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The demography of tree species response to climate: sapling and canopy tree growth

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Abstract. Despite the clear need to predict the effects of climate change on the distribution and abundance of temperate tree species, there is still only a rudimentary understanding of how climate influences key demographic processes that determine the current distribution and abundance of tree species. We use data from the U.S. Forest Service Forest Inventory and Analysis (FIA) program to quantify the relationships between two key climate variables—mean annual temperature and effective growing season precipitation—and rates of sapling and canopy tree growth for the 50 most common tree species in the eastern United States. Our models include the effects of tree size, competition, and anthropogenic nitrogen (N) deposition, both to avoid confounding effects and to provide context for the importance of variation in climate relative to other factors known to influence tree growth. The 50 species show a broad range of relationships between size and growth, in contrast to predictions of metabolic theory. The 50 species differ widely in shade tolerance, and both saplings and canopy trees show a wide range of competitive responses to total stand basal area. The competitive responses of canopy trees were more sensitive than were saplings to the size of an individual relative to the median size of trees in the stand. As has been shown in other studies with FIA data, species responses to N deposition also varied widely and were related to the type of mycorrhizal association of the tree species. Relationships between the two climate variables and tree growth were surprisingly modest, and bore little obvious relationship to the distributions of the species along climate gradients. For over a quarter of the species, there was no statistical support for a relationship between 5-yr average growing season precipitation and 5-yr average growth, and for most of the remaining species, the relationship was effectively flat over a wide range of precipitation. Responses to regional variation in mean annual temperature were stronger, but again showed little obvious correlation with the distribution of abundance of most species along the temperature gradient.

Key words: climate responses of temperate trees; competition; eastern United States; Forest Inventory and Analysis; nitrogen deposition; precipitation; sapling and canopy tree growth; temperature.

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Introduction

Understanding the effects of climate change on the geographic distribution and abundance of tree species and the functioning of forest ecosystems has important ecological and economic implications. Paleoecological studies have provided much of the scientific foundation for our understanding of the relationships between climate (and climate change) and tree species distribution and abundance (e.g., Jackson and Whitehead 1991, Prentice et al. 1991, Williams et al. 2004). The expectation of unprecedented rates of climate change during this century has prompted efforts to develop a variety of model-based assessments to predict future changes in the distribution of tree species and forest ecosystems. The models fall into three general classes: (1) process models based on ecophysiology and biogeochemistry (e.g., Sitch et al. 2008, Tang and Beckage 2010), (2) statistical models that relate the current geographic distribution of species and ecosystems to climate variables (e.g., Sykes and Prentice 1996, Iverson and Prasad 1998, Thompson et al. 1998, Box et al. 1999), and (3) population dynamic models that incorporate the effects of climate on the demography of component species (e.g., Bugmann 1996, Scheller and Mladenoff 2005). The three approaches have very different empirical foundations and lead to very different projections of future distributions of tree species under climate change (Loehle and LeBlanc 1996, Iverson and Prasad 1998, Bolliger et al. 2000, Tang and Beckage 2010).

Despite a pressing need to be able to predict the effects of climate change on the distribution and abundance of temperate tree species, we still have only rudimentary understanding of how ecophysiological and demographic processes determine the current distributions of those species, and how different aspects of climate influence key ecophysiological and demographic processes that determine the abundance of tree species (Holt et al. 2005, Parmesan et al. 2005). It seems clear that climate must play a preeminent role in at least the range boundaries of temperate tree species (Simova et al. 2015), but it is much less clear how important climate is in determining the spatial distribution and abundance of a species within its range, particularly given the myriad other factors that influence the presence and abundance of tree species within a stand (Morin et al. 2007, Canham and Thomas 2010). There is also a growing recognition that temperate tree species distributions are likely to be in disequilibrium with current climate, given long generation times for temperate trees and pervasive human impacts and natural variation in climate over the past millennium (Canham 2014, Jackson and Blois 2015).

The limitations of statistical "climate envelope" models have been widely debated, particularly their potential to overestimate future shifts in species distributions under climate change, largely because of the assumption that species can track climate change without time lags (Davis et al. 1998, Jeschke and Strayer 2008). A number of studies have pointed out that early versions of both process and population dynamic models also suffered from this limitation because of fundamental flaws in the assumptions about the nature of the direct effects of climate variables (particularly temperature) on tree growth and survival (e.g., Pacala and Hurtt 1993, Loehle and LeBlanc 1996). Schenk (1996) reviewed early approaches to modeling temperature effects on growth and survival, and concluded that very few of the models were based on assumptions and processes that were consistent with the empirical research on temperature effects on plant performance. More recent models have sought to address these concerns through more detailed mechanistic models of ecophysiological processes (e.g., Ise and Moorcroft 2010, Gustafson et al. 2015). We suggest, however, that the most significant current limitation in our ability to refine the predictions of the impacts of climate change on the distribution of tree species is that rigorous empirical analyses of the effects of climate on tree growth and survival have lagged far behind the models (Saxe et al. 2001, Way and Oren 2010).

Networks of national forest inventory plots have become an important source of data for analysis of the distribution and dynamics of tree species (e.g., Iverson and Prasad 1998, Canham and Thomas 2010, Lichstein et al. 2010, Thomas et al. 2010). Here, we use data from the U.S. Forest Service Forest Inventory and Analysis (FIA) program to quantify the relationships between two key climate variables and rates of sapling and canopy tree growth for the 50 most common tree species in the eastern United States, across the full range of climatic conditions present within that region.

