Climate sensitivity of understory trees differs from overstory trees in temperate mesic forests

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Abstract. The response of understory trees to climate variability is key to understanding current and future forest dynamics. However, analyses of climatic effects on tree growth have primarily focused on the upper canopy, leaving understory dynamics unresolved. We analyzed differences in climate sensitivity based on canopy position of four common tree species (*Acer rubrum*, *Fagus grandifolia*, *Quercus rubra*, and *Tsuga canadensis*) using growth information from 1,084 trees across eight sites in the northeastern United States. Effects of canopy position on climate response varied, but were significant and often nonlinear, for all four species. Compared to overstory trees, understory trees showed stronger reductions in growth at high temperatures and varied shifts in precipitation response. This contradicts the prevailing assumption that climate responses, particularly to temperature, of understory trees are buffered by the overstory. Forest growth trajectories are uncertain in compositionally and structurally complex forests, and future demography and regeneration dynamics may be misinferred if not all canopy levels are represented in future forecasts.

Key words: canopy position; climate–growth relationship; forest structure; generalized additive models; tree rings.

INTRODUCTION

Forests cover approximately 30% of the global land surface and are key to a variety of ecosystem services including hosting biodiversity and the regulation of global carbon, climate, and hydrological cycles (Bonan 2008, Pan et al. 2011, Trumbore et al. 2015). Large, canopy-dominant trees often regulate many dynamics such as ecosystem water, carbon, and nutrient cycling (Lutz et al. 2018), but juveniles in the understory are key to future forest health and resilience to global change (Dey et al. 2019). However, geographic distributions of mature, overstory individuals do not reflect the locations of successful regeneration (McEwan et al. 2011, Zhu et al. 2012). This mismatch highlights the implicit assumption in many distribution studies that overstory dynamics are mirrored in the understory. Many of the biotic and abiotic factors that influence tree growth and survival, such as microclimate and competition, are not uniform within a region and explain spatial and temporal heterogeneity in forest composition and function (Canham et al. 2006, Gómez-Aparicio et al. 2011, Foster et al. 2016). Variation in microclimate and relative competition pressure within a single location can be pronounced for trees above and below the forest canopy and may lead to differences in both tree growth rates and climate sensitivity (Clark et al. 2012, 2014, Rollinson et al. 2016). Thus, the growth and climate response of the understory trees representing potential regeneration may not be accurately inferred from the study of canopy-tree dynamics alone.

Differences between the climate response of overstory and understory trees may be greatest in forests with dense, multi-layered canopies, such as those of the eastern United States. Dense forest canopies result in microclimate conditions beneath the canopy that can be distinct from those experienced by the upper-most trees (Ishii et al. 2004, von Arx et al. 2012, Davis et al. 2019). Relative to understory trees, the upper-most trees in the canopy profile experience greater wind shear, higher levels of incoming solar radiation, increased temperatures, and lower relative humidity (Baldocchi and

Meyers 1988, Renaud et al. 2011, von Arx et al. 2012, Davis et al. 2019). Studies in some regions of the United States have suggested that reduced climate stress below the forest canopy reduces climate sensitivity and a buffered response in the understory (Martín-Benito et al. 2008, Carnwath et al. 2012, Davis et al. 2019). However, competition for light and space is increased for understory individuals, leading to increased stress and reduced resources both aboveground and belowground (Canham et al. 1994, Ricard et al. 2003, Onoda et al. 2014). The impact of this resource asymmetry and overall forest canopy structure on individual tree growth is still being resolved, but increased stress from other factors may lead to higher climate vulnerability and sensitivity rather than a buffered response (Orwig and Abrams 1997, He et al. 2005, Canham and Murphy 2016, Fahey et al. 2016, Hardiman et al. 2018).

Current methods for analyzing the interannual variability in tree growth using dendrochronology have long been complicated by the strong temporal trends in annual growth due to changes in tree diameter and exogenous influences such as disturbances (Cook 1985, Peters et al. 2015). Traditional methods for tree-ring analysis have relied heavily upon a priori detrending, aggregation into site-level chronologies to achieve univariate linear correlations between climate variables, and interannual variability in tree growth (Cook and Peters 1997, Peters et al. 2015). These approaches may remove important nonlinearities in individual climate responses that are the result of underlying biophysical processes or interactions among multiple co-occurring factors that influence individual tree growth (Canham and Uriarte 2006, Clark et al. 2011, Canham et al. 2018). Thus, disentangling the ecologically complex differences in climate sensitivities of individual trees in different canopy positions with differences in primary stressors requires use of flexible, multivariate, and nonlinear analytical methods that allow unexpected ecological patterns to emerge across multiple sites (Rollinson et al. 2021, Polansky and Robbins 2013).

To determine whether canopy position influenced species' observed climate sensitivity in the Northeastern U.S. (NEUS), we used growth information from overstory, middle-canopy, and understory tree growth of four species abundant across eight forests in this region. Using 120 yr of climate data and growth from 1,084 individual trees, we fit generalized additive mixed models to estimate simultaneous nonlinear responses to temperature, precipitation, and vapor pressure deficit (VPD) at the species level. We evaluated the importance of canopy position in mediating climate responses by comparing change in species' climate sensitivity and model performance between a naïve model where all trees were grouped together, and one where climate responses were allowed to vary by canopy position. We then describe the ecological impacts and how climate response varies among canopy classes within a species by analyzing the model-estimated climate sensitivity.

