

Quantifying climate–growth relationships at the stand level in a mature mixed-species conifer forest

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Abstract

A range of environmental factors regulate tree growth; however, climate is generally thought to most strongly influence year-to-year variability in growth. Numerous dendrochronological (tree-ring) studies have identified climate factors that influence year-to-year variability in growth for given tree species and location. However, traditional dendrochronology methods have limitations that prevent them from adequately assessing stand-level (as opposed to species-level) growth. We argue that stand-level growth analyses provide a more meaningful assessment of forest response to climate fluctuations, as well as the management options that may be employed to sustain forest productivity. Working in a mature, mixed-species stand at the Howland Research Forest of central Maine, USA, we used two alternatives to traditional dendrochronological analyses by (1) selecting trees for coring using a stratified (by size and species), random sampling method that ensures a representative sample of the stand, and (2) converting ring widths to biomass increments, which once summed, produced a representation of stand-level growth, while maintaining species identities or canopy position if needed. We then tested the relative influence of seasonal climate variables on year-to-year variability in the biomass increment using generalized least squares regression, while accounting for temporal autocorrelation. Our results indicate that stand-level growth responded most strongly to previous summer and current spring climate variables, resulting from a combination of individualistic climate responses occurring at the species- and canopy-position level. Our climate models were better fit to stand-level biomass increment than to species-level or canopy-position summaries. The relative growth responses (i.e., percent change) predicted from the most influential climate variables indicate stand-level growth varies less from year-to-year than species-level or canopy-position growth responses. By assessing stand-level growth response to climate, we provide an alternative perspective on climate–growth relationships of forests, improving our understanding of forest growth dynamics under a fluctuating climate.

KEYWORDS

biomass increment, canopy position, climate change, dendrochronology, forest carbon cycle, Howland Forest, tree growth response

1 | INTRODUCTION

Understanding forest response to a changing climate requires that we identify the climate variables most strongly influencing forest demographics, including tree growth rates. However, quantifying climate–growth relationships in forest systems presents numerous challenges due to the diverse factors that influence tree growth response. For example, response to climate varies among tree species (Drobyshev, Gewehr, Berninger, & Bergeron, 2013; Friedrichs et al., 2009), among canopy positions (Martín-Benito, Cherubini, Del Río, & Cañellas, 2008), among individuals within a tree species (Foster, Finley, D'Amato, Bradford, & Banerjee, 2016), by tree size or age (Foster et al., 2016; Mérian & Lebourgeois, 2011), across competition gradients (Sánchez-Salguero et al., 2015), across a range of stand densities (D'Amato, Bradford, Fraver, & Palik, 2013), among soil conditions (Edvardsson et al., 2015; Gewehr, Drobyshev, Berninger, & Bergeron, 2014), and among elevations (Primicia et al., 2015). In addition, within a given site, gradual changes in stand development interact with climate to govern long-term variability in tree growth (Kardol, Todd, Hanson, & Mulholland, 2010; Primicia et al., 2015).

Although these and other recent studies have shed much light on drivers of annual variability in tree growth, very few studies have evaluated the influence of climate on growth at the level of the forest stand, as opposed to individual trees or species (but see D'Amato et al., 2013; Foster, D'Amato, & Bradford, 2014). When individual tree growth is aggregated to the stand-level, small annual changes could result in substantial interannual variability in stand-level growth, and in mixed-species stands it may reveal that stand-level growth responds somewhat differently to climate than do the component species. Because forest management typically operates at the stand level, we argue that stand-level growth analyses provide a more meaningful assessment of forest vulnerability to climate fluctuations, as well as the management options that may be employed to sustain forest productivity (Clark et al., 2016; D'Amato et al., 2013).

Much of the previous work on climate–growth relationships has relied on dendrochronological (tree-ring) methods because such data provide long-term information with annual resolution. Tree-ring series from a given species are routinely standardized in such studies, a process whereby long-term size- or age-related growth trends are removed from individual tree-ring series, resulting in a unitless index of annual growth (Cook, 1987). These standardized chronologies are then combined (within a species) to produce a single species-specific chronology (e.g., Biondi & Qeadan, 2008). The resulting chronology is used to investigate correlations with climate variables using as many years as possible and employing a variety of statistical analyses.

Recent work has proposed an alternative to the traditional tree-ring analyses, namely the use of annual volume or biomass increments (also derived from tree-ring series; Bouriaud, Bréda, Dupouey, & Granier, 2005; Lara, Bravo, & Maguire, 2013; Foster et al., 2014) instead of ring widths. This approach produces time series in units typical of ecological studies, thus making them compatible with a

large body of literature addressing forest productivity, particularly when expressed on a per-unit-area basis. Further, biomass increments can be directly summed by species or by area without the need for standardization to remove tree size-related trends in radial growth as done in traditional dendrochronology techniques (Foster et al., 2016). That is, summing annual biomass increments from trees within a stand inherently weights trees based on their rate of biomass accumulation: trees accruing more biomass are thus more influential on stand-level growth. Thus, species- or stand-level biomass increment, in comparison to traditional standardized ring-width chronologies, may be more informative for assessing climate effects on overall forest growth (see Foster et al., 2016).

Another common procedure used in dendrochronological studies involves sampling relatively large, presumably old trees whose growth is limited by a particular resource of interest (e.g., water stress in an arid environment). Individual trees are often nonrandomly selected for sampling in environments that support fewer trees to avoid the confounding factors of tree–tree competition. These sampling strategies are intended to maximize the climate signal of interest, and by doing so they have provided invaluable insights into past climate variability (Lara & Villalba, 1993; Sheppard, Comrie, Packin, Angersbach, & Hughes, 2002). While these techniques are suitable for climate reconstructions, they likely do not capture the range of growth patterns of trees occurring in typical forest systems (Carrer, 2011; Foster et al., 2016; Nehrbass-Ahles et al., 2014). Assessing factors influencing climate–growth relationships for forest systems, particularly complex systems of mixed-species composition and stratified canopies, requires an alternate sampling strategy, particularly where the intent is to evaluate stand-level growth response.

Our specific objectives in this study were to (1) identify the climate variables that most strongly influence stand-level, species-level and canopy-position biomass growth, and (2) quantify the magnitude of biomass growth response under the observed ranges of climate variables. We hypothesized that each species would respond to a unique set of climate variables, and that the stand as a whole would respond to some combination of species-level response variables. We also hypothesized that growth of lower canopy positions (i.e., suppressed and intermediate) would be less sensitive to climate fluctuations than the upper positions (i.e., dominant and codominant) because the latter have greater water needs (D'Amato et al., 2013; Martín-Benito et al., 2008) and may be more negatively affected by drought (Bennett, McDowell, Allen, & Anderson-Teixeira, 2015). Lastly, we hypothesized stand-level growth would be buffered from climate extremes by individualistic responses among species and canopy positions, and therefore show growth responses of lesser magnitude than those at the species-level to the most influential climate variables.

We conducted this work at the Howland Research Forest, a mixed-species (*Picea rubens*–*Tsuga canadensis*), multiaged forest of central Maine, USA. This site conveniently provides a mix of species and canopy positions with potentially different climate responses, and it includes a relatively long-term permanent-plot and associated

detailed climate data. We selected trees for coring based on a random stratified (by species and size class) method, which ensured a representative sample of our study site (Nehrbass-Ahles et al., 2014), and we then summed the resulting annual biomass increments to assess annual variability in stand-level growth. Our approach benefits from a relatively flexible unit of measure (i.e., annual biomass increment), which may be calculated at different levels of organization (i.e., stand-level, species-level, and canopy position). Viewing forest growth at these levels yields information on the dynamic nature of climate–growth relationships, and it provides insights into the applicability of these methods in complex mixed-species forests. In addition, models projecting future forest productivity may benefit from these alternative perspectives of climate–growth relationships, because plant physiological response to climate is sometimes misrepresented by ecosystem models (Richardson et al., 2012).