Methods

Study region, plots, and species

Plot and tree data were obtained from the website of the U.S. Forest Service FIA program (http://apps.fs.fed.us/fiadb-downloads/datamart.html, data downloaded in September of 2012) for the 31 eastern U.S. states (all states east of Minnesota south to Louisiana). We used data from plots censused under the nationally standardized (annualized) protocols established in 1999 (Woudenberg et al. 2010), although some states used effectively the same design prior to that, so the census years in our compiled data set ranged from 1998 to 2012. For each state, we selected census cycles for which both the current and previous censuses were conducted using the new national standard plot design, to allow determination of plot and tree conditions at the time of the previous census. We then used average annual diameter growth (change in diameter between the two censuses, divided by the census interval) as the primary response variable. Average remeasurement intervals for species varied from 4.4 to 5.0 yr. Plots that were not classified as "forestland" were excluded from the data set. We also excluded plots in southern pine forest types as the focus of our broader research effort was on the deciduous and mixed deciduous/conifer forests of the eastern United States. This left a total of 114,584 plots distributed across the 31-state study region. True plot locations were obtained from the U.S. Forest Service under a security memorandum.

Each FIA plot consists of four circular subplots, with 36.6 m between subplot centers. All trees ≥12.7 cm diameter at breast height (dbh) are censused in the 7.32 m radius subplots. Saplings (stems ≥2.5 and <12.7 cm dbh) are censused in a single 2.07 m radius microplot within each subplot. Our analyses focus on the 50 most common tree species in our plot data set (Table 1), with separate analyses for each of the 50 species. Sample sizes for species ranged from 900 to 81,113 adults and 224 to 19,345 saplings in 971 to 35,500 subplots. Because of the wide spacing between subplots, and because neighborhood-scale canopy tree abundance within a subplot is used in the analyses to characterize competition, we treat each subplot as a separate sample location.

While there is a rich literature relating plant performance to a wide range of climatic variables (e.g., Thuiller et al. 2003), we have chosen a priori to focus our analyses on two primary climate variables: annual mean temperature and effective growing season precipitation (total annual precipitation minus runoff during winter months). Our reasons are based on both pragmatism and principle. Within our study region, mean annual temperature has an extremely high correlation with both mean monthly temperatures for all months of the year, and with various metrics based on growing degree days. And much of the scientific and policy debate about the effects of climate change has been couched in terms of changes in mean annual temperature. While plant survival may be more closely related to water deficits, we have chosen to test for a relationship between growth and a measure of water supply rather than deficit. For studies with sites that occur within a fairly narrow range of mean annual temperature, total annual precipitation is a reasonable measure of water supply. But when sites occur across a broad range of temperature regimes, total annual precipitation will give a biased over estimate of supply of water for sites with cold winter months where a significant fraction of total annual precipitation is lost via runoff. Thus, we have used a calculation of "effective precipitation," defined as total annual precipitation minus rainfall received in winter months above available water storage capacity.

We compiled annual and monthly temperature and precipitation data for each plot using bilinear interpolation of the 800 m resolution PRISM climate data (http://www.prism.oregonstate.edu/), using only data from the specific years and months between the current and previous censuses of a given plot. The calculation of runoff required estimates of monthly potential and actual evapotranspiration (PET and AET). We used the National Elevation Dataset compiled by the U.S. Geological Survey at 1/3 arc-second resolution for digital elevation data to calculate incident solar radiation, by month, for each plot location, using solar radiation routines in ArcGIS Version 10 (ESRI 2011). Available water storage capacity in the top 100 cm of soil at each plot location was extracted from the U.S. Department of Agriculture Soil Survey Geographic (SSURGO) database. The monthly solar radiation data and soil water storage capacity data were then combined with monthly temperature and precipitation data to calculate monthly PET and AET using the Turc method (Lu et al. 2005, Dyer 2009). The sum of rainfall received in winter months above available water storage capacity was treated as runoff and subtracted from total annual precipitation to generate our measure of effective precipitation.

A number of recent studies have documented effects of anthropogenic nitrogen (N) deposition on tree growth in temperate forests (e.g., Thomas et al. 2010). We used regional maps of total annual wet deposition of nitrate and ammonium generated by the National Trends Network

Table 1. Total sample size for each of the 50 study species, broken down by numbers of adults vs. saplings, and the number of unique plots and subplots in which individuals of each species occurred.

