–899.

Hagan, D. L., T. A. Waldrop, M. Reilly, and T. M. Shearman. 2015. Impacts of repeated wildfire on long-unburned plant communities of the southern Appalachian Mountains. International Journal of Wildland Fire 24:911–920.

Hansen, A. J., L. B. Phillips, R. Dubayah, S. Goetz, and M. Hofton. 2014. Regional-scale application of lidar: variation in forest canopy structure across the southeastern US. Forest Ecology and Management 329:214–226.

Hawthorne, S., and C. F. Miniat. 2018. Topography may mitigate drought effects on vegetation along a hillslope gradient. Ecohydrology 11: https://doi.org/10.1002/eco.1825

Helvey, J. D., J. D. Hewlett, and J. E. Douglass. 1972. Predicting soil moisture in the southern Appalachians. Soil Science Society of America Journal 36:954–959.

Hicks, D. J., and B. F. Chabot. 1985. Deciduous forest. Pages 257–277 *in* B. F. Chabot and H. A. Mooney, editors. Physiological ecology of North American plant communities. Springer, Dordrecht, The Netherlands.

Hwang, T., L. E. Band, C. F. Miniat, C. Song, P. V. Bolstad, J. M. Vose, and J. P. Love. 2014. Divergent phenological response to hydroclimate variability in forested mountain watersheds. Global Change Biology 20:2580–2595.

Hwang, T., C. Song, P. V. Bolstad, and L. E. Band. 2011. Downscaling real-time vegetation dynamics by fusing multi-temporal MODIS and Landsat NDVI in topographically complex terrain. Remote Sensing of Environment 115:2499–2512.

Kabrick, J. M., J. L. Villwock, D. C. Dey, T. L. Keyser, and D. R. Larsen. 2014. Modeling and mapping oak advance reproduction density using soil and site variables. Forest Science 60:1107–1117.

Kane, V. R., R. J. McGaughey, J. D. Bakker, R. F. Gersonde, J. A. Lutz, and J. F. Franklin. 2010. Comparisons between field-and LiDAR-based measures of stand structural complexity. Canadian Journal of Forest Research 40:761–773.

Kelty, M. J., E. M. Gould, and M. J. Twery. 1987. Effects of understory removal in hardwood stands. Northern Journal of Applied Forestry 4:162–164.

Kirkby, M. 1988. Hillslope runoff processes and models. Journal of Hydrology 100:315–339.

Kloeppel, B. D., B. D. Clinton, J. M. Vose, and A. R. Cooper. 2003. Drought impacts on tree growth and mortality of southern Appalachian forests. Pages 43–55 *in* D. Greenland, D. Goodin, and R. Smith, editors. Climate variability and ecosystem response at Long-Term Ecological Research sites. Oxford University Press, Oxfordshire, UK.

Knoepp, J. D., and W. T. Swank. 1998. Rates of nitrogen mineralization across an elevation and vegetation gradient in the southern Appalachians. Plant and Soil 204:235–241.

Knoepp, J. D., and J. M. Vose. 2007. Regulation of nitrogen mineralization and nitrification in southern Appalachian ecosystems: separating the relative importance of biotic vs. abiotic controls. Pedobiologia 51:89–97.

Knoepp, J. D., J. M. Vose, and W. T. Swank. 2008. Nitrogen deposition and cycling across an elevation and vegetation gradient in southern Appalachian forests. International Journal of Environmental Studies 65:391–410.

Koch, G. W., and A. L. Fredeen. 2005. Transport challenges in tall trees. Pages 688 *in* C. K. Boyce, N. M. Holbrook, and M. A. Zwieniecki, editors. Vascular transport in plants. Academic Press, San Diego, California, USA.

Leuzinger, S., G. Zotz, R. Asshoff, and C. Körner. 2005. Responses of deciduous forest trees to severe drought in Central Europe. Tree Physiology 25:641–650.

Lewis, M. E. 1989. Americans and their forests: a historical geography. Cambridge University Press, Cambridge, UK.