2 | MATERIALS AND METHODS

2.1 | Site description

The Howland Research Forest of central Maine, USA, is located in the transition zone between the eastern deciduous forest and the boreal forest in eastern North America. The climate is damp and cool, with average annual temperatures of $5.9 \pm 0.8^\circ\text{C}$ and mean precipitation of 112 ± 21 cm/year that is evenly distributed throughout the year. The warmest month is July with an average temperature of 19.7°C , and the coldest month is January with an average temperature of -9.6°C . Mean elevation at the site is 60 m above sea level. Soils are spodosols, formed in well- to poorly drained glacial till with little change in elevation. The site supports a mature mixed-aged, structurally diverse spruce–hemlock forest, consisting of roughly 90% conifer, and 10% deciduous tree species (Hollinger et al., 1999). The most abundant species are red spruce (*Picea rubens*), eastern hemlock (*Tsuga canadensis*), northern white-cedar (*Thuja occidentalis*), red maple (*Acer rubrum*), and white pine (*Pinus strobus*). The site has evidence of previous logging (evenly distributed, well-decayed cut stumps), but has been unmanaged for roughly a century.

2.2 | Field data collection

We measured tree growth on a 3-hectare mapped forest plot ($150 \text{ m} \times 200 \text{ m}$) established by the Laboratory for Terrestrial Physics at NASA's Goddard Space Flight Center (see Ranson et al., 2001; Weishampel, Sung, Ransom, LeJeune, & Shugart, 1994). In 1989, all trees ≥ 3.0 cm diameter at breast height (DBH) were mapped, measured (DBH and height), and tagged using a unique identification number, recording ca. 7,800 stems. This large mapped plot is subsequently referred to as the NASA plot. In 2015, we remeasured all living and dead standing trees >10 cm at breast height (DBH, 1.37 m) in the NASA plot (Table 1) and assigned one of four canopy positions to each tree (dominant, codominant,

TABLE 1 Species composition and sampling of all living trees ≥ 10 cm DBH in the 3-ha NASA plot. Sample size refers to the total number of cored trees used for the analysis

Species	Living trees	Sample size	Mean DBH \pm SD (cm)	Maximum DBH (cm)
<i>Picea rubens</i>	1,395	142	20.1 ± 7.1	45.2
<i>Tsuga canadensis</i>	868	88	20.5 ± 8.1	50.1
<i>Thuja occidentalis</i>	336	35	18.8 ± 6.4	40.9
<i>Acer rubrum</i>	281	31	18.2 ± 6.7	41.3
<i>Pinus strobus</i>	153	17	33.3 ± 17.2	68.5
<i>Abies balsamea</i> ^a	65	8	11.7 ± 1.5	16.9
<i>Betula alleghaniensis</i> ^a	13	2	25.8 ± 12.5	56.3
<i>Betula papyrifera</i> ^a	12	2	19.0 ± 7.5	31.5
All species (stand)	3,123	325	20.4 ± 8.7	68.5

The mean and maximum diameter at breast height (DBH) is reported for all trees in the plot. Species marked with asterisks (^a) were excluded from species-level analyses due to low abundance.

intermediate, or suppressed; Smith, Larson, Kelty, & Ashton, 1997). A subset of the living trees (ca. 10%) were selected for coring in a random stratified (by species and diameter class, using 10–20, 20–30, >30 cm classes) manner for detailed growth analysis, resulting in 325 trees. The stratified random sampling technique ensured a representative sample of trees in the stand. The selection reflected the size distribution and abundance of each species in the NASA plot, ranging from overstory dominant to understory suppressed. We extracted one increment core from each selected tree at breast height with a standard 5.2 mm diameter increment borer. Cores were air-dried and secured to wooden mounts, then sanded and polished using increasingly fine sandpaper. We measured ring widths to the nearest 0.01 mm using a Velmex sliding stage (Velmex Inc., Bloomfield, NY, USA) with MeasureJ2X software (VoorTech Consulting, Holderness, NH, USA) and stereomicroscope. We performed cross-dating using species-specific marker years, usually light (narrow band of latewood) or narrow rings, followed by statistical confirmation using COFECHA software (Holmes, 1983).

Tree ring-width measurements were used to back-calculate diameters for every year since 1982, corresponding to the first year detailed weather data are available. First, we estimated inside bark diameters using species-specific bark factors (Dixon & Keyser, 2011). When possible, we compensated for off-center piths by adjusting ring widths, so that cumulative ring width equaled half the inside bark diameter in 2015, following methods and justification presented by Frelich (2002). We sequentially subtracted ring widths from 2015 inside bark diameter to estimate each year's diameter inside bark. We then added predicted bark thickness back to each year's inside bark diameters for use in allometric equations. We estimated whole-tree biomass for each cored tree from 1982 to 2015 using Young's locally developed whole-tree allometric equations (Young, Ribe, & Wainwright, 1980) which include the bole, branches, leaves, and coarse roots. Young's equations estimate whole-tree dry biomass directly, without the need to convert volume to mass, as required by

other allometric equations. Using diameter-based allometric equations assumes that whole-tree biomass increment is responding proportionally to ring width; it does not account for potential variation in growth allocation in response to resource availability (e.g., fine root production in response to a drought). We then summed annual biomass increments from the cored trees at the species and stand level for each year from 1982 to 2015. Summing annual biomass increments maintains the signals from individual trees while homogenizing the effect of tree-level factors such as tree size and crowding. Species-level biomass increments thus represent the relative annual contribution of that species to the total stand-level biomass increment.

2.3 | Climate data collection

We considered a wide variety of climate variables for analysis. Daily temperature (minimum, mean, and maximum), total precipitation, and vapor pressure deficit were summarized for each season from 1982 to 2015 using the interpolated PRISM gridded climate dataset (Daly et al., 2008). Potential evapotranspiration was calculated using methods presented by Hargreaves and Samani (1982) and converted to precipitation divided by potential evapotranspiration (P/PET). P/PET values >1 generally indicate adequate moisture, while values <1 indicate moisture deficit. Growing degree days were calculated using a baseline temperature of 5°C. Stream flow data from the Penobscot River at West Enfield were collected through the USGS National Water Information System from 1982 to 2015 (U.S. Geological Survey 2016) and used as an index of water availability. All climate variables were summarized at the seasonal level, characterized by three-month intervals beginning in the previous spring (previous March to previous May) to current summer (June to August), resulting in six seasons for each climate variable. We chose a 33-year period for our analyses (1983 to 2015) based on the temporal extent of daily information available through the PRISM gridded dataset. We acknowledge the uncertainty arising from unknown growth of trees that died prior to 2015, which becomes increasingly limiting as we extend further back in time; we return to this topic under *Uncertainties*, below. The full list of climate variables used for analysis is presented in Table 2.

TABLE 2 Climate variables used for stand-level, species-level and canopy-position analyses. Where appropriate, climate variables were summarized for each 3-month season, including the previous year

Variable	Abbreviation	Units
Average maximum daily temperature	Tmax	°C
Average mean daily temperature	Tmean	°C
Average minimum daily temperature	Tmin	°C
Growing degree days	GDD	°C
Total monthly precipitation	Precip	cm
Vapor pressure deficit	VPD	kPa
Precipitation over potential evapotranspiration	P/PET	cm
Streamflow (Penobscot River at Enfield)	Flow	m ³ /s

2.4 | Statistical analysis

Our intent was to assess the influence of various climate variables in controlling the annual variability of stand-level biomass growth (sum of biomass increment from all individuals of all eight species), species-level biomass growth (sum of biomass increments from individuals of that species), as well as canopy position (sum of biomass increments from individuals in each of four canopy positions: dominant, codominant, intermediate and suppressed, regardless of species). To remove long-term growth trends that may be related to factors other than climate (e.g., competition or stand dynamics), we created a standardized index for the biomass increments summarized at the stand-level, species-level, and canopy position by dividing the observed annual total growth by fitted total growth based on a linear regression of biomass growth increments over time. This step reduces the chance of observing spurious relationships between co-occurring trends in tree growth and climate, and it allows us to report the relative influence of each climate variable on tree growth as a percentage.