Species	Acronym	Total sample size	No. of adults	No. of saplings	No. of unique plots	No. of unique subplots
Abies balsamea	ABBA	39,271	19,926	19,345	4581	10,667
Acer rubrum	ACRU	98,452	81,113	17,339	16,437	35,500
Acer saccharum	ACSA	69,719	58,346	11,373	9521	22,157
Betula alleghaniensis	BEAL	13,270	11,035	2235	3592	6674
Betula lenta	BELE	7784	6462	1322	2115	3749
Betula papyrifera	BEPA	18,336	14,830	3506	4328	7387
Carya alba	CAAL	10,195	8621	1574	4322	6420
Carpinus caroliniana	CACA	3297	900	2397	1448	1851
Carya glabra	CAGL	10,842	9699	1143	4540	6839
Carya ovata	CAOV	8072	7272	800	2974	4505
Cornus florida	COFL	5925	1842	4083	3097	4109
Fagus grandifolia	FAGR	22,800	16,567	6233	5102	9524
Fraxinus americana	FRAM	16,575	13,948	2627	5703	8947
Fraxinus nigra	FRNI	5483	4066	1417	1525	2276
Fraxinus pennsylvanica	FRPE	6100	4892	1208	2359	3346
Juniperus virginiana	JUVI	11,104	9090	2014	2597	4535
Liquidambar styraciflua	LIST	18,622	14,545	4077	3739	7741
Liriodendron tulipifera	LITU	23,222	21,097	2125	5610	10,186
Nyssa sylvatica	NYSY	11,879	8173	3706	5187	7499
Ostrya virginiana	OSVI	8720	3770	4950	3414	4948
Oxydendrum arboreum	OXAR	8789	7135	1654	2935	5208
Picea glauca	PIGL	6571	5624	947	1722	2755
Picea rubens	PIRU	13,268	9946	3322	1844	4106
Pinus banksiana	PIBA	2396	2172	224	550	971
Pinus echinata	PIEC	6750	6465	285	1939	3173
Pinus resinosa	PIRE	17,700	17,163	537	1397	3014
Pinus strobus	PIST	22,041	19,685	2356	4057	7893
Pinus taeda	PITA	12,068	10,712	1356	2510	4519
Pinus virginiana	PIVI	5572	5127	445	1474	2311
Populus balsamifera	POBA	3605	2754	851	742	1179
Populus grandidentata	POGR	11,882	9489	2393	2294	3752
Populus tremuloides	POTR	39,715	27,983	11,732	5139	10,675
Prunus serotina	PRSE	19,421	15,610	3811	7170	10,787
Quercus alba	QUAL	41,005	38,404	2601	9719	19,048
Quercus coccinea	QUCO	9345	8970	375	3134	5168
Quercus falcata	QUFA	5716	5137	579	2257	3427
Quercus macrocarpa	QUMA	4791	4374	417	1220	2088
Quercus nigra	QUNI	6315	4523	1792	1725	3095
Quercus prinus	QUPR	21,459	20,719	740	3674	8017
Quercus rubra	QURU	27,649	25,695	1954	8314	14,114
Quercus stellata	QUST	12,674	11,781	893	3221	5655
Quercus velutina	QUVE	18,056	16,823	1233	5858	9798
Robinia pseudoacacia	ROPS	3938	3534	404	1427	1998
Sassafras albidum	SAAL	5812	4275	1537	2401	3186
Thuja occidentalis	THOC	9326	8489	837	1502	2664
Tilia americana	TIAM	12,411	11,129	1282	3109	5100
Tsuga canadensis	TSCA	21,935	19,870	2065	3271	6846
Ulmus alata	ULAL	4047	2481	1566	1881	2687
Ulmus americana	ULAM	9498	7051	2447	4179	5940
Ulmus rubra	ULRU	3568	2809	759	1927	2545

of the National Atmospheric Deposition Program (NADP, 2015). Data for annual nitrate and ammonium wet deposition were downloaded from the NADP website (http://nadp.sws.uiuc.edu/ntn/annualmapsByYear.aspx). We then extracted the deposition data for each FIA plot location, using only the data from the years from the beginning to the end of the census interval used for a given plot. Average annual wet nitrate and ammonium deposition (kg·ha^{-1}·yr^{-1}) were then combined for an estimate of average total annual wet N deposition during the census interval.

A maximum-likelihood model of sapling and adult tree growth

As in our previous analyses of tree growth using FIA data (Canham et al. 2006, Thomas et al. 2010), we assume that diameter growth is a multiplicative function of terms representing (1) an ontogenetic effect of plant size, (2) a measure of neighborhood competition, and (3) terms representing environmental effects. As in Thomas et al. (2010), the latter terms include explicit measures of (1) nitrogen deposition, (2) temperature, and (3) precipitation. To minimize potential parameter trade-offs inherent in any multiplicative model, the five sets of factors above are scalars (0–1) which are multiplied by an estimated potential growth rate (PG) representing expected growth at optimal levels of all of the factors. Thus, the basic model is as follows:

$$\begin{aligned}\text{Growth} = {} & \text{PG} \times \text{size} \times \text{competition} \times \text{nitrogen} \\ & \times \text{temperature} \times \text{precipitation.}\end{aligned} \tag{1}$$

Both growth and PG are in units of mm/yr diameter growth. The other terms are dimensionless scalars (0–1). The FIA plots span the full range of edaphic conditions within the region, and field crews assign a site class code (an ordinal measure from 1 to 7) based on estimates of growth for individual site trees (O'Connell et al. 2014). We grouped the seven site index codes into three general site index classes (FIA plot variable SITECLCD 1–2 = 1, SITECLCD 3–4 = 2, SITECLCD 5–7 = 3) to ensure adequate sample sizes within the three classes, and estimated separate PG parameters for each of the three classes.

The ontogenetic effect of plant size on diameter growth is modeled as a three parameter lognormal function of diameter at breast height (dbh):

$$\text{Size} = e^{-0.5\left(\frac{\ln\left((\text{dbh}+S_p)/S_0\right)}{S_b}\right)^2} \tag{2}$$

where dbh (cm) is measured at the beginning of the census interval, and S_p, S_0, and S_b are estimated parameters. The S_p parameter shifts the lognormal to the left to allow nonzero intercepts at zero dbh. The size term was fit with a single set of parameters for all stems (adults and saplings).

In previous studies with FIA data, we have used a species-specific and distance-dependent neighborhood competition index (NCI) to model the effects of competition (e.g., Canham et al. 2006). For the current study, we used a simpler competition function based on total tree basal area (m^2) in the subplot where an individual tree was located, and included a term to factor in the size of the target tree relative to the mean size of neighbors:

$$\text{Competition} = e^{-\alpha \times \text{BAratio}^{\gamma} \times \text{totalBA}^{\beta}} \tag{3}$$

where α, β, and γ are estimated parameters. For adult trees, totalBA is the total basal area of all other trees in the 7.32 m radius subplot at the time of the first census. For saplings, totalBA includes the basal area of all adult trees in the subplot, plus the basal area of all other saplings in the 2.07 m microplot. BAratio is the ratio of the mean basal area of individual trees used in the calculation of totalBA to the basal area of the target tree or sapling, at the time of the first census. The parameters α and β determine the shape of the decline in growth with increasing neighbor abundance. The parameter γ determines whether sensitivity of the target tree to crowding varies as a function of its size relative to the mean size (basal area) of neighbors. When γ is positive, target trees are more sensitive to crowding when they are smaller than the mean size of neighbors, and vice versa when γ is negative. Separate sets of the three parameters were fit for saplings and adults because of prior research supporting the assumption that saplings and adults differ in their responses to crowding, and because initial tests showed that fitting separate competition parameters for saplings and adults yielded superior models (in terms of AIC).