Lienard, J., I. Florescu, and N. Strigul. 2015. An appraisal of the classic forest succession paradigm with the shade tolerance index. PLoS ONE 10:e0117138. https://doi.org/10.1371/journal.pone.0117138

Lipscomb, M. V., and E. T. Nilsen. 1990. Environmental and physiological factors influencing the natural distribution of evergreen and deciduous ericaceous shrubs on northeast- and southwest-facing slopes of the Southern Appalachian Mountains. II. Water relations. American Journal of Botany 77:517–526.

Lorimer, C. G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. Ecology 61:1169–1184.

Lowe, P. R. 1977. An approximating polynomial for the computation of saturation vapor pressure. Journal of Applied Meteorology 16:100–103.

Maclean, J. E., R. J. Mitchell, D. F. R. P. Burslem, D. Genney, J. Hall, and R. J. Pakeman. 2017. Understory plant community composition reflects invasion history decades after invasive *Rhododendron* has been removed. Journal of Applied Ecology. https://doi.org/10.1111/1365-2664.12973

Mallik, A. U. 2003. Conifer regeneration problems in boreal and temperate forests with ericaceous understory: role of disturbance, seedbed limitation, and keytsone species change. Critical Reviews in Plant Sciences 22:341–366.

Malpica, J. A. 2007. Hue adjustment to IHS pan-sharpened IKONOS imagery for vegetation enhancement. IEEE Geoscience and Remote Sensing Letters 4:27–31.

Martin, J. G., B. D. Kloeppel, T. L. Schaefer, D. L. Kimbler, and S. G. McNulty. 1998. Aboveground biomass and nitrogen allocation of ten deciduous southern Appalachian tree species. Canadian Journal of Forest Research 28:1648–1659.

McNab, W. H. 1989. Terrain shape index: quantifying the effects of minor landforms on tree height. Forest Science 35:91–104.

McNab, W. H. 1993. A topographic index to quantify the effect of mesoscale landform on site productivity. Canadian Journal of Forest Research 23:1100–1107.

Meiners, T., D. Smith, T. Sharik, and D. E. Beck. 1984. Soil and plant water stress in an Appalachian oak forest in relation to topography and stand age. Plant and Soil 80:171–179.

Mitchell, S. J. 2013. Wind as a natural disturbance agent in forests: a synthesis. Forestry: An International Journal of Forest Research 86:147–157.

Monk, C. D., D. T. McGinty, and F. P. Day Jr. 1985. The ecological importance of *Kalmia latifolia* and *Rhododendron maximum* in the deciduous forest of the southern Appalachians. Bulletin of the Torrey Botanical Club 112:187–193.

Morin, X., C. Augspurger, and I. Chuine. 2007. Process-based modeling of species' distributions: What limits temperate tree species' range boundaries? Ecology 88:2280–2291.

Moser, K. W., M. J. Ducey, and P. M. S. Ashton. 1996. Effects of fire intensity on competitive dynamics between red and black oaks and mountain laurel. Northern Journal of Applied Forestry 13:119–123.

Myers, R. H., D. C. Montgomery, G. G. Vining, and T. J. Robinson. 2010. Random effects in generalized linear models. Pages 319–407 *in* R. H. Myers, D. C. Montgomery, G. Geoffrey Vining, and T. J. Robinson, editors. Generalized linear models: with applications in engineering and the sciences. Second edition. John Wiley & Sons Inc, Hoboken, New Jersey, USA.

Næsset, E. 2002. Predicting forest stand characteristics with airborne scanning laser using a practical two-stage procedure and field data. Remote Sensing of Environment 80:88–99.

Nagamatsu, D., Y. Hirabuki, and Y. Mochida. 2003. Influence of micro-landforms on forest structure, tree death and recruitment in a Japanese temperate mixed forest. Ecological Research 18:533–547.

Narayanaraj, G., P. V. Bolstad, K. J. Elliott, and J. M. Vose. 2010. Terrain and landform influence on (*Tsuga canadensis* (L.) Carrière) eastern hemlock distribution in the southern Appalachian Mountains. Castanea 75:1–18.

Nilsen, E. T., B. D. Clinton, T. T. Lei, O. K. Miller, S. W. Semones, and J. F. Walker. 2001. Does *Rhododendron maximum* L. (Ericaceae) reduce the availability of resources above and belowground for canopy tree seedlings? American Midland Naturalist 145:325–343.