Methods

Site descriptions and climate data

We sampled eight locations throughout the NEUS, from Maine to west-central Massachusetts, that range across slightly differing elevations and proximities to the Atlantic Ocean (Fig. 1; Table 1). This region covers the transitions from northern hardwood species at the southern distribution and lower elevations to lowland coniferous forest in the north and upper elevations (Braun 1950, Dyer 2006). These sites were part of a larger study developed to understand long term dynamics and climate-growth relations in a region and forest similar to the eddy flux plots in the northeast and provide context for long-term research in those forests (D'Orangeville et al. 2018, Dye et al. 2019). All eight sites showed overlapping intra-annual temperature, precipitation, and maximum vapor pressure deficit (VPDmax) variability that facilitate use of multiple sites to estimate species- and canopy strata-based climate responses (Appendix S1: Fig. S2, Appendix S1: Fig. S7). This study design is unbiased and ecologically representative, with fewer samples being used to constrain climate responses at the margins of that species distribution, even though the representation of species among sites and climate space is unbalanced as a result. Climate data for each site, including mean growing season temperature, precipitation, and VPDmax, were extracted for the period 1895–2014 from the gridded monthly PRISM climate data set with approximate 4 km resolution (PRISM *Climate Group*). Although the PRISM dataset should not be used to describe regional climate change (PRISM *Climate Group*), the data used to estimate climate responses in our study contain an average growing season warming of 0.24°C and increased precipitation of 90 mm over our study temporal domain, which are consistent with climate change assessments for this region (Easterling et al. 2017, Vose et al. 2017). We defined the growing season as May–September (Barford et al. 2001) and all data presented are for this temporal window.

Field techniques

We described stand structure and species composition at each site using two to three nested circular plots following (Dye et al. 2016). In the innermost nest (0–13 m), we sampled trees ≥10 cm in DBH, in the middle nest (13.1–20 m) we sampled trees ≥20 cm DBH, and in an outer nest (20.1–30 m), we sampled trees ≥30 cm DBH. Due to density and stand characteristics, only Gill Brook, North Round Pond, Goose Egg, and Pisgah were sampled using this outer ring. Species, DBH, and canopy position were recorded for each tree within the plots. Canopy classes were defined as follows: overstory trees. dominant and co-dominant individuals in the uppermost canopy stratum whose crown is emergent and taller than neighboring trees or those with crowns
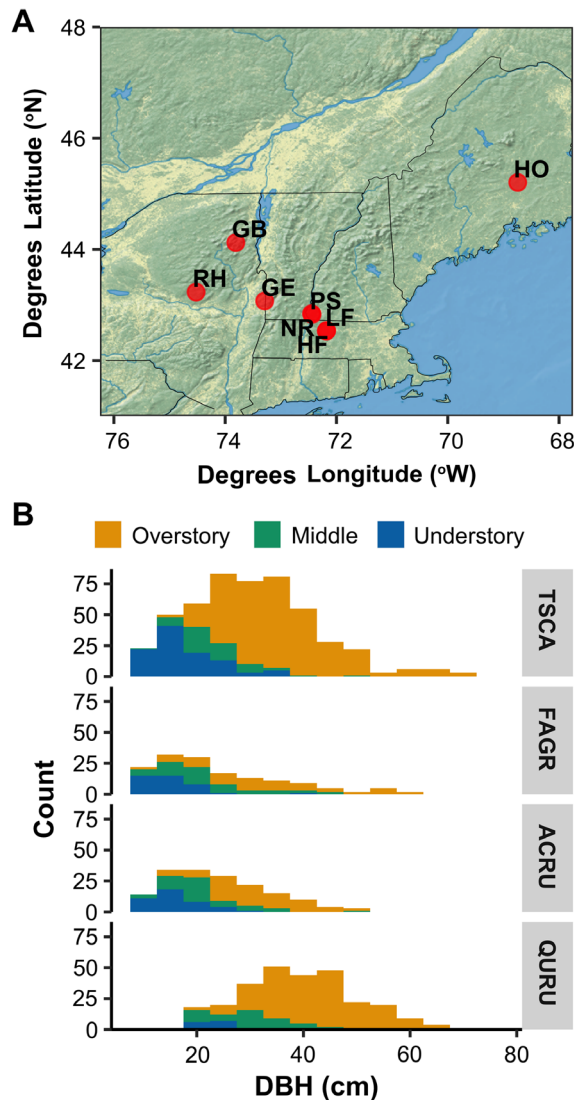
FIG. 1. (A) Map of the eight populations sampled in the eastern United States and (B) stacked histograms detailing diameter at breast height (DBH) distributions of overstory (gold), middle (green), and understory (blue) trees are also shown for *Acer rubrum* (ACRU), *Fagus grandifolia* (FAGR), *Quercus rubra* (QURU), and *Tsuga canadensis* (TSCA) across all sites sampled. North Round Pond (NR) and the Pisgah Tract (PS) are proximal populations and have overlapping site points. The same is true for the Harvard Forest (HF) population and the Lyford Plots (LF). These pairs of sites are indicated by a single point. See Table 1 for all site names.

of similar height as their neighbors; middle-canopy trees, intermediate trees where most of their crown is shaded by taller trees, but where they have some access to sunlight through small gaps in the forest canopy; and understory trees, where a tree's entire crown was fully overtopped by adjacent trees with the potential to show suppressed growth.