The effects of nitrogen deposition on sapling and adult tree growth were fit with a simple Gaussian function:

$$\text{Nitrogen} = e^{-0.5\left(\frac{\text{Ndeposition} - N_0}{N_b}\right)^2} \tag{4}$$

where Ndeposition is the average annual wet nitrogen deposition ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) at the plot location, and N_0 and N_b are estimated parameters. Again, because of both prior research and initial tests, separate sets of parameters were estimated for both saplings and canopy trees.

There is no consensus in the literature on the most appropriate functional forms of the response of tree diameter growth to variation in either temperature or effective precipitation. Our approach is to use a functional form that is flexible enough to faithfully fit the data but with parameters that have interpretable effects on the shape of the function. We did initial tests on a number of simpler alternatives including Gaussian and lognormal functions, but settled on a compound double logistic function with three parameters that controlled the shape of the function at the low end of the temperature or precipitation gradient and three parameters that controlled the shape of the function at the high end of the gradient. The functional form was flexible enough to allow different nonzero tails at each end of the gradient and different shapes of rising and falling responses, with a broad plateau at intermediate temperature or effective precipitation if dictated by the data:

$$\text{Climate response} = \left[\text{low}_a + \left(\frac{1-\text{low}_a}{1+\left(\frac{\text{low}_b}{C}\right)^{\text{low}_c}}\right)\right] \times \left[\text{hi}_a + \left(\frac{1-\text{hi}_a}{1+\left(\frac{C}{\text{hi}_b}\right)^{\text{hi}_c}}\right)\right] \tag{5}$$

where C is either effective precipitation or mean annual temperature during the period between the first census and second census, and the other terms are estimated parameters. Temperature was converted to degrees Kelvin to avoid discontinuities in the function at 0°C. By inverting the position of the climate variable in the two parts of the function, and making the low_c and hi_c parameters strictly positive, the first half of the function allows for a rising response at the low end of the temperature or precipitation gradient, while the second half of the function allows a falling response at the high end of the gradient. But the low_b and hi_b parameters determine over what range of the climate variable the function either rises or falls, and are allowed to vary enough that Eq. 5 can fit monotonically increasing or decreasing responses within the range of the data (see Figs. 1 and 2 for illustration of the range of shapes Eq. 5 can take). For both the temperature and precipitation effects in Eq. 1, separate sets of parameters were estimated for saplings and adults, because initial tests showed that models that allowed separate climate responses of juveniles and adults were always superior (in AIC) to simpler models that tried to fit both life stages with a single climate response. While this required a large number of estimated parameters (6 parameters × 2 climate variables × 2 life history stages), the sample sizes for all 50 species were also very large (Table 1).

For each of the 50 species, initial model testing and development was made using the global optimization algorithm in our likelihood package in R (R Core Team 2014). Given the very large sample sizes, large number of parameters, and large number of iterations required for convergence of the optimization routine, the final models were fit using an implementation of the optimization algorithm in Java. This reduced the computational demand by more than an order of magnitude. While tree growth data are often heteroscedastic, initial tests showed that a simple homogeneous variance normal distribution was appropriate for the likelihood function. We also tested variants of Eq. 1 in which either or both of the climate variables were dropped from the model. Alternate models were then compared using AIC to choose the most parsimonious model with or without one or both of the climate variables. Uncertainty in the maximum-likelihood parameter estimates was assessed using 2-unit support intervals. Goodness of fit of the models was assessed with R^2. We tested for bias using the slope of the relationship between observed and predicted growth.

RESULTS

The best models explained an average of 14% of variation in growth for the 50 species (range