Nilsen, E. T., J. F. Walker, O. K. Miller, S. W. Semones, T. T. Lei, and B. D. Clinton. 1999. Inhibition of seedling survival under *Rhododendron maximum* (Ericaceae): Could allelopathy be a cause? American Journal of Botany 86:1597–1605.

Nowacki, G. J., and M. D. Abrams. 2008. The demise of fire and "mesophication" of forests in the eastern United States. BioScience 58:123–128.

Oren, R., and D. E. Pataki. 2001. Transpiration in response to variation in microclimate and soil moisture in southeastern deciduous forests. Oecologia 127:549–559.

Osnas, J. L. D., J. W. Lichstein, P. B. Reich, and S. W. Pacala. 2013. Global leaf trait relationships: mass, area, and the leaf economics spectrum. Science 340:741–744.

Pallardy, S. G. 2008. Physiology of woody plants. Elsevier, Amsterdam, The Netherlands.

Parker, G. G., J. P. O'Neill, and D. Higman. 1989. Vertical profile and canopy organization in a mixed deciduous forest. Vegetatio 85:1–11.

Peterson, C. J. 2007. Consistent influence of tree diameter and species on damage in nine eastern North America tornado blowdowns. Forest Ecology and Management 250:96–108.

Plocher, A. E., and K. L. Carvell. 1987. Population dynamics of rosebay rhododendron thickets in the southern Appalachians. Bulletin of the Torrey Botanical Club 114:121–126.

Purves, D. W., and S. Pacala. 2008. Predictive models of forest dynamics. Science 320:1452–1453.

Putz, F. E., G. G. Parker, and R. M. Archibald. 1984. Mechanical abrasion and intercrown spacing. American Midland Naturalist 112:24–28.

R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Rambo, T. R., and M. P. North. 2008. Spatial and temporal variability of canopy microclimate in a Sierra Nevada riparian forest. Northwest Science 82:259–268.

Reich, P. B., and P. Bolstad. 2001. Productivity of evergreen and deciduous temperate forests. Pages 245–283 *in* J. Roy, H. Mooney, and B. Saugier, editors. Terrestrial global productivity. Academic Press, San Diego, California, USA.

Reich, P. B., M. B. Walters, D. S. Ellsworth, J. M. Vose, J. C. Volin, C. Gresham, and W. D. Bowman. 1998. Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: a test across biomes and functional groups. Oecologia 114:471–482.

Rodriguez-Iturbe, I., G. K. Vogel, R. Rigon, D. Entekhabi, F. Castelli, and A. Rinaldo. 1995. On the spatial organization of soil moisture fields. Geophysical Research Letters 22:2757–2760.

Ryan, M. G., N. Phillips, and B. J. Bond. 2006. The hydraulic limitation hypothesis revisited. Plant, Cell and Environment 29:367–381.

Ryan, M. G., and B. J. Yoder. 1997. Hydraulic limits to tree height and tree growth. BioScience 47:235–242.

Schafer, K. V. R., R. Oren, J. D. Tenhunen, K. V. R. Schäfer, R. Oren, and J. D. Tenhunen. 2000. The effect of tree height on crown level stomatal conductance. Plant, Cell and Environment 23:365–375.

Secord, J., and A. Zakhor. 2007. Tree detection in urban regions using aerial LiDAR and image data. IEEE Geoscience and Remote Sensing Letters 4:196–200.

Shugart, H. H. 1984. A theory of forest dynamics: the ecological implications of forest succession. Springer-Verlag, New York, New York, USA.

Swift, L. J., G. Cunningham, and J. Douglass. 1988. Climatology and hydrology. Pages 35–55 *in* D. A. Crossley Jr., and W. T. Swank, editors. Forest hydrology and ecology at Coweeta. Springer-Verlag, New York, New York, USA.

Swift Jr., L. W., K. Elliott, R. D. Ottmar, and R. E. Vihnanek. 1993. Site preparation burning to improve southern Appalachian pine – hardwood stands: fire characteristics and soil erosion, moisture, and temperature. Canadian Journal of Forest Research 23:2242–2254.