Tree diameter at breast height (DBH) ranged from 10 to 76.5 cm across all sites (only trees ≥10 cm were sampled; Table 1). However, the tallest trees based on relative canopy position were not always the largest diameter trees, indicating size alone is not a criterion for describing canopy position. Tree diameters ranged from 11.8 to 76.5 cm, 10.2 to 53.0 cm, and 10.0 to 38.8 cm, for the overstory, middle, and understory trees, respectively (Fig. 1). The oldest trees were found at the Gill Brook site, and the youngest trees were found at the Goose Egg site (Table 1). However, all sites had individuals more than one-hundred years, and the understory was not dramatically younger than the overstory, with individuals as old as 174 yr (Appendix S1: Fig. S1).

Two increment cores were collected from each tree 90°–180° relative to one another at breast height. All samples were cross dated to ensure accurate assessment of tree responses to interannual variability in temperature, precipitation, and VPD (Appendix S1: Table S2) (Stokes and Smiley 1968). Multiple cores collected from the same tree were averaged to calculate the mean annual ring width for that tree. In the case where only one core from a tree could be verifiably cross dated, the dated core was used to represent the growth for the entire tree. The diameter of each tree was reconstructed for each year by subtracting annual ring width increments from the DBH observed in the field (Davis et al. 2009, Dye et al. 2016, Alexander et al. 2018). Ring-width measurements were transformed into basal area increment (BAI), as BAI considers the geometry of the tree and better illustrates productivity than traditional ring-width increments (Phipps and Whiton 1988, Phipps 2005, Babst et al. 2014).

Growth model descriptions

We analyzed growth responses to climate across canopy strata in the four species with representation across multiple sites and present in all canopy positions: *Tsuga canadensis* (L.) Carr, *Quercus rubra* L., *Fagus grandifolia* Ehrh., and *Acer rubrum* L. (Appendix S1: Table S1; Fig. 1; *n* = 1,084). We were unable to reconstruct relative canopy position back through time, so we categorically grouped trees and compared their sensitivity based on observed canopy position at the time of sampling. However, all canopy groups had growth information available throughout the analysis period of 1985–2014, indicating that canopy position is not collinear with age in our study (Appendix S1: Fig. S1). We used log-transformed basal area increment (BAI) as the response variable in all analyses. All effects were estimated using generalized additive mixed models (GAMMs) using the gamm function in the mgcv R package to allow for nonlinear climate and size effects without prescribing a priori functional forms such as lognormal or exponential (Polansky and Robbins 2013, Wood 2017, Simpson 2018). An overview of models follows, but more detail can be found in Appendix S1: Section S1.

TABLE 1. Details for study sites including, site name, site abbreviation (Abb.), latitude, longitude, DBH range of trees sampled, number of trees sampled, range of the innermost year present from the sampled trees (Inner Year Range), and the age (mean ± SD) of trees at the site (calculated from innermost year present in samples).

Site name	Abb.	Latitude (°N)	Longitude (°W)	DBH (cm) range	Trees sampled	Inner year range	Age (yr)
Gill Brook	GB	44.122	73.809	10.2–68.5	63	1576–1984	144 ± 79
Goose Egg	GE	43.072	73.290	10.1–58.0	100	1681–1994	137 ± 47
Lyford Plots	LF	42.531	72.183	10.3–76.5	116	1861–1986	95 ± 22
North Round Pond	NR	42.845	72.447	10.2–72.2	196	1754–1977	116 ± 45
Pisgah	PS	42.829	72.439	10.2–65.6	238	1675–1963	109 ± 44
Rooster Hill	RH	43.231	74.523	10.0–66.0	119	1828–1966	112 ± 35
Harvard Forest	HF	42.539	72.176	10.1–53.0	118	1896–1974	85 ± 19
Howland	HO	45.205	68.742	10.2–64.4	134	1809–1970	108 ± 33

Note: Only trees ≥10 cm were sampled.

We fit two sets of models to determine the relative influences of canopy class on species-based climate responses on tree growth: a model without a single climate response for each species and one in which climate responses varied by canopy position (Table 2). All models included year and size effects to include temporally varying, non-climatic influences on growth. Year effects were estimated using a four-knot thin plate regression spline fit by sampling plot to capture stand dynamics such as suppression or release events that may have influenced growth through time. Four knots were chosen for year effects to provide greater flexibility than size and climate effects and approximated one knot for every 30 yr in our analyses. Size effects were estimated for each species using three-knot thin-plate regression splines fit to reconstructed DBH. Three knots were chosen for the size to allow for a flexible functional form, but enough rigidity that the effect mirrored biological hypotheses and subsequent studies could mirror with more prescribed forms (e.g., logistic). Together, the year and size effects are analogous to *a priori* detrending that is more common in traditional tree-ring analyses so that effects of climate can be analyzed in the remaining interannual variation (Cook 1985, Cook and Peters 1997, Peters et al. 2015). However, a priori detrending prevents quantitative comparison of size or disturbance-based constraints on growth as well as interactions with low-frequency changes in climate over the analysis period (Peters et al. 2015; Rollinson et al., *in press*).