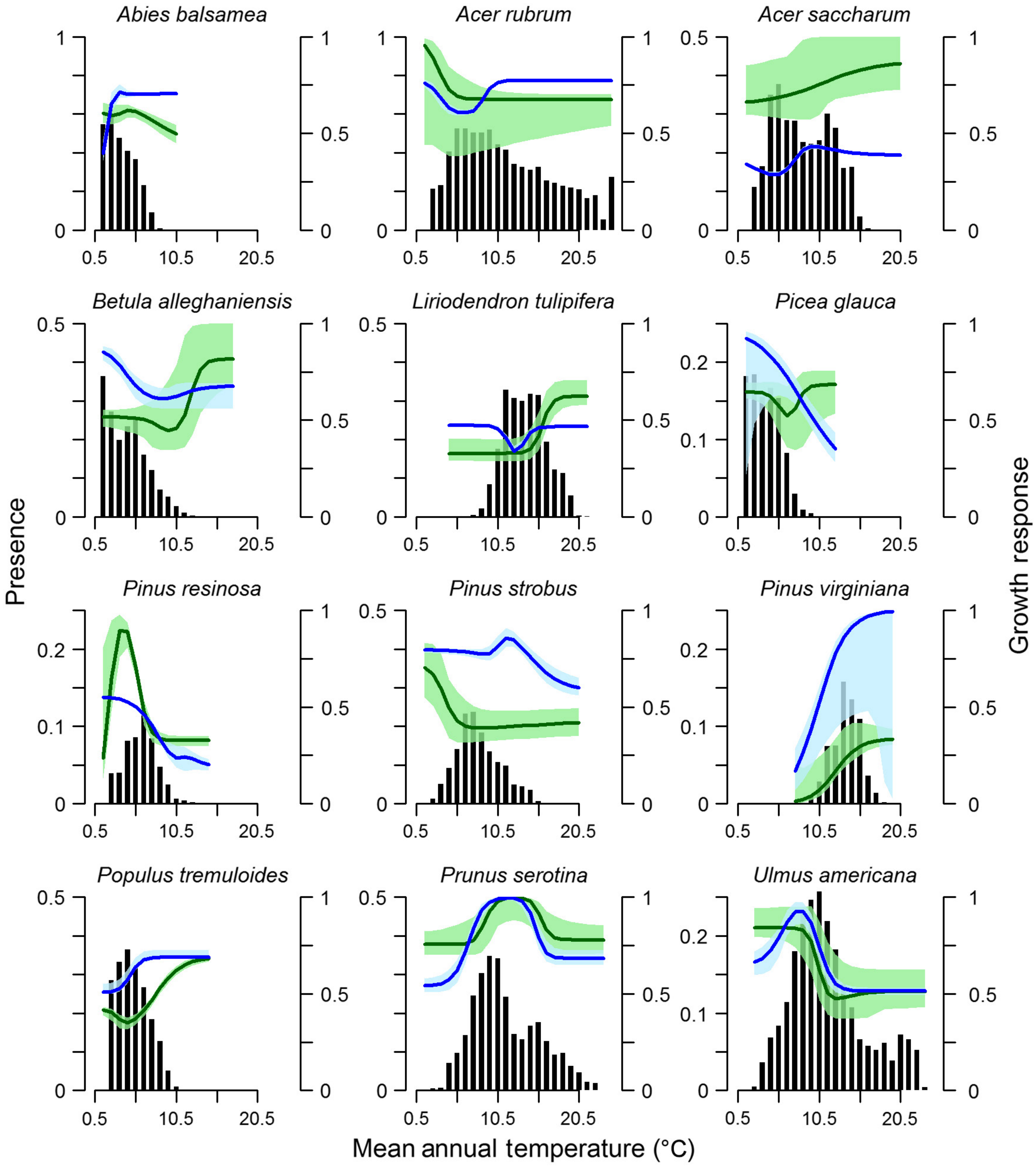

Fig. 1. Expected responses (fraction of potential growth, right-hand axis) to variation in mean annual temperature of saplings (green line) and canopy trees (blue line) for 12 representative tree species. Lines are plotted only over the range of temperature in which a species occurred. The shaded areas around each line are 2-unit support limits on the predicted responses. The histograms (black bars) show the fraction of plots (left-hand axis) in 1-degree intervals of mean annual temperature in which canopy trees of a given species occurred.

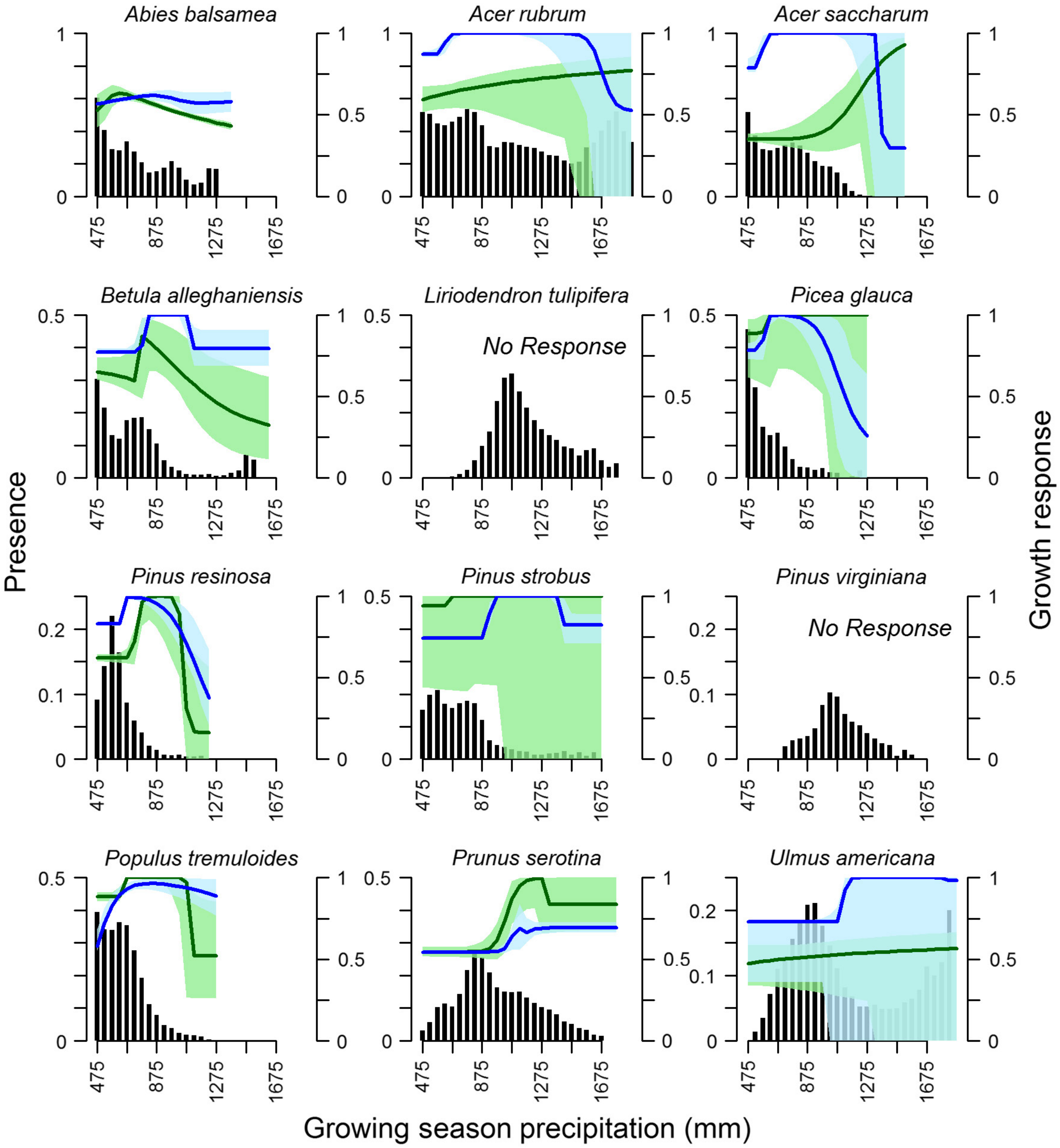

Fig. 2. Expected responses (fraction of potential growth, right-hand vertical axis) to variation in effective growing season precipitation of saplings (green line) and canopy trees (blue line) for 12 representative tree species. The shaded areas around each line are 2-unit support limits on the predicted responses. Lines are plotted only over the range of the data for a given species. The histograms (black bars) show the fraction of plots (left-hand vertical axis) in which canopy trees of a given species occurred.