Given the large number of potential covariates, the likely strong correlations among them, and possible nonlinear relationships, a non-parametric variable selection method was used prior to the final parametric approach. For each level of annual biomass increment (stand-level, species-level, and canopy position; the response variables), we screened the large set of previous- and current-year climate variables using the random forest variable selection method coded in the VSURF package (Genuer, Poggi, & Tuleau-Malot, 2015) in R (R Core Team, 2017). This method calculated importance values and out-of-bag error for all climate variables, and eliminated variables that were unimportant for predicting biomass increment based on a data-driven threshold for variable importance. We used the default parameters from the VSURF model (Genuer et al., 2015), which uses a variable importance score averaged over 50 forests with 2,000 trees, five variables per node, and an approximate 35% out-of-bag sample. This process narrowed our selection to ca. 10–20 variables for each response level.

Using these selected climate variables, we tested the effect of each individual climate variable on biomass increment using generalized least squares (GLS) regression (nlme package in R). We eliminated the variables that did not have significant relationships ($p < .05$) with biomass increment, and ranked the variables based on the model's corrected Akaike's information criterion (AICc) scores (subsequently referred to as AIC). With the remaining climate variables demonstrating significant relationships, we used a stepwise, forward selection regression procedure to build multivariate regression models with different combinations of seasonal climate variables that retained significant relationships following inclusion of other variables. We avoided using collinear variables (e.g., precipitation and P/PET from the same season) by selecting ones that best fit the multivariate models based on AIC scores, allowing us to determine which models, and hence which climate variables (including meaningful interactions), were best supported by the data (Burnham & Anderson, 2002). We selected the final multivariate model for each

level of biomass increment based on the lowest AIC scores. We used a second-order autoregressive process to account for temporal autocorrelation. Each model was tested to ensure it met the general assumptions of GLS models, including the distribution of residuals. To prevent model overparameterization and avoid collinearity, we also tested each variable's variance inflation factor (except in models with interactions). Model fit for each of the response levels was evaluated using pseudo R^2 (correlation of predicted vs. observed growth; Canham, Lepage, & Coates, 2004) and root mean square error (RMSE).

The fact that the predictor variables differed between our climate-growth analyses and the traditional dendrochronological analyses precludes any direct comparison between the two. Specifically, to avoid overfitting our regression models, we condensed monthly climate variables (predictors) into four seasonal variables; in contrast, the standard dendrochronological analyses, as well as the various associated software packages (Biondi and Waikul 2004, Bunn, 2008; R Core Team 2017), require monthly values as input. Our methods also differ in that (1) our response variable is the sum (by species or stand) of annual biomass increments, whereas typical response-function analyses use averages of standardized ring widths, and (2) our analyses rely on least squares regressions, whereas the typical dendrochronological analyses employ bootstrapped response-function analysis (see Biondi and Waikul 2004). Further, sampling typically used in dendrochronological analyses of climate-growth relationships excludes trees in subcanopy positions, whereas our sampling purposefully employed trees of all canopy positions. Nevertheless, in an attempt assess similarities between the two approaches, we compared climate responses using species-level biomass increment (our approach) to those of the standardized species-level ring-width chronologies (more traditional approach), in both cases using GLS regression. To facilitate the comparison of our approach to the traditional analysis, we excluded trees in the intermediate and suppressed canopy positions. Following the traditional approach, we standardized ring-width series using a 67% cubic smoothing spline curve (dplR package in R). We averaged the ring-width indices to produce species-level chronologies and tested these chronologies in the same GLS regression models used for biomass increment. Doing so allowed us to assess the efficacy of biomass increment in comparison to traditional techniques. We return to this topic in the Discussion.

Finally, to demonstrate the potential magnitude of stand-level, species-level and canopy-position biomass growth changes attributable to the selected climate variables, we modeled the percent annual change in biomass accumulation across the full range of observed climate variables. We thus report how stand-level, species-level, and canopy-position biomass growth respond to climate fluctuations based on the range of recorded seasonal measurement over the 33-year period (1983 to 2015) using the GLS regression models described above. By addressing the percent change in biomass increment in this manner, we can quantify the effect of climate variability at these various levels to better understand factors influencing biomass accumulation rates.

2.5 | Uncertainties

Although we believe our stratified random sampling strategy produced results representative of the forest at Howland, we note that the biomass increment responses are heavily influenced by large trees. That is, large trees accumulate disproportionately more biomass than smaller trees (Stephenson et al., 2014), and therefore have greater influence on stand-level biomass gain. This natural weighting system was appropriate for our intended purpose, namely to quantify the annual variability in stand-level biomass increment. However, while these methods are appropriate for the purpose employed here, they are not necessarily applicable for generalizations across individual trees of different diameters. For example, large diameter trees may have a higher water demand than small trees per unit area (D'Amato et al., 2013; Mérian & Lebourgeois, 2011), and we predict stand-level increments in stands dominated by large trees are likely more sensitive to water stress than those dominated by smaller trees.

As mentioned previously, the unknown growth of trees that died during our period of interest (1983 to 2015) creates uncertainty in our stand-level, species-level, and canopy-position reconstructions of biomass growth. This limitation has persistently plagued ecological studies using tree rings, because most such studies rely on individuals that have survived to present day. Numerous authors have pointed to the challenges created by unknown past mortality, such as estimating tree longevities, forest age structure, forest disturbance rates, and growth rates (e.g., Foster et al., 2014; Fox, 1989; Frelich, 2002; Johnson, Miyanishi, & Kleb, 1994). We observed in our data that the majority of trees that died since 1989 (plot establishment) were small, suppressed, and presumably slow growing prior to death, meaning that they contributed little to overall forest growth. Thus, we feel that our use of surviving trees provides a depiction of species- or stand-level growth suitable for assessing the influence of climate variables over this time period.

3 | RESULTS

The stand was clearly dominated by *Picea rubens* and *Tsuga canadensis* (Table 1). The stand as a whole had a basal area of 40.6 m²/ha and density of 1,041 trees/ha (considering stems ≥ 10 cm dbh) in 2015, which is typical of this forest type and developmental stage (Puhlick et al., 2016). The diameter distribution, based on the complete inventory, displayed a 'reverse J' form also typical of this developmental stage (Figure 1). As expected, tree biomass was concentrated in the dominant and codominant canopy positions (Figure 2); this distribution is provided to aid in interpretation of the canopy-position analyses (below).

The summed stand-level biomass increment from all cored trees (Figure 3a) illustrates the year-to-year variability in biomass accumulation at Howland Forest. We express these data in total kilograms of dry biomass from the cored trees (10% sample of 3 hectares). Biomass increment peaked in 1986, followed by a steep decline into

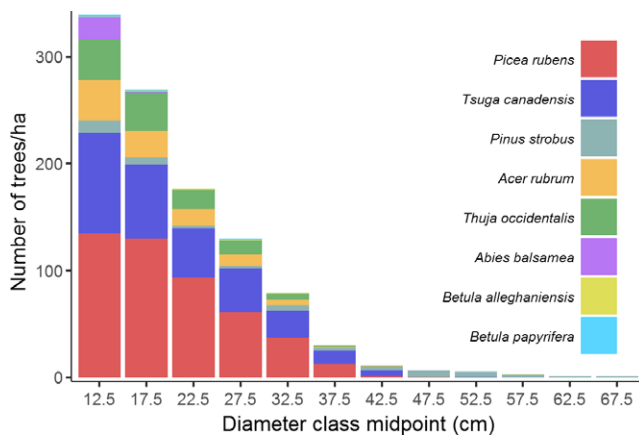


FIGURE 1 Tree diameter distribution of NASA plot in Howland Forest as of year 2015. Colored sections represent the number of trees in each 5-cm diameter class by species