In both sets of models, temperature, precipitation, and VPD effects were estimated using three-knot thin plate regression splines. Three knots were chosen for the climate effects to allow for flexible responses that could vary among canopy positions with the same mathematical formulation, but with enough rigidity that the effects mirrored biological hypotheses and avoided overfitting the data. In the model canopy position model, climate splines were fit separately for each canopy class. Change in model performance through the addition of canopy-position-based climate effects for each species was assessed through changes in the fixed effects R^2 (gam component of gamm), linear mixed effects Akaike information criterion (AIC; lme component of gamm), and fixed effects RMSE. Models for *Fagus grandifolia* and *Quercus rubra* also included hierarchical random intercepts for individual trees nested within plots nested within sites. Due to challenges achieving model convergence, models for *Tsuga canadensis* and *Acer rubrum* did not have plot random effects but maintained hierarchical random intercepts for individual trees nested within sites. Random, categorical, year effects were not included in our models because of the plot-based year terms and because our model uses interannual variability in temperature, precipitation, and VPD to explain interannual variation in growth. Models of a global climate response for each species included a fixed effect for plot and those where climate responses varied among canopy positions included fixed effects of plot and canopy position.

The sensitivity of estimated climate responses at both the species and canopy-position level to data representation at individual sites was analyzed through

TABLE 2. Comparison of multiple measures for model evaluation for all formulations used to determine impacts of species (spp) and canopy class (cc) on tree response to climate.

Species	n	R^2 spp	R^2 cc	ΔR^2	AIC spp	AIC cc	ΔAIC	RMSE spp	RMSE cc	ΔRMSE
TSCA	496	0.407	0.424	0.017	136876	136437	−439	1.079	1.064	−0.015
FAGR	148	0.445	0.449	0.004	46700	46692	−8	1.36	1.354	−0.006
ACRU	165	0.351	0.355	0.004	58441	58428	−13	1.507	1.501	−0.006
QURU	275	0.466	0.472	0.006	67165	67147	−18	0.805	0.8	−0.005

Notes: Climate variables investigated include mean growing season temperature, cumulative growing season precipitation, and mean growing season maximum vapor pressure deficit. Δ indicates the difference between the species-only (spp) and canopy class-informed (cc) models.

supplemental "leave-one-out" analyses. In these analyses, a single site was excluded from analysis of each species using the same models described above so as to determine if estimated species' responses to climate were influenced by inclusion of sites with particular disturbance histories or climatic ranges, such as the low temperatures at Rooster Hill (RH) and Gill Brook (GB; Appendix S1: Fig. S2). Although briefly summarized below, these analyses were not the focus of this manuscript. Full results for all four species can be found in Appendix S1: Fig. S8–S16.

Evaluation of influence of species and canopy on climate response

To aid in ecological interpretation, we compared statistically estimated partial effects and sensitivities based on model parameters rather than compare the model-estimated spline coefficients that do not directly translate to ecologically relevant parameters. We present differences in the partial effects of temperature, precipitation, and VPD on growth based on species and canopy position in two ways. First, the partial climate effect sizes across species and canopy strata were calculated using spline parameters and their associated uncertainty to create 100 posterior estimates of relative effect of climate on growth for each climate effect group (i.e., species and/or canopy class). All partial effects presented in figures and texts have been transformed into effects on relative BAI by taking the exponent of the model-estimated values. Because splines in the mgcv R package used to estimate nonlinear climate effects are 0 centered, the exponent of partial effects becomes 1 centered and 0 bounded. Values that are additive in the log-formulation of the model become multiplicative when transformed back to BAI-space, resulting in the partial climate effects being relative growth scalars. To further facilitate ecological interpretation of results, we then multiplied the scalar by 100 so that partial effects could be presented as percent of relativized growth. Mean differences in growth rates due to species, canopy class, plot, or site are accounted for by categorical model intercept terms (see Appendix S1: Section S1 for more detail).

In text, we describe growth responses to climate as sensitivity, which is the instantaneous slope calculated from the first derivative of the model-estimated partial effects described above. As sensitivity is defined as the slope of the climate response of relativized growth, sensitivity units are percent change in growth per change in unit of climate (°C, mm precipitation, or kPA VPD). We calculated sensitivity values using the same 100-member posterior distribution as partial effects estimation (see Appendix S1: Section S2). Ranges of conditions for statistical sensitivity are defined as regions where the first derivative in this distribution was significantly different from zero ($P < 0.05$). Because we present results generated from a simulated posterior distribution, we cannot rely on standard statistical comparisons due to our

artificial n for simulated effects. Climate sensitivities are presented in text as the mean value and standard deviation among simulated ensemble members over the specified range of conditions (e.g., above or below a threshold).