2–42%) and were unbiased: Slopes of regression of observed on predicted growth ranged from 0.99 to 1.01 (Table 2). For 32 of the 50 species, the best model included both climate variables. For seven of the species, inclusion of temperature effects did not improve the model (based on AIC), and for 13 of the species, inclusion of effective precipitation did not improve the model (Table 2). Inclusion of the two climate variables in the model increased R^2 by an average of only 2.5% (in absolute units of R^2, across the 50 species; range 0–7.5%).

Ontogenetic effects of tree size on growth

More than half (27) of the species showed an essentially monotonic increase in diameter growth as a function of diameter (*size* term in Eq. 1; Appendix S1), after the other terms in the equation had been factored out. This group included both species of *Acer*, all three species of *Carya*, the three species of *Fraxinus,* and all nine species of *Quercus*, but only two of the conifer species (*Tsuga canadensis* and *Thuja occidentalis*). Eighteen of the species showed a basically flat response or a very slight decline in diameter growth with increasing diameter (Appendix S1). This group included all three species of *Betula* and six of the 10 species of conifers (five of the six species of *Pinus,* and *Picea glauca*). Finally, a much smaller group of five species showed a lognormal shape, with a rapid rise to a peak growth at a relatively small adult tree size, and then a gradual but pronounced decline in growth with increasing diameter. This group included one of the understory species (*Cornus florida*) with a small maximum diameter, but also included *Fagus grandifolia*, one of the late successional dominant trees in the study region, but a species in which larger trees in the northern portion of its range have been heavily impacted by beech bark disease (Appendix S1).

Interspecific differences in responses of saplings and canopy trees to competition

As expected, saplings of the 50 species differed widely in their response to canopy competition (competition term in Eq. 1; Appendix S1). For a 2 cm dbh sapling beneath a canopy with a mean dbh of 20 cm and a total basal area of 40 m^2/ha, predicted growth would be reduced to 31% of potential growth, averaged across the 50 species, but with a range from 1.5% to 75% of potential growth (the very shade-intolerant *Pinus resinosa* and the understory tree *Carpinus caroliniana*, respectively). Sensitivity of saplings to the competitive effects of neighbors (primarily canopy trees) did not vary much with sapling size: γ parameters (Eq. 3) for saplings averaged just 0.071 and were effectively zero for more than a quarter of the species (Appendix S2). Thus, growth of 10 cm dbh saplings of the 50 species under the same canopy would be reduced on average to 37% of potential growth. As expected, the four species with the least reduction in growth beneath a closed canopy were understory species (*Carpinus caroliniana, Oxydendron arboretum, Cornus florida, Ostrya virginiana,* and *Ulmus alata*), and the least sensitive of the canopy species was the very shade-tolerant *Fagus grandifolia* (Appendix S1). Nine of the 10 species most sensitive to canopy competition as saplings were species of either *Quercus* or *Pinus*.

Sensitivity of canopy trees to competition was more strongly influenced by the size of the individual relative to the mean size (basal area) of neighbors (Appendix S1). The γ parameters for adults were consistently larger than for saplqings, averaging 0.319 (range 0–1.00) (Appendix S2). Seven of the nine species of *Quercus* and four of the six species of *Pinus* were among the dozen species with the highest estimated γ parameters, and thus, the species in which sensitivity to competition was greatest when the target tree size was small relative to mean canopy tree size (Appendix S2). Growth of a 15 cm dbh individual in a stand with a total basal area of 40 m^2/ha and a mean adult tree size of 30 cm dbh averaged just 33% of potential growth (across the 50 species), but ranged from 4% to 64%. Growth of a 30 cm dbh tree in the same stand averaged 47.9% of potential growth (range 23–78% among the 50 species).

Interspecific differences in responses to N deposition

Responses of the 50 tree species to regional variation in nitrogen (N) deposition varied widely among species, and as reported in a previous study with a subset of 24 of these species sampled in a smaller region (Thomas et al. 2010), responses differed depending on the characteristic mycorrhizal associations of the tree species (Appendix S3).

Table 2. Comparison of differences in Akaike information criterion (AIC) among four alternate models: the full model in Eq. 1 and models in which either or both of the climate variables (temperature and precipitation) were omitted.