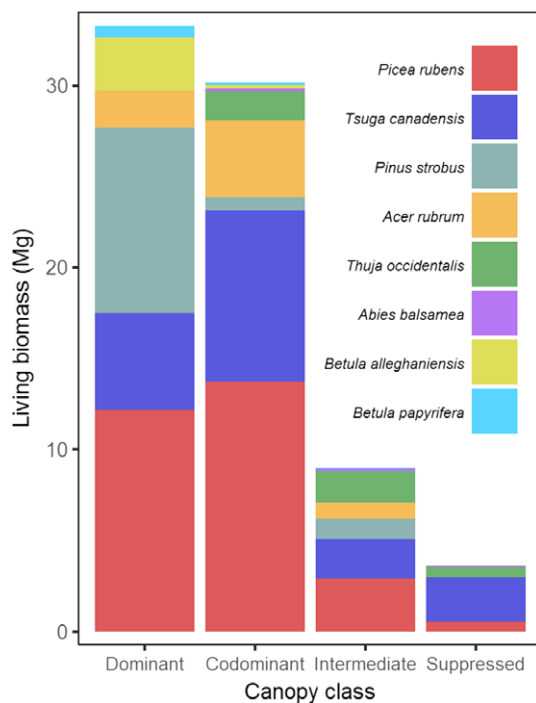


FIGURE 2 Biomass stored in living trees at each canopy position by species in year 2015 based on the randomly selected cored trees (10% sample of the 3-ha NASA plot). Colored sections represent relative amount of biomass in each class by species. The legend is listed in reverse order stacked

the early 1990s and a gradual recovery until a 2010 maximum. Species-level biomass increments represent the relative contributions of each species to stand-level biomass accumulation (Figure 3b). Species displayed different magnitudes of biomass increment and unique year-to-year variability. *Picea rubens* represented the greatest proportion of stand-level biomass accumulation over much of the study period, which is not surprising given that this species represents roughly half of the trees in the stand. In recent years, however, biomass increments for *Tsuga canadensis* and *Pinus strobus* have at times

surpassed *Picea rubens* biomass increments. This trend is particularly striking for *Pinus strobus*: despite representing only 5% of the total stems, in recent years it has contributed to stand-level growth at a rate roughly equivalent to that of the two dominant species (Figure 3b). Biomass increment summed by canopy position (species pooled) demonstrated marked differences in average biomass accumulation and long-term trends among positions (Figure 4). The dominant canopy position's biomass increment had an increasing trend over the sampling period, annually accruing more biomass than any other canopy position, and the highest per tree averages ($7.9 \pm 0.7 \text{ kg tree}^{-1} \text{ year}^{-1}$). Similar to the dominant canopy position, the codominant position demonstrated an increasing trend over the sampling period, and accrued $2.8 \pm 0.3 \text{ kg tree}^{-1} \text{ year}^{-1}$. In contrast, intermediate and suppressed canopy positions had decreasing biomass increment trends over the sampling period and lower average annual biomass accumulation ($1.7 \pm 0.2 \text{ kg tree}^{-1} \text{ year}^{-1}$ and $1.0 \pm 0.2 \text{ kg tree}^{-1} \text{ year}^{-1}$, respectively).

The variable selection process was effective in producing climate models that best fit each standardized stand-level, species-level, and canopy-position annual biomass increment (Table 3). Each of the models listed in Table 3 identified climate variables with significant relationships to tree growth while accounting for second-order autocorrelation, and they explained growth better than other combinations of climate variables (tested using AIC). Log transforming climate variables tended to improve the distribution of residuals and allowed the models to characterize nonlinear relationships. Interestingly, the four conifer species demonstrated significant growth responses to climate variables; however, *Acer rubrum* did not show significant relationships with any of the seasonal climate variables tested.

Several similarities emerged among the most important climate variables for the stand- and species-level analyses (Table 3). Previous summer and current spring climate variables seem to be particularly important predictors for biomass growth. Previous year precipitation (previous summer in particular) variables consistently demonstrated positive relationships with growth (i.e., above average rainfall in the previous growing season consistently produced above average growth). Precipitation and P/PET were strongly correlated, but these variables were not interchangeable; precipitation contributed to the best model for the stand and for *Tsuga canadensis*, while P/PET was better fit for *Picea rubens* and *Pinus strobus* models. Our models also suggest that temperature influences both previous and current year growth. Higher previous summer temperatures were consistently negatively associated with growth (for the stand, *Picea rubens*, *Tsuga canadensis*, and *Thuja occidentalis*), while warm spring temperatures were positively associated with growth (for the stand, *Tsuga canadensis*, and *Pinus strobus*).

Analyses revealed a significant interaction between the previous summer climate variables for *Picea rubens*: the species' growth was highest following cool and damp summers. Similarly, the stand and *Tsuga canadensis* also had the highest growth rates following cool, damp summers. These two levels (stand and *Tsuga canadensis*) shared all three of their most influential climate variables, each also

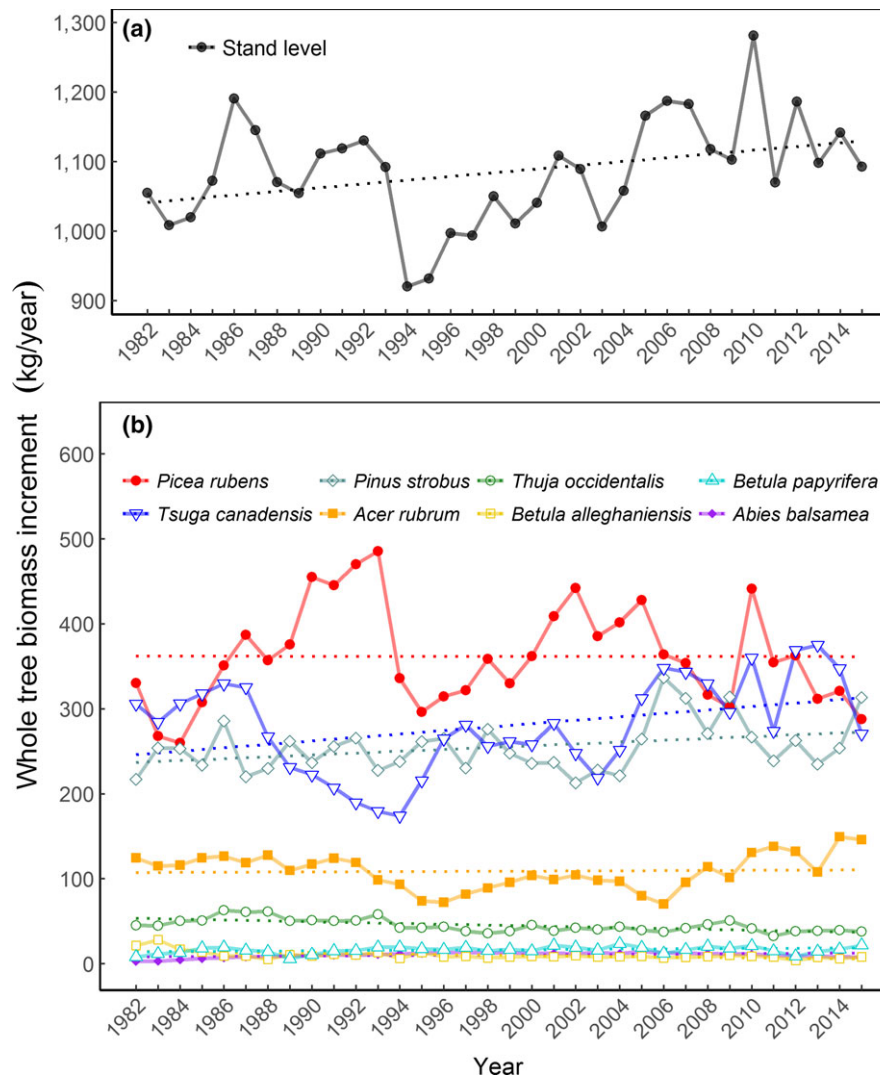


FIGURE 3 Annual stand-level (top panel) and species-level (lower panel) biomass increment summed from cored trees since 1982. Note that the magnitude in growth shown in the lower panel is in part a function of each species' abundance within the stand, given that biomass increments are summed within a species. Fitted linear regression lines (dotted) shown to emphasize overall growth trends

showing positive growth responses to warm spring temperatures. Their models did, however, differ in magnitude of response and error associated with the climate variables, with the *Tsuga canadensis* model having greater error and lower pseudo R^2 associated with growth predictions (Table 3).

Climate responses at different canopy positions (species pooled) also revealed similarities to the stand-level relationships (Table 3). Previous summer precipitation or P/PET had significant positive relationships with biomass increment for all canopy positions (a relationship also documented at the stand-level). Biomass increments for the dominant and intermediate canopy positions demonstrated significant positive relationships with spring temperature variables. Codominant and suppressed canopy positions did not respond significantly to spring temperature; instead, these positions responded negatively to previous summer temperature. In contrast to the stand-level, all canopy positions except the intermediate position demonstrated positive relationships with

previous fall temperatures, a climate variable not among the most influential at the stand- or species-level. Climate models fit all canopy positions fairly well, but pseudo R^2 values were highest among dominant and codominant positions. No canopy position fit the climate data better than did the stand-level biomass increment (Table 3).