RESULTS

Species-only model

Species responses to climate in the model naive of canopy position showed expected variation in climate–growth relationships (Fig. 2). *Quercus rubra* ($n = 275$) showed the highest explained variance ($R^2 = 0.466$) and lowest RMSE (0.805), whereas *Acer rubrum* ($n = 165$) had the lowest performing species-based models of tree growth (Table 2, $R^2 = 0.351$, RMSE = 1.507). The two northern-distributed and late-successional species *Tsuga canadensis* and *Fagus grandifolia* increased growth under cool and wet conditions, whereas *Quercus rubra* shows increased growth under warm and dry conditions (Fig. 2). With the exception of *Fagus grandifolia* precipitation response, species displayed highly nonlinear sensitivities to climate. *Fagus grandifolia* showed a linear sensitivity of $0.06 \pm 0.01\%$ BAI/mm for precipitation. However, *Fagus grandifolia* was insensitive to VPD at the species-level and only sensitive to temperatures below 15.8°C ($-7.70 \pm 2.78\%$ BAI/°C). In contrast, *Tsuga canadensis* only showed growth sensitivity to changes in temperatures below 16.3°C with a mean sensitivity of -9.77 ± 2.09 %BAI/°C. This result parallels the observed *Tsuga canadensis* response to VPD, which only showed reduced growth at VPD below 77.7 kPA ($-0.84 \pm 0.23\%$ BAI/kPa). Although *Tsuga canadensis* showed overall positive relationships to precipitation, it was only significantly sensitive to annual growing season precipitation below 708 mm ($0.04 \pm 0.01\%$ BAI/mm). *Quercus rubra* showed responses to temperature and precipitation nearly opposite that of *Tsuga canadensis* with increasing growth rates at temperatures below 16.7°C ($10.85 \pm 1.50\%$ BAI/°C) and reduced growth with growing season precipitation above 226 mm ($-0.09 \pm 0.01\%$ BAI/mm). Without consideration of canopy position, *Quercus rubra* showed the greatest sensitivity to VPD with strong sensitivity below 78.6 kPA ($-2.21 \pm 0.15\%$ BAI/kPa). *Acer rubrum* showed the overall lowest sensitivity to temperature and precipitation, with temperature sensitivity only significant above 13.3°C, which includes positive sensitivity of $9.84 \pm 3.91\%$ BAI/°C up to 15.3°C and negative sensitivity of $-10.79 \pm 3.72\%$ BAI/°C above 16.7°C. *Acer rubrum* was only sensitive to precipitation above 580 mm ($-0.08 \pm 0.03\%$ BAI/mm) and to low VPD ($-1.34 \pm 0.42\%$ BAI/kPa below 76.3 kPA).

Canopy position model

Comparisons of climate responses among canopy groups reveal high within-species variability that can be
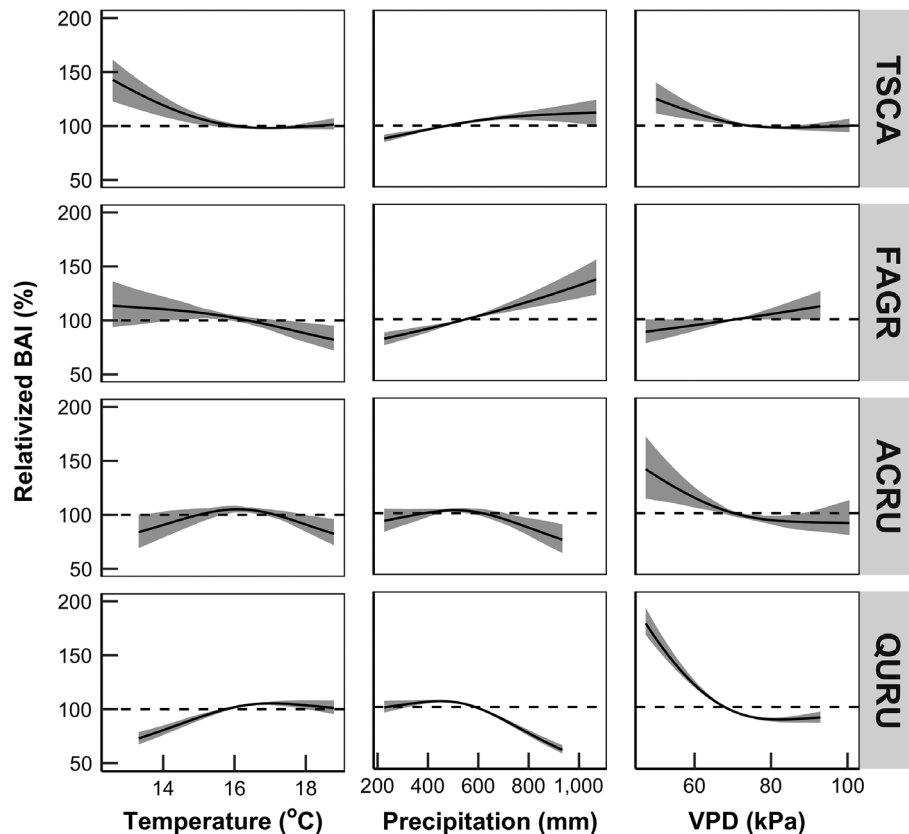
FIG. 2. Partial climate effects on relativized basal area increment (BAI) from the global species model (Table 2) where canopy position is ignored. Species codes are TSCA, *Tsuga canadensis*; FAGR, *Fagus grandifolia*; ACRU, *Acer rubrum*; and QURU, *Quercus rubra*. Partial climate effects were fit conditionally in a single generalized additive mixed model (GAMM) that included mean growing season temperature (Tmean), cumulative growing season precipitation (Precip), and mean growing season daily maximum vapor pressure deficit (VPDmax). Each curve consists of the mean response (heavy line) and 95% confidence interval (ribbon). The dashed horizontal line (relativized BAI = 100%) represents mean growth rate for individual trees; values greater than 100% indicate increased growth and values below 100% indicate reduced growth.