			ΔAIC			
Species	Best model	R^2 (%)	Full Model	No climate effects	No temp effects	No precipitation effects
Abies balsamea	Full	20.3	0	3209	954	92
Acer rubrum	Full	12.4	0	1587	505	117
Acer saccharum	Full	16.7	0	2411	1226	1590
Betula alleghaniensis	Full	9.3	0	210	115	187
Betula lenta	No temperature	7.4	119	154	0	171
Betula papyrifera	Full	8.4	0	96	103	22
Carpinus caroliniana	No precipitation	13.5	16	182	24	0
Carya alba	No temperature	10.8	41	30	0	31
Carya glabra	No temperature	13.0	45	24	0	7
Carya ovata	Full	13.0	0	45	2	26
Cornus florida	No precipitation	4.5	69	207	58	0
Fagus grandifolia	Full	15.7	0	427	184	164
Fraxinus americana	No precipitation	12.3	3	33	37	0
Fraxinus nigra	Full	8.3	0	77	81	74
Fraxinus pennsylvanica	No climate	10.3	23	0	31	108
Juniperus virginiana	Full	14.2	0	316	84	109
Liquidambar styraciflua	Full	9.2	0	622	53	111
Liriodendron tulipifera	No precipitation	13.7	651	590	694	0
Nyssa sylvatica	Full	10.4	0	186	141	253
Ostrya virginiana	No temperature	5.4	9	254	0	59
Oxydendrum arboreum	No precipitation	1.9	27	60	82	0
Picea glauca	Full	23.8	0	284	221	87
Picea rubens	Full	21.1	0	218	21	202
Pinus banksiana	Full	33.0	0	131	100	157
Pinus echinata	No precipitation	15.8	59	44	69	0
Pinus resinosa	Full	42.2	0	1130	817	495
Pinus strobus	Full	27.0	0	847	77	233
Pinus taeda	Full	24.7	0	530	246	249
Pinus virginiana	No precipitation	19.6	33	173	100	0
Populus balsamifera	Full	9.2	0	147	95	62
Populus grandidentata	Full	17.7	0	214	17	77
Populus tremuloides	Full	12.3	0	649	470	406
Prunus serotina	Full	11.6	0	654	235	112
Quercus alba	Full	16.9	0	1727	154	2647
Quercus coccinea	No precipitation	13.5	40	209	130	0
Quercus falcata	No climate	11.4	34	0	27	28
Quercus macrocarpa	Full	15.2	0	48	38	1
Quercus nigra	No temperature	17.2	93	5	0	66
Quercus prinus	No precipitation	13.3	33	760	371	0
Quercus rubra	Full	16.8	0	716	280	128
Quercus stellata	No precipitation	9.3	18	178	1	0
Quercus velutina	Full	12.7	0	407	252	132
Robinia pseudoacacia	Full	9.5	0	146	115	71
Sassafras albidum	Full	11.9	0	96	99	24
Thuja occidentalis	Full	6.0	0	21	16	98
Tilia americana	Full	10.2	0	390	72	18
Tsuga canadensis	Full	17.4	0	520	178	43
Ulmus alata	Full	12.1	0	168	20	193
Ulmus americana	Full	21.4	0	579	307	15
Ulmus rubra	No precipitation	12.8	47	114	153	0

Notes: The best model has a ΔAIC of zero. Also reported is the R^2 of the best model.

Adults of 18 of the 50 species showed a strong monotonic increase in growth with increasing N deposition across the range of deposition in the study plots (i.e., <10 kg·ha^{-1}·yr^{-1}). These included 10 of the 17 species (59%) with arbuscular mycorrhizal associations, but only eight of the 33 species (18%) with ectomycorrhizal associations. The ectomycorrhizal species showing a positive response included six of the nine species of *Quercus*. The remaining seven species with arbuscular mycorrhizae and more than half (17 of 33) of the species with ectomycorrhizae showed no response of adult tree growth to variation in N deposition. The only species with a consistently negative response to variation in N deposition were 10 of the 33 species (30%) with ectomycorrhizae (Appendix S3).

Thomas et al. (2010) focused only on canopy trees, but our analysis here allows us to compare responses of saplings vs. adults to N deposition. As with adults, saplings of roughly half of the species (26 of 50) had no response to the gradient of N deposition (although a different set of species than for adults). Saplings of only 13 of the 50 species showed a monotonic increase in growth across the N deposition gradient, and only five of these are associated with arbuscular mycorrhizae (*Fraxinus pennsylvanica, Juniperus virginiana, Liquidambar styraciflua, Liriodendron tulipifera,* and *Oxydendron arboretum*). Saplings of only one species—*Fagus grandifolia*—showed a strong monotonic decline in growth across the deposition gradient. But saplings of a larger group of 10 species (only two of which, *Nyssa sylvatica* and *Robinia pseudoaccacia*, are associated with arbuscular mycorrhizae) had a strongly Gaussian response, with peak growth at intermediate levels of N deposition (Appendix S3).

Interspecific differences in responses to climate

The compound logistic functional form we used to test for responses of both saplings and canopy trees to variation in mean annual temperature is capable of taking on a very wide range of shapes, and the 50 species do indeed show an enormous diversity of shapes in their response to regional variation in temperature (12 representative species shown in Fig. 1, figures for all 50 species are in Appendix S1). For many of the species, there is a significant portion of their temperature range for which growth of either or both saplings and canopy trees does not vary. Prominent examples include *Acer rubrum* and *A. saccharum*, the two most common species in the data set (Fig. 1). A small set of six species (two angiosperms *Betula alleghaniensis* and *Ulmus americana*, and four conifers *Picea glauca*, *Pinus banksiana*, *P. resinosa*, and *P. taeda*) had pronounced declines in expected adult tree growth across the warmer end of their current distribution (Fig. 1; Appendix S1). But by far the most common response among the 50 species (if there was any response to variation in temperature at all) was for an approximately monotonic increase in expected sapling or adult growth with increasing temperature (Appendix S1). In contrast, virtually all of the species show much more canonical and approximately Gaussian distributions of the fraction of plots of a given temperature in which they were present (Fig. 1; Appendix S1; Canham and Thomas 2010).

Responses to variation in effective precipitation (average annual precipitation minus winter runoff) showed even weaker patterns than the responses to variation in temperature (12 representative species shown in Fig. 2, figures for all 50 species are in Appendix S1). Despite pronounced variation in the distributions of the 50 species along the precipitation gradient, there was much more modest or effectively no variation in expected growth rates of either saplings or canopy trees along the precipitation gradient (Fig. 2; Appendix S1). Support intervals on the predicted responses were often quite large, particularly at the edges of the range of the distribution of a species along the gradient, where sample sizes were more limited.