Tajchman, S. J., H. Fu, and J. N. Kochenderfer. 1997. Water and energy balance of a forested Appalachian watershed. Agricultural and Forest Meteorology 84:61–68.

Tajchman, S. J., M. H. Harris, and E. C. Townsend. 1988. Variability of the radiative index of dryness in an Appalachian watershed. Agricultural and Forest Meteorology 42:199–207.

Thiffault, N., and R. Jobidon. 2006. How to shift unproductive *Kalmia angustifolia – Rhododendron groenlandicum* heath to productive conifer plantation. Canadian Journal of Forest Research 36:2364–2376.

Thomsen, J. E., G. Bohrer, A. M. Matheny, V. Y. Ivanov, L. He, H. J. Renninger, and K. V. R. Schäfer. 2013. Contrasting hydraulic strategies during dry soil conditions in *Quercus rubra* and *Acer rubrum* in a sandy site in Michigan. Forests 4:1106–1120.

Tromp-van Meerveld, H. J., and J. J. McDonnell. 2006. On the interrelations between topography, soil depth, soil moisture, transpiration rates and species distribution at the hillslope scale. Advances in Water Resources 29:293–310.

Tyree, M. T. 2003. Hydraulic limits on tree performance: transpiration, carbon gain and growth of trees. Trees 17:95–100.

VanLear, D. H., D. B. Vandermast, C. T. Rivers, T. T. Baker, C. W. Hedman, D. B. Clinton, and T. A. Waldrop. 2002. American chestnut, rhododendron, and the future of Appalachian cove forests. Pages 214–220, SRS GTR-48. USDA Forest Service, Southern Research Station, Asheville, North Carolina, USA.

Vose, J. M., B. D. Clinton, N. H. Sullivan, B. D. Clinton, and P. V. Bolstad. 1995. Vertical leaf area distribution, light transmittance, and application of the Beer-Lambert Law in four mature hardwood stands in the southern Appalachians. Canadian Journal of Forest Research 25:1036–1043.

Vose, J. M., and K. J. Elliott. 2016. Oak, fire, and global change in the Eastern USA: What might the future hold? Fire Ecology 12:160–179.

Waldrop, T. A., and H. P. Brose. 1999. A comparison of fire intensity levels for stand replacement of Table Mountain Pine (*Pinus pungens* Lamb.). Forest Ecology and Management 113:115–166.

Werling, J. A., and S. J. Tajchman. 1984. Soil thermal and moisture regimes on forested slopes of an Appalachian watershed. Forest Ecology and Management 7:297–310.

Western, A. W., R. B. Grayson, G. Böschl, and G. R. Willgoose. 1999. Observed spatial organization of soil moisture indices. Water Resources Research 35:797–810.

White, P. S., and R. I. Millert. 2008. Topographic models of vascular plant richness in the southern Appalachian high peaks. Journal of Ecology 76:192–199.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs 26:1–80.

Wurzburger, N., and R. L. Hendrick. 2007. Rhododendron thickets alter N cycling and soil extracellular enzyme activities in southern Appalachian hardwood forests. Pedobiologia 50:563–576.

Wurzburger, N., and R. L. Hendrick. 2009. Plant litter chemistry and mycorrhizal roots promote a nitrogen feedback in a temperate forest. Journal of Ecology 97:528–536.

Wyckoff, P. H., and J. S. Clark. 2002. The relationship between growth and mortality for seven co-occurring tree species in the southern Appalachian Mountains. Journal of Ecology 90:604–615.

Yeakley, J. A., W. T. Swank, L. W. Swift, G. M. Hornberger, and H. H. Shugart. 1998. Soil moisture gradients and controls on a southern Appalachian hillslope from drought through recharge. Hydrology and Earth System Sciences 2:41–49.

Yin, X., E. A. Lantinga, A. D. H. C. M. Schapendonk, and X. Zhong. 2003. Some quantitative relationships between leaf area index and canopy nitrogen content and distribution. Annals of Botany 91:893–903.

Zar, J. H. 1999. Biological statistics. Prentice Hall, Upper Saddle River, New Jersey, USA.