attributed to canopy position (Fig. 3). Allowing climate sensitivity to vary by canopy position improved all measures of model performance for all four species (Table 2). *Tsuga canadensis* showed the greatest improvement across all metrics, where improvements in R^2, AIC, and RMSE was more than twice that seen in other species. In the supplemental site-exclusion analyses, the naive model did not show higher R^2 or lower RMSE than the canopy-based model for any of the 26 site–species combinations (Appendix S1: Table S3, Appendix S1: Figs. S8–S16). The naive model showed lower AIC values in only two instances: *Fagus grandifolia* without Gill Brook (GB) and *Quercus rubra* without Harvard Forest (HF). AIC values were the same or similar (within 2 AIC points) for *Fagus grandifolia* without North Round Pond (NR) and *Quercus rubra* without Lyford (LF).

All species except *Quercus rubra* showed reduced growth of understory trees under warm conditions, despite sometimes opposite trends in the overstory (Fig. 3). Growth of overstory *Tsuga canadensis* decreased −10.67 ± 2.42% BAI/°C at temperatures below 15.7°C,

but increased 7.79 ± 1.32% BAI/°C above 16.3°C. In contrast, understory *Tsuga canadensis* showed consistent and strong negative growth sensitivity of −25.4 ± 2.61% BAI/°C at temperatures above 15.4°C. *Fagus grandifolia* displayed the greatest similarity in growth sensitivity between the understory and overstory with mean sensitivity of −11.55 ± 3.99% BAI/°C and −19.96 ± 5.61% BAI/°C above 16.2° and 15.5°C, respectively. *Acer rubrum* was not sensitive to temperature in the overstory, but middle-canopy trees showed parabolic-shaped temperature sensitivity (15.40 ± 5.86% BAI/°C at 13.3–15.4°C, −19.01 ± 6.41% BAI/°C above 16.7°C) and understory showed negative sensitivity above 16.1 (−30.33 ± 6.16% BAI/°C). Despite overall positive temperature sensitivity of overstory *Quercus rubra* (11.14 ± 1.46% BAI/°C below 17.0°C), growth of understory trees was only sensitive to temperatures above 16.2°C, where it showed decreasing growth in warmer years (−10.51 ± 4.16% BAI/°C).

Fewer species displayed differences in precipitation sensitivity among canopy positions, but for all species,
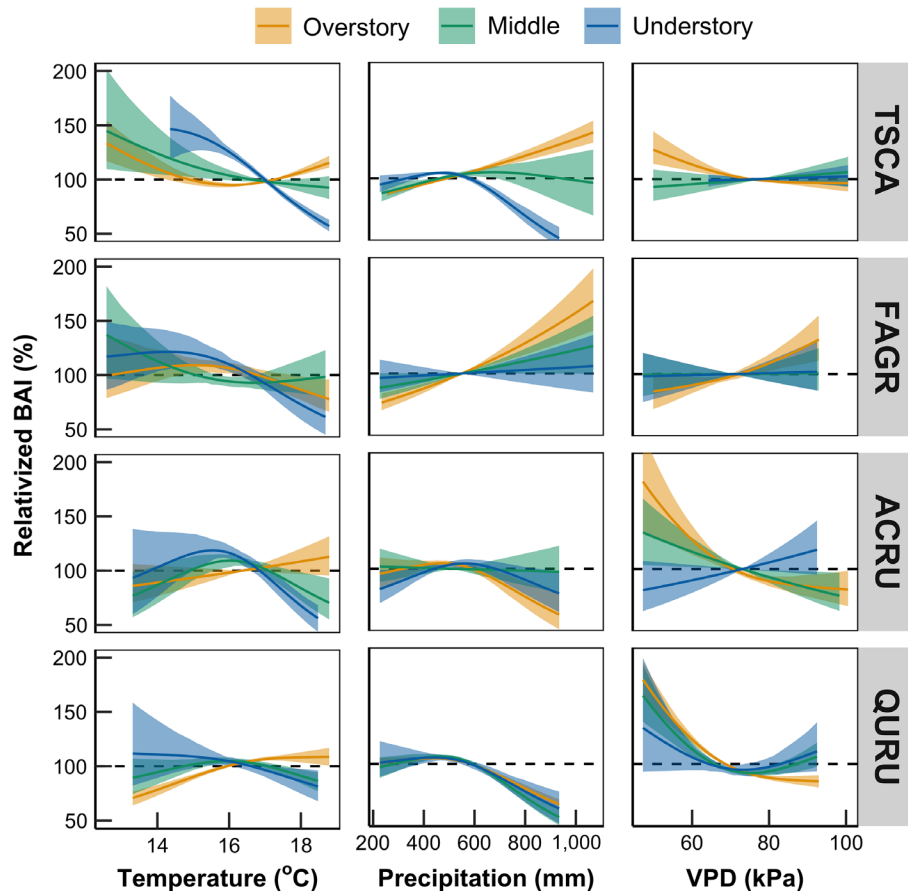
Fig. 3. Partial climate effects on relativized BAI from the canopy position model (Table 2) that describe tree responses to climate as a function of both canopy position (colors) and species (rows). Canopy positions are indicated as follows: overstory (yellow), middle (green), and understory (blue). Species codes are TSCA, *Tsuga canadensis*; FAGR, *Fagus grandifolia*; ACRU, *Acer rubrum*; and QURU, *Quercus rubra*. Partial climate effects were fit conditionally in a single generalized additive mixed model (GAMM) that included mean growing season temperature (Tmean), cumulative growing season precipitation (Precip), and mean growing season daily maximum vapor pressure deficit (VPDmax). Each curve consists of the mean response (heavy line) and 95% confidence interval (ribbon). The dashed horizontal line (relativized BAI = 100%) represents mean growth rate for individual trees; values greater than 100% indicate increased growth and values below 100% indicate reduced growth.