The results using the traditional standardized ring widths within our GLS regression approach (using dominant and codominant trees) show very similar climate responses, pseudo R^2 , and root mean square error to our analyses using species-level biomass increment (Table 3 and Table 4). Only one of the climate variables selected for the cumulative biomass increment analyses was not significant using standardized ring widths (maximum daily spring temperature for *Tsuga canadensis*). That is, model selection using standardized ring widths selected the same set of climate variables as those identified for the biomass increment, with the exception of spring temperature for *Tsuga canadensis*.

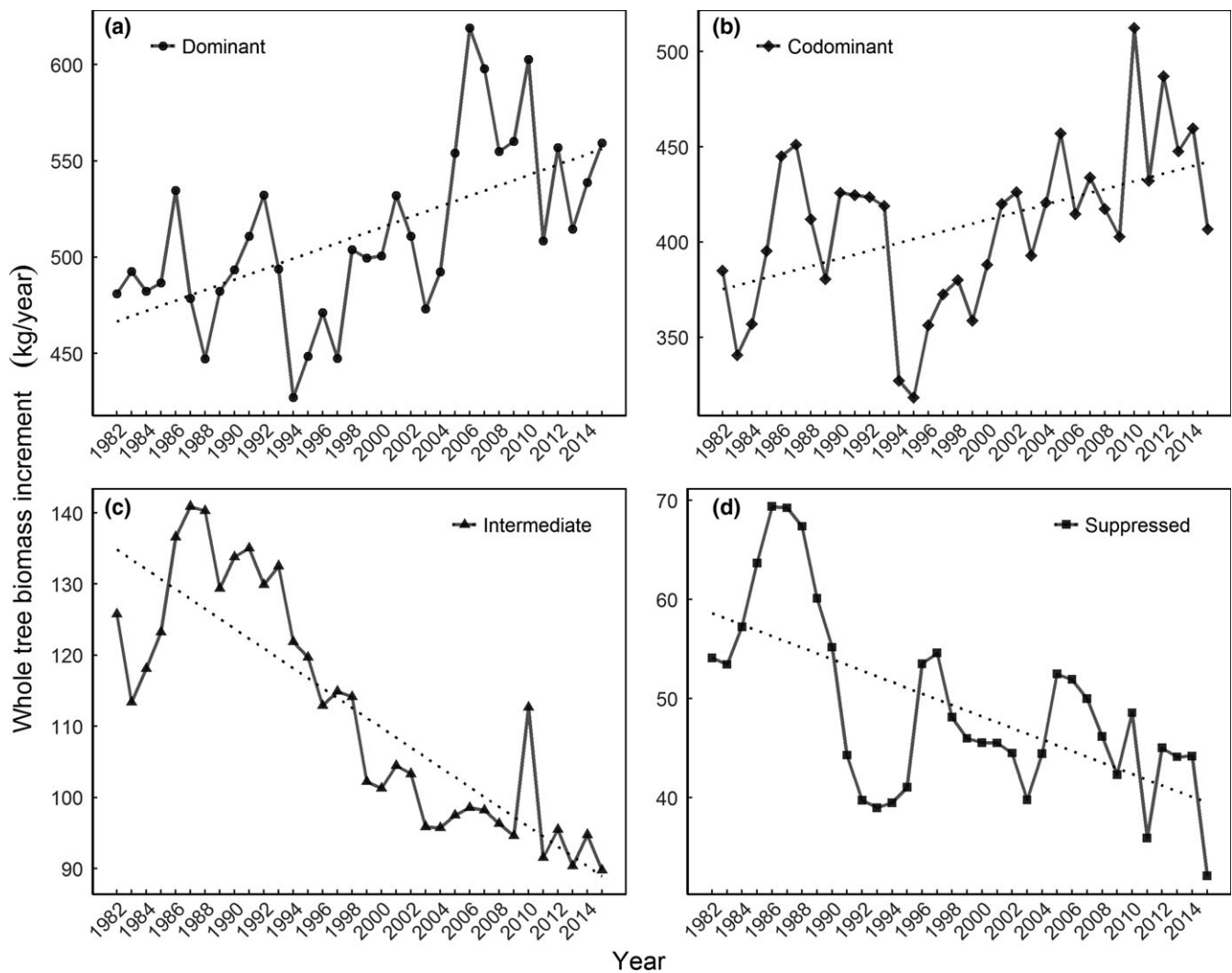


FIGURE 4 Annual canopy-level biomass increment since 1982. Note that the magnitude in growth is in part a function of the abundance within each canopy position, given that biomass increments are summed for all species at a given canopy position. Fitted linear regression lines (dotted) shown to emphasize overall growth trends. Note the scale of the vertical axes differs among panels

To further quantify the effect of the climate variables on biomass growth, we used the models described in Table 3 to determine the percent change in biomass growth (i.e., growth anomalies) in response to observed ranges of the most important climate variables (Figures 5 and 6). Results revealed striking changes in biomass growth resulting from climate variable minima and maxima (observed in this study). For example, a cool, damp summer followed by an average spring can result in 35.1% and 17.1% above average biomass increment for *Picea rubens* and *Tsuga canadensis*, respectively (Figure 5b,c). When compared to the species-level, stand-level growth responses were relatively resistant to climate anomalies, as evidenced by flatter response surfaces (Figure 5a), with less error associated with the responses (Table 3). For example, a hot and dry summer followed by an average spring resulted in a 15.4% growth reduction in *Tsuga canadensis* yet only an 8.5% reduction in stand-level growth.

The magnitude of growth response to influential climate variables differed markedly by canopy position (Figure 6). The dominant canopy position responded with 8.2% greater growth with combined

wet summers and warm falls of the previous year, followed by average spring temperatures. Wet and cool summers followed by warm falls resulted in 20.1% and 18.2% greater growth the following year for codominant and suppressed canopy positions, respectively. The intermediate canopy position demonstrated 9.9% greater growth with a cool, damp summer followed by average spring temperatures.

4 | DISCUSSION

We quantified the effects of annual climate variation on biomass increment summed at the stand-level, species-level, and by canopy position using models containing the most influential climate variables. We explored the applicability of using biomass increment for climate-growth analysis as an alternative to traditional dendrochronology techniques based on ring widths. We also assessed the contributions of species and canopy position to climate response for the stand as a whole. Our results indicate that climate variables differentially

TABLE 3 Model selection displaying the best-fit climate variables for standardized stand-, species- and canopy-level annual biomass increments (the response variables) based on AIC scores, while accounting for second-order autocorrelation

Response level	N	Climate variable	<i>b</i>	SE	<i>p</i> -value	Pseudo <i>R</i> ²	RMSE
Stand	325	Precip <i>p</i> summer	0.123	0.031	.001	.75	0.04
		Tmax spring	0.180	0.061	.006		
		Tmin <i>p</i> summer	−0.349	0.117	.006		
<i>Picea rubens</i>	142	P/PET <i>p</i> summer	11.160	3.745	.006	.39	0.15
		Tmean <i>p</i> summer	−1.984	0.503	<.001		
		P/PET × Tmean	−3.790	1.287	.006		
<i>Tsuga canadensis</i>	88	Precip <i>p</i> summer	0.196	0.051	.001	.46	0.17
		Tmin <i>p</i> summer	−0.597	0.189	.004		
		Tmax spring	0.205	0.097	.043		
<i>Thuja occidentalis</i>	35	Tmax <i>p</i> summer	−1.325	0.425	.004	.61	0.10
		Tmax summer	−1.666	0.426	<.001		
<i>Pinus strobus</i>	17	P/PET <i>p</i> fall	0.139	0.048	.007	.59	0.09
		GDD spring	0.155	0.069	.033		
Dominant	65	P/PET <i>p</i> summer	0.074	0.026	.009	.69	0.05
		Tmax <i>p</i> fall	0.255	0.119	.042		
		GDD spring	0.141	0.030	<.001		
Codominant	147	P/PET <i>p</i> summer	0.170	0.033	<.001	.71	0.08
		Tmin <i>p</i> summer	−0.769	0.151	<.001		
		Tmax <i>p</i> fall	0.550	0.159	.002		
Intermediate	66	Precip <i>p</i> summer	0.082	0.034	.021	.53	0.06
		Tmin <i>p</i> summer	−0.330	0.129	.017		
		Tmax spring	0.148	0.066	.034		
Suppressed	47	P/PET <i>p</i> summer	0.156	0.047	.002	.48	0.13
		Tmin <i>p</i> summer	−0.723	0.209	.001		
		Tmax <i>p</i> fall	0.616	0.227	.014		