the understory response was similar to or lower than the overstory in wet growing seasons (Fig. 3). Overstory *Tsuga canadensis* and *Fagus grandifolia* display nearly linear, positive sensitivity to precipitation (0.06 ± 0.01% BAI/mm and 0.10 ± 0.02% BAI/mm, respectively). However, these positive effects of increased precipitation were diminished in understory trees of these same species, with middle-canopy trees showing precipitation responses that were between overstory and understory. In the case of *Tsuga canadensis*, understory trees showed slight positive sensitivity to precipitation between 226 and 410 mm (0.05 ± 0.02% BAI/mm), but strong negative sensitivity at levels above 502 mm (−0.20 ± 0.03% BAI/mm). Understory *Fagus grandifolia* was insensitive to precipitation. Understory precipitation response of *Quercus rubra* and *Acer rubrum* was statistically similar to that of overstory and middle-canopy trees of those same species. For *Quercus rubra*, trees in all canopy

positions showed similar trends as observed in the species-only model with a cross-group sensitivity of −0.14 ± 0.01% BAI/mm above 500 mm, although overstory *Quercus rubra* also showed slight, positive precipitation sensitivity below 368 mm (0.02 ± 0.01% BAI/mm). Overstory and understory *Acer rubrum* displayed negative precipitation sensitivity with wetter conditions (−0.15 ± 0.04% BAI/mm above 531 mm and −0.10 ± 0.05% BAI/mm above 637 mm, respectively). However, understory *Acer rubrum* also showed positive sensitivity at low precipitation (0.09 ± 0.05% BAI/mm below 474 mm).

For all four species, overstory trees show sensitivity to VPD and understory trees were insensitive to VPD. As seen in the species-only model, *Tsuga canadensis*, *Acer rubrum*, and *Quercus rubra* showed decreasing growth with increasing VPD below 81 kPa (−0.84 ± 0.22% BAI/kPa, −2.13 ± 0.51% BAI/kPa, and −2.13 ± 0.18%

BAI/kPa, respectively). In contrast, overstory *Fagus grandifolia* showed a nearly linear, positive sensitivity to VPD between 66.5 kPa and 92.9 kPa (1.26 ± 0.38% BAI/kPa). Despite trends in the overstory, the only significant VPD growth sensitivity in the understory was for *Quercus rubra* under a narrow range of VPD conditions (86.2 to 92.5 kPA, 1.19 ± 0.74% BAI/kPa).

Discussion

Quantification of the variable growth sensitivity along the vertical canopy profile is important to accurately represent species' responses to climate variability and change. Our results demonstrate that including information about canopy position in analyses of species-level climate response not only improves model performance (Table 2) but reveals stark differences among canopy strata (Fig. 3). Furthermore, climate responses to interannual variability in temperature, precipitation, and VPD across canopy positions and particularly in the understory were often highly nonlinear (Fig. 3). Despite impacts of canopy buffering on understory microclimatic conditions (Davis et al. 2019), only sensitivity to VPD was consistently reduced in understory trees. Relative sensitivity to temperature and precipitation among canopy classes varied by species, but all understory trees showed greater growth reductions relative to overstory trees in the warmest growing seasons. Altered climate sensitivity in the understory may be the result of asymmetric competition for resources, including light (Canham et al. 1994, 2006, Ricard et al. 2003). Although strong competition in the understory may suppress growth and reduce the absolute magnitude of growth variation in response to interannual climate variability, we demonstrate that this does not necessarily hold true for relativized growth. In some instances, understory trees may experience increased competition stress because smaller canopies (Vertessy et al. 1995) and root systems (Jacquart et al. 1992, Le Goff and Ottorini 2001, Bolte et al. 2013) relative to overstory trees may reduce their ability to acquire resources such as light, water, and nutrients (Callaway and Walker 1997, Linares et al. 2010, Gleason et al. 2017).

Overstory trees showed varied temperature sensitivities among the four species, but all understory trees showed reduced growth under warmer temperatures. If cooler below-canopy temperatures caused understory trees to be buffered from climate stress, we would expect the understory to display a similar functional form of temperature response as the overstory, but with reduced sensitivity (Martín-Benito et al. 2008, Carnwath et al. 2012, Davis et al. 2019). The temperature sensitivity of overstory trees (Fig. 3) generally resembled the overall species-level sensitivity if canopy position was ignored (Fig. 2). However, understory trees diverged from the response seen in the overstory for most species, with *Fagus grandifolia* showing the greatest similarity between overstory and understory (Fig. 3). These results suggest that temperature dimensions of drought indices may be important for explaining previous results that showed greater impacts of drought on understory individuals and trees under strong competition (Orwig and Abrams 1997, Gleason et al. 2017).

Although significant temperature sensitivity was observed in both overstory and understory trees of all four species, precipitation sensitivity was most consistently observed in overstory trees. For *Quercus rubra* and *Acer rubrum*, there was little or no variation in precipitation sensitivity among trees of different canopy positions (Fig. 3). For *Quercus rubra* in particular, which is more xeric than the other species, this may be due to their deep-rooting strategy that provides early access to groundwater, leading to little ontological variability in growth response to precipitation (Burns and Honkala 1990). For the remaining two species, *Fagus grandifolia* and *Tsuga canadensis*, overstory trees showed positive sensitivity to precipitation, while understory trees saw reduced or negative sensitivity (Fig. 3). Increased precipitation has been shown to promote increased leaf area, causing a decrease in the quality of light that infiltrates the canopy profile (Grier and Running 1977, Canham et al. 1994, Onoda et al. 2014). Therefore, although high precipitation may benefit the canopy in forests dominated by these species, it could lead to increased asymmetric competition for the understory and subsequent reduced growth, even in shade-tolerant species.

The only consistent evidence for buffered understory sensitivity in our study was for VPD, to which no species was sensitive in the understory despite significant overstory sensitivity. We correlated tree growth with climate extracted from a large-scale gridded product, which most accurately reflects open or above-canopy climate conditions. Understory conditions during the leaf-on growing season are cooler and more humid than at the canopy surface, which experiences greater VPD variability (Renaud et al. 2011). Lack of understory sensitivity to VPD may be further compounded by reduced light availability and overall reduced photosynthetic rates despite variations in large-scale evaporative demand (Davis et al. 2019). VPD is linked more directly to plant transpiration than precipitation alone, but is often not directly measured by meteorological stations and its calculation relies on other temporally and spatially dynamic variables such as specific humidity and surface pressure (Anderson 1936). Although VPD is linked to leaf-level processes and has been correlated with overstory tree growth in univariate dendrochronological studies (Williams et al. 2013), other large-scale meta analyses have noted that VPD may not improve predictive power over other climate metrics (Iio et al. 2014, Law et al. 2019, Grossiord et al. 2020).

Despite their widespread use in ecological analyses, our results highlight that flexible nonlinear methods, such as generalized additive mixed models, can reveal unexpected responses in tree-growth data. As *Tsuga canadensis* precipitation sensitivity and *Acer rubrum* temperature sensitivity demonstrate, even if canopy trees

show a linear climate response, understory trees of the same species may display a nonlinear trend (Fig. 3). Traditional methods for analyzing tree-ring data often rely on a priori detrending methods, often through the use of splines, to remove nonlinear growth trends related to age, size, or exogenous disturbance, ideally leaving a linear relationship with climate to explain residual interannual variability (Cook and Peters 1997, Peters et al. 2015). However, many physical and chemical processes underlying biological processes are nonlinear as well as emergent responses of tree growth to interacting effects of soil nutrients and climate (Farquhar et al. 1980, Ryan and Waring 1992, Burkett et al. 2005, Bonan 2008, Lombardozzi et al. 2015). Our method accommodates nonlinear responses to multiple climate influences but may still be subject to the challenges of disentangling covarying long-term trends in ecological data (Cade 2015; Rollinson et al., *in press*). As climate conditions continue to change under anthropogenic radiative forcing, nonlinear and multivariate methods that can accommodate a variety of phenomena such as compounding effects or threshold responses are essential analytical tools across ecological disciplines (Liang and Camarero 2018, Moore 2018; Rollinson et al., *in press*).

Field-based ecological studies are often complicated by unbalanced representation of data, and such non-ideal data distribution can pose analytical challenges due to variation in climate conditions (Canham et al. 2018) or disturbance histories (Rydval et al. 2018). In our study, species and canopy positions were unevenly distributed between sites (Appendix S1: Table S1), but 86% of our site exclusion models indicated that allowing species' response to climate to vary by canopy position is statistically justified based on AIC, and 100% of models based on other metrics of model performance (Appendix S1: Table S3). Although balanced studies with even group representation across species, sites, and canopy positions would be statistically ideal, it is an unachievable benchmark for empirical studies without biasing sample representation. In our study, GAMMs allowed the uncertainty associated with climate response and sensitivity to vary across the range of climate conditions observed for each species and canopy position based on the data density (Appendix S1: Fig. S7).

Consideration of variation in climate sensitivity of tree growth throughout the vertical canopy profile is important for understanding and describing potential forest responses to climate variability and change. Individual-level variation in climate sensitivity is important for describing species responses to climate (Canham et al. 2006, Clark et al. 2012, Rollinson et al. 2016), and we demonstrate that relative canopy position is an important factor that can be readily assessed in the field (Bechtold and Randolph 2018). Species showed considerable variability in their climate responses, but understory trees generally showed more cohesive responses to climate variables, particularly negative effects of increasing temperatures on relative growth and insensitivity to

VPD (Fig. 3). The microclimatic and ecophysiological mechanisms behind canopy position-based differences in climate sensitivity warrant more investigation and will be important for providing pathways for integrating competition effects into forest simulations used to project forest responses to climate change (Price et al. 2001, Fisher et al. 2018).

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