Regression coefficients (*b*), standard error (SE), and *p*-values for the generalized least squares regression are based on full models containing the listed variables with log transformations. Model fits for each response level are expressed in pseudo *R*² (correlation between observed and predicted values) and root mean square error (RMSE). Refer to Table 2 for climate variable descriptions. The prefix *p* indicates the variable is from the previous year. Note that *Acer rubrum* showed no significant relationships and is thus not included.

influenced stand-level, species-level, and canopy-position growth, which allowed us to quantify the magnitude of growth variation across observed ranges of these variables. Our approach has a distinct advantage over traditional species-level dendrochronological analyses because it allows us to characterize stand-level growth, which we argue provides a more meaningful assessment of forest vulnerability to climate fluctuations (see also Clark et al., 2016; Foster et al., 2014). Further, unlike traditional dendrochronological approaches, our stratified random selection of trees allowed us to capture a wide range of individual growth responses representative of the stand as a whole (Carrer, 2011). We believe these methods represent a valid approach to testing the effects of climate on stand-level growth.

By first developing stand- and species-level biomass increments, we were able to identify each species' relative contribution to stand-level annual productivity. These species-level contributions (Figure 3b) suggest a temporal shift in relative biomass accumulation at the site. Based on the high abundance of *Picea rubens*, we expected

the species to maintain the highest biomass increment throughout the time series. However, an increase in *Tsuga canadensis* and to a lesser extent *Pinus strobus* biomass increments resulted in an equivalence of these two species with *Picea rubens*, meaning that the three species were contributing similarly to biomass accumulation as of 2015 (Figure 3b). Besides *Tsuga canadensis* and *Thuja occidentalis* (increasing and decreasing trends, respectively, since 1982), other species have shown relatively stable long-term growth. We note the surprisingly high annual biomass contributions of *Pinus strobus*, relative to its low abundance in the stand: although *Pinus strobus* represented only 5% of the stems (and approximately 16% of the stand's living biomass), it accumulated more biomass than any other species in 2009 and 2015. Working in a similar forest type, Fajvan and Seymour (1993) found that *Pinus strobus*, through differences in shade tolerance and height growth, came to dominate the upper canopies when mixed with *Picea rubens* and *Tsuga canadensis*, presumably leading to enhanced growth relative to these associates.

Response level	N	Climate variable	b	SE	p-value	Pseudo R ²	RMSE
<i>Picea rubens</i>	110	P/PET <i>p</i> summer	10.846	3.867	.009*	.45	0.13
		Tmean <i>p</i> summer	-2.165	0.514	<.001*		
		P/PET × Tmean	-3.674	1.328	.010*		
<i>Tsuga canadensis</i>	46	Precip <i>p</i> summer	0.197	0.054	.001*	.42	0.12
		Tmin <i>p</i> summer	-0.578	0.199	.007*		
		Tmax spring	0.184	0.103	.084		
<i>Thuja occidentalis</i>	12	Tmax <i>p</i> summer	-1.162	0.349	.002	.70	0.08
		Tmax summer	-0.069	0.015	<.001		
<i>Pinus strobus</i>	14	P/PET <i>p</i> fall	0.089	0.042	.042*	.49	0.08
		GDD spring	0.142	0.061	.027*		

Regression coefficients (*b*), standard error (SE), and *p*-values for the generalized least squares regression are based on full models containing the listed variables with log transformations. Model fits for each response level are expressed in pseudo *R*² (correlation between observed and predicted values) and root mean square error (RMSE). Refer to Table 2 for climate variable descriptions. The prefix *p* indicates the variable is from the previous year. Note that *Acer rubrum* showed no significant relationships and is thus not included. Asterisks indicate statistical significance.

TABLE 4 Response of standardized ring-width chronologies (using dominant and codominant trees) to climate variables selected in biomass increment analysis (Table 3)

We also documented dramatically different biomass growth trends and magnitudes according to canopy position. The dominant canopy position is composed of inherently large trees that accumulated biomass at much higher rates than trees in other canopy positions. Dominant and codominant canopy positions demonstrated significant increasing trends in biomass increment over the sampling period, yet the intermediate and suppressed positions had decreasing trends over the same period. The more rapid biomass growth in upper canopy positions was expected and is well supported in the literature (e.g., Oliver & Larson, 1996). However, the magnitude of the differences among canopy positions was surprising: the dominant position exhibited biomass increments roughly an order of magnitude greater than the suppressed positions (Figure 4a,d). Although these differences can be explained in part by species abundances (e.g., *Pinus strobus*, the fastest growing species, was most abundant in the dominant position, Figure 2), we note that the other species, particularly the two most dominant (*Picea rubens* and *Tsuga canadensis*), occurred in roughly similar proportions across canopy positions (Figure 2). These results clearly point to the benefits, in terms of increased growth, afforded by greater light availability in the upper canopy.

Results support our first hypothesis stating each species responds to a unique set of climate variables, and the stand would thus respond to a combination of these climate variables. Our results also point to several similarities among the most influential climate variables at the stand-level and species-levels. It is perhaps self-evident that the stand-level biomass increment reacted similarly to that of its dominant component species, which are long-lived and shade-tolerant. That is, *Picea rubens*, *Tsuga canadensis*, and *Thuja occidentalis* seem to be driving the stand-level response to previous summer temperature. These species and the stand as a whole are particularly sensitive to previous summer climate anomalies, when compared to other species (Table 3 and Figure 5). Warm temperatures have been shown to reduce photosynthesis rates of *Picea rubens* (Day, 2000;

Vann, Johnson, & Casper, 1994), and have been associated with growth reductions the following year for *Picea rubens* (Conkey, 1979), *Tsuga canadensis* (Cook & Cole, 1991), and *Thuja occidentalis* (Housset, Girardin, Baconnet, Carcaillet, & Bergeron, 2015).

By aggregating growth from all species, we are inherently homogenizing responses from species with different ecological traits (i.e., shade tolerances). Unlike *Picea rubens* and *Tsuga canadensis*, *Pinus strobus* did not respond significantly to previous summer climate variables, perhaps because its intermediate shade tolerance (the least shade-tolerant of the species assessed) and more southerly range suggest a higher tolerance to warm summers. The positive stand-level response to spring temperature was likely influenced by higher growth of *Pinus strobus* and *Tsuga canadensis*. Growth of cool-weather conifers of North America is thought to be limited by spring temperature (Rossi et al. 2008). Above average spring temperatures are associated with early leaf-out phenology (Morin et al., 2009; Polgar & Primack, 2011) resulting in increased spring photosynthesis rates and ultimately higher annual carbon gain (Black et al., 2000; Hollinger et al., 2004; Keenan et al., 2014). *Acer rubrum* did not demonstrate marked fluctuations in growth in response to spring or summer climate variables. As the species at Howland Forest with the largest geographical distribution, *Acer rubrum* may exhibit greater plasticity to fluctuating climate conditions, and ultimately be more resistant to a changing climate. Previous studies have shown that climate differentially affects co-occurring species (Friedrichs et al., 2009; Miyamoto, Griesbauer, & Green, 2010), thereby corroborating our findings of diverse species-level responses.

Previous work has shown dominant trees to be more responsive to climate fluctuations than trees in lower canopy positions (Martín-Benito et al., 2008; Carnwath, Peterson, & Nelson, 2012; Lebourgeois, Eberlé, Mérian, & Seynave, 2014). We thus hypothesized that upper canopy positions (i.e., dominant and codominant) would be more sensitive to climate fluctuations than the lower positions (i.e.,

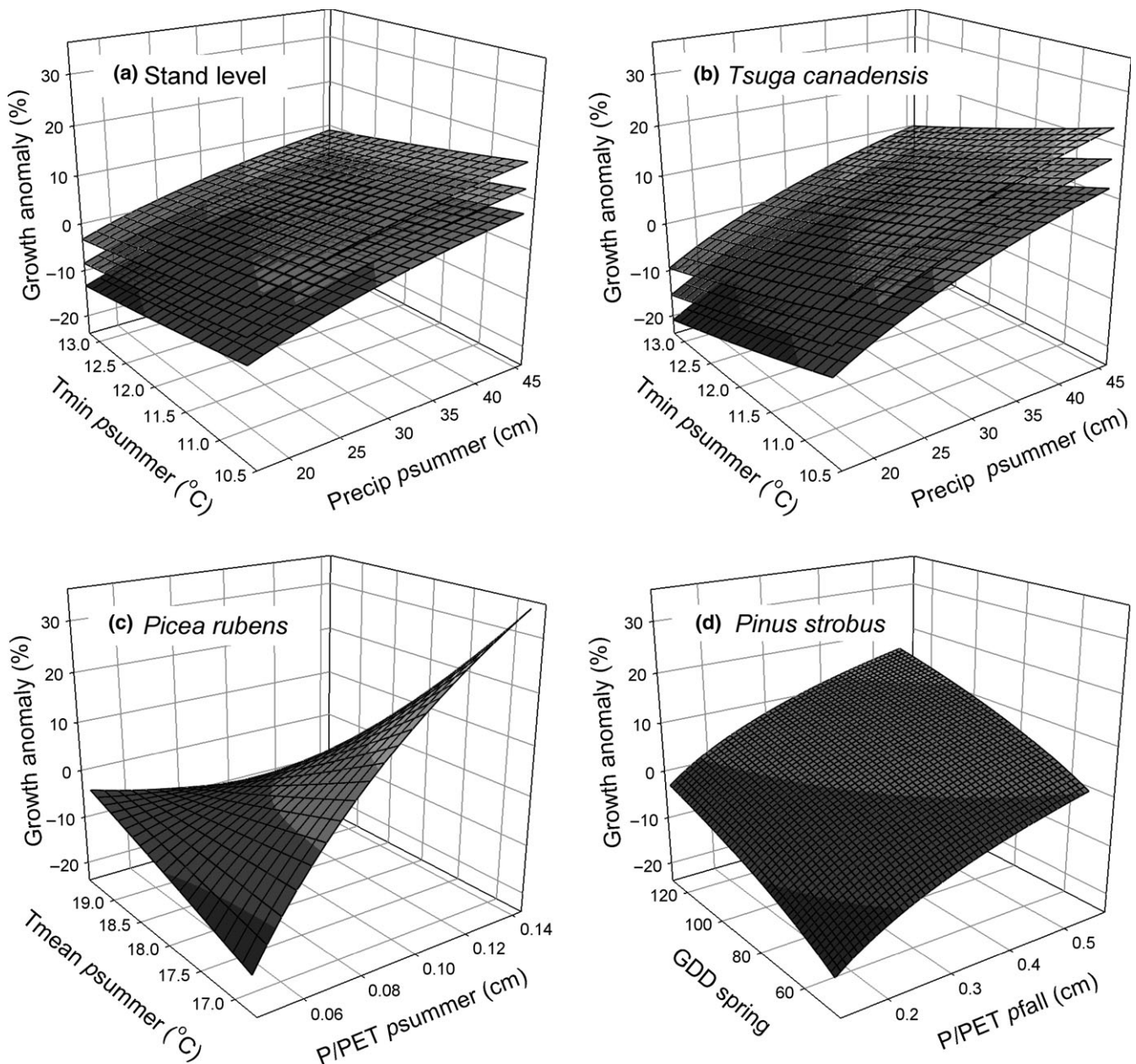


FIGURE 5 Model results demonstrating how growth varies as a function the most important climate variables for the entire stand as well as the three most productive species, *Picea rubens*, *Tsuga canadensis*, and *Pinus strobus*, across the range of observed values for each climate variable. Growth anomaly is the percent deviation from the mean annual biomass increment given a set of climate conditions. For the stand level and for *Tsuga canadensis*, which each had three important climate variables, we show the effect of spring temperature (the third variable) as the series maximum (top), mean (middle), and minimum (bottom) surfaces over the range of observed variables. The prefix *p* indicates the variable is from the previous year; Table 2 provides climate variable descriptions

suppressed and intermediate). Our data did not support this hypothesis: although sensitivity (as assessed by the response surfaces shown in Figure 6) varied among positions, no trend from upper to lower canopy positions was evident. We note that our analysis was confounded by the necessity, given our sample sizes, to pool species for each canopy position, which may have masked potential trends. Canopy positions in general responded to similar climate variables despite having subsets of trees representing different relative species abundances, size distributions, and presumably, levels of

competition. However, as above, the magnitude of responses varied greatly between canopy positions. We suspect the minor differences in climate variable selection and the magnitude of response is in part due to relative species abundances. For example, the codominant and suppressed canopy positions had the highest relative growth response to their most influential climate variables, shared the most influential climate variables, and had the highest relative contribution of *Tsuga canadensis* growth. Likewise, higher abundance of *Pinus strobus* in the dominant canopy position may have influenced the

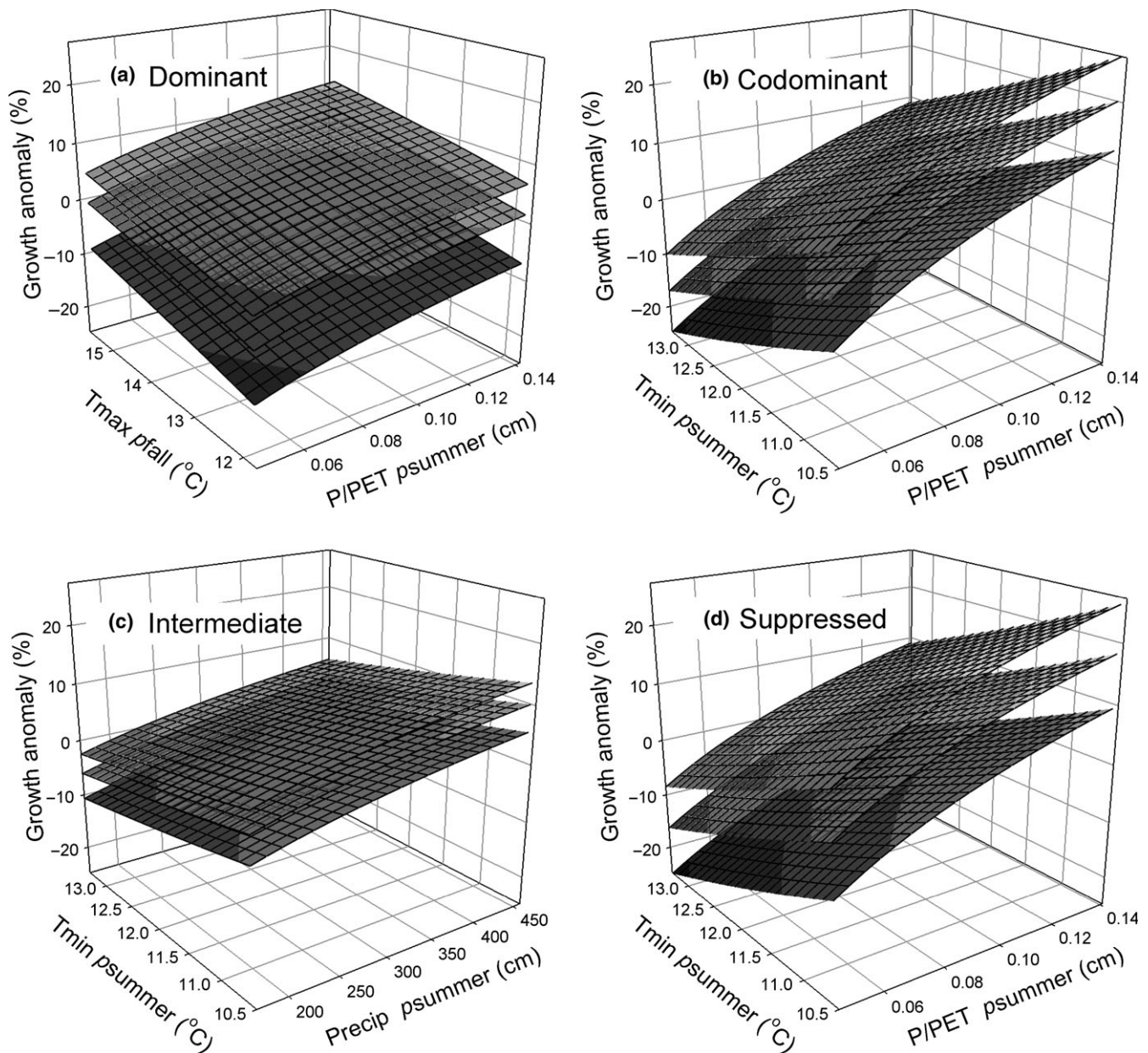


FIGURE 6 Model results demonstrating how growth varies as a function the most important climate variables for the canopy positions (species pooled), across the range of observed values for each climate variable. Growth anomaly is the percent deviation from the mean annual biomass increment given a set of climate conditions. Each canopy position responded significantly to three important climate variables; variation for the third variable is shown as three distinct surfaces. The third climate variable for the dominant and intermediate canopy positions was spring temperature (growing degree days and maximum temperature respectively), and the third variable for codominant and suppressed positions was maximum temperature of the previous fall. These variables are presented as maximum (top), mean (middle), and minimum (bottom) surfaces over the range of observed variables. The prefix *p* indicates the variable is from the previous year; Table 2 provides climate variable descriptions

significant positive relationship with spring growing degree days and the smaller growth responses to extreme summer temperatures. Although our results do not support our hypothesis that upper canopy positions would be more sensitive to climate, our models do suggest that climate is more important for determining growth at the dominant and codominant positions, which have a stronger relationship with climate variables than do intermediate and suppressed positions.

Our final hypothesis stated that stand-level growth would be buffered (i.e., less responsive to climate fluctuations) by individual responses among species as well as canopy positions. Our results support this hypothesis based on the lower magnitude of response the stand has to the most influential climate variables compared to the species-level and canopy-position responses (Figures 5 and 6). Through the different ecological responses provided by this species mix, it appears that stand-level growth is more resistant to climate

fluctuations. The stand-level climate model had the lowest associated RMSE and highest pseudo R^2 (Table 3), suggesting that growth pooled across species, when compared to growth of individual species, is better predicted by climate variables. Similar results were found when model fits from individual canopy positions were compared to those at the stand level.

As stated above, the fact that predictor variables differed between our analyses and the traditional dendrochronological analyses precludes any direct comparison between the two. However, when standardized ring width (as in typical dendrochronological analyses) is substituted for cumulative biomass increment in our GLS regression approach, the results produce very similar climate responses, pseudo R^2 , and RMSEs across species. In fact, these regression diagnostics did not indicate that one metric of tree growth was better fit for the climate data than the other. Only one significant climate variable in the cumulative biomass increment analyses (maximum daily spring temperature for *Tsuga canadensis*) was not significant when evaluated using standardized ring widths. We did not expect these two growth metrics to produce such similar results. Because large trees accumulate biomass at a higher rate, larger trees are inherently weighted higher in biomass increment than in standardized ring widths (where all trees are weighted equally). Excluding trees in lower canopy positions from the traditional approach likely contributed to the close relationship we found. We argue that the similarity in results from these two approaches supports the use of summed biomass increments to address climate–growth relationships at the stand level. D'Amato et al. (2013) similarly found close agreement between analyses of summed stand-level basal-area increments and traditional ring-width analyses when addressing climate–growth relationships. Our approach may not demonstrate substantial improvements over traditional species-level climate–growth analyses in terms of identifying climate variables significantly affecting individual species growth. However, the added rigor of the stratified random sampling ensures a representative sample of the stand, and the use of allometric equations employs units (e.g., Mg/ha) typically used in ecosystem productivity studies. Further, using biomass increment has distinct advantages over the traditional dendrochronological analyses because it (1) allows us to assess climate–growth relationships at the stand level (i.e., the level at which forest management occurs), an important consideration in mixed-species forests, and (2) provides a method to determine the magnitude of various climate drivers on overall growth, illustrating a direct relationship between climate and the carbon balance of the forest on a per-unit-area basis. However, it is important to note that our approach has disadvantages because it (1) requires a detailed forest inventory from which to randomly select representative trees, and (2) is limited to the most recent several decades, due to unknown growth of trees that have died, a problem that compounds as temporal depth is extended.

Both species- and stand-level results show marked fluctuations in biomass growth over the study period. Our results demonstrate that seasonal climate variables explained much of the year-to-year variability, with R^2 values ranging from .38 to .59 at the species level. However, as in other dendrochronological studies of climate–growth relationships, additional factors not apparent in seasonal (or

monthly) climate summaries influence growth (Cook & Briffa, 1990; Foster et al., 2016). For example, *Picea rubens* can be affected by winter injury (i.e., rapid freezing of foliage) in New England (Boyce, 1995), which is known to cause growth reductions in the years following the event (Kosiba, Schaberg, Hawley, & Hansen, 2013). Although this phenomenon is more prevalent at high elevations in the region (Lazarus, Schaberg, DeHayes, & Hawley, 2004) (our site lies at 60 m a.s.l.), we recognize the potential influence of such events on biomass growth and the confounding effect they would have on analyses based on seasonal averages.

In forests not limited by water, climate change may have positive effects on forest productivity (see Boisvenue & Running, 2006). Indeed, other studies have recently documented increased *Picea rubens* growth response to elevated temperature (Kosiba, Schaberg, Rayback, & Hawley, 2017) and to reduced acid deposition inputs (Engel et al., 2016). However, in contrast to these studies, our data suggest we could see declines in *Picea rubens* growth under projected warming trends due to its sensitivity to high-temperatures (Vann et al., 1994; this study). Our results suggest that stand-level growth, through differential responses to climate fluctuations, was stabilized over the observed period owing to a mix of species-level responses. That is, enhanced growth in one species at times compensated for slow growth in another (Figure 3b). Previous studies have shown that maintaining species richness stabilizes ecosystem productivity by increasing community-level resistance to climate extremes (Isbell et al., 2015; Lebourgeois, Gomez, Pinto, & Mérian, 2013), given that species-rich communities have greater functional diversity and thus greater resistance to climate fluctuations. In fact, despite the growth limitations imposed on component species due to previous summer climate variables, stand-level productivity at Howland Forest shows little evidence of stress from recent temperature and precipitation trends. Instead, annual biomass accumulation appears to be increasing (Keenan et al., 2013, this study) as development continues.

A changing climate is likely to affect forest productivity (Boisvenue & Running, 2006; Morin et al., 2009) and alter tree species distributions (Iverson, Prasad, & Matthews, 2008). Although climate–growth relationships are known for many tree species, much remains unknown regarding climate–growth responses of forest stands because of difficulties scaling growth of individuals to trees across sizes, species, and stands. We combined the use of two approaches not typically used in such studies: (1) we collected a large random sample (stratified by size and species) of forest trees for coring, which ensures an adequate representation of the stand as a whole, and (2) we used biomass increment as an alternative to traditional tree-ring chronologies for analyses. Together, these approaches allowed us to clarify the influence of climate on growth at the stand-level, species-level, and by canopy position for a multiaged, mixed-species conifer forest. We demonstrate a direct connection between climate and stand-level biomass growth, which can be expressed on a per-unit-area basis, making it comparable to typical studies of ecosystem productivity. Stand-level growth responds to climate in a manner somewhat similar to that of its dominant species, but stand-level models have lower associated error than those

of individual species. We find that the mix of these tree species confers resistance to climate fluctuations for the stand as a whole, in part due to the differences in climate sensitivity and growth strategies of component species. Of course, past disturbance regulates species composition and stand structure, and therefore has a significant role in resistance to climate fluctuations. The approach described here provides an alternative perspective from the stand-level while still accounting for individual species variability, thereby improving our understanding of forest growth dynamics under a fluctuating climate.

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