Discussion

Ontogeny and the importance of plant size

Our models include the effects of plant size for both practical and theoretical reasons. Traditional growth studies used relative growth rates (RGR) rather than absolute growth in large part to control for differences among treatment groups or populations in the sizes of individuals that could obscure the effects of other independent variables (climate in our case). But RGR assumes an underlying linear ontogenetic relationship between growth and size that is clearly not appropriate over a broad range of plant sizes. Allometric scaling models, including metabolic theory, posit a power law relationship between biomass and biomass growth, typically with a theoretical expectation of a common exponent across species (Enquist et al. 1999). A variety of studies have challenged the fit between empirical data and the expected value of the scaling exponent, and its consistency across species (Muller-Landau et al. 2006, Coomes and Allen 2009). Our models predict diameter growth as a function of stem diameter, and because of the nonlinear relationship between stem diameter and biomass, an asymptotic power law relationship between biomass and biomass growth will result in a unimodal and approximately lognormal shape to the relationship between diameter and diameter growth for at least some values of the power law exponent. But the broad range of shapes of the estimated relationships between stem diameter and diameter growth for the 50 species analyzed here (Appendix S1) suggests that there indeed is a broad range of ontogenetic size relationships possible among tree species (Franceschini and Schneider 2014, Iida et al. 2014).

The importance of including competition in models of climate responses

As with the size term, the competition term is included in our general model (Eq. 1) to control for the effects of competition and avoid confounding any climate-based differences in the average intensity of competition with underlying direct effects of climate on tree growth. The functional form for the NCI used here is simpler than in previous studies that are spatially explicit and account for species-specific differences in both competitive effects and responses (Canham et al. 2004, 2006). Those more complex formulations for NCI yield much better goodness of fit (R^2), but do so at the cost of a much greater computational burden in both parameter estimation and implementation of the resulting relationships in forest simulation models. Nonetheless, even the simple formulation for competitive effects used here confirms that the absolute degree of crowding in a stand and the size of an individual relative to the mean size of neighbors combine to have the greatest impact on predicted growth of any of the terms in the model (Appendix S1).

Interspecific differences in responses to nitrogen deposition

Our analyses of responses of saplings and canopy trees to regional variation in nitrogen deposition confirm a previous study (Thomas et al. 2010) with a smaller set of species from a more limited study area. Roughly half of the 50 species we examined showed variation in growth along the N deposition gradient as saplings, and a different set of roughly half of the 50 species also responded as adults. In general, species with arbuscular mycorrhizae were more likely than species with ectomycorrhizae to show a positive response to N deposition, over at least some portion of the gradient. A significant fraction of the ectomycorrhizal species (but none of the arbuscular mycorrhizal species) had negative responses to N deposition. And while the Thomas et al. (2010) study focused only on canopy trees, our results show that saplings typically had different responses to N deposition than did canopy trees of the same species, and that saplings were more likely to have Gaussian rather than monotonic responses over the range of wet N deposition in the eastern United States. The analysis by Thomas et al. (2010) revealed that high ambient levels of N deposition were associated with a significant net increase in aboveground tree biomass averaged across the northeastern and north-central United States. But the wide range of species-specific positive and negative responses to N deposition suggests that at a local scale, species composition, including the relative balance of ectomycorrhizal vs. arbuscular mycorrhizal tree species, will be an important determinant of the net effect of N deposition on forest productivity and carbon storage (Phillips et al. 2013). It is also important to note that while anthropogenic N deposition represents an input of a nutrient often considered to limit tree growth in this region, it is also associated with soil acidification and depletion of base cations (Likens et al. 1998). The wide range of positive to negative responses to N deposition may thus reflect indirect effects due to interspecific differences in sensitivity to soil acidification and supply of base cations (Bigelow and Canham 2007, Fowler et al. 2015).

Climatic controls of tree growth and distribution

After controlling for the effects of plant size, competition, and N deposition, the relationships between the two climate variables and geographic variation in tree growth were surprisingly modest, and bore little obvious relationship to the distributions of the species along climate gradients

(Appendix S1). For over a quarter of the species, there was no statistical support for a relationship between 5-yr average effective growing season precipitation and 5-yr average growth, and for most of the remaining species the relationship was effectively flat over a wide range of precipitation. And yet there was striking variation in the distribution of most of the species along the precipitation gradient. Responses to regional variation in mean annual temperature were stronger, but again showed little obvious correlation with the distribution of abundance of most species along the temperature gradient (Appendix S1).

Studies of climate–growth relationships always face the challenge of selecting appropriate climate metrics to use as independent variables. Our approach has been to select variables a priori because of the well-known problems with a posteriori selection based on goodness of fit of variables among the literally hundreds of possible permutations of temperature and precipitation data than can be generated for any location. While there is a rich ecophysiological literature on leaf-level responses to variation in temperature and water relations, stem diameter growth represents just one component of whole-tree carbon gain and attempts to develop general scaling rules from short-term, leaf-level responses to whole-plant, longer term growth have not led to consensus on climate variables most appropriate for inclusion in models of annual or longer term average tree diameter growth.

This problem is particularly acute with assessment of the impact of variation in precipitation, as soil water supply and plant water status reflect the combined effects of precipitation modified by temperature, solar radiation, topography, and soils. And while mean annual temperature has a very high correlation with monthly and seasonal temperature variables at any given location, measures of seasonal and annual rainfall totals have a much weaker relationship to seasonal or annual water deficits. For example, across the >100,000 plots in our data set, the correlation between our measure of "effective" precipitation and growing season water deficit was only 0.24 because of variation in topography, temperature, and soil water-holding capacity within a given precipitation regime. Thus, it is possible and even likely that there are stronger relationships between tree growth and other measures of water supply or water stress for many of the 50 species. Much of the variation in soil water supply and various measures of potential plant water stress would occur as fine-scale variation due to topography and soils within a given temperature and precipitation regime. Nonetheless, most of the 50 tree species studied here show clear niche differentiation in at least presence (frequency of occurrence) within stands along the precipitation gradient (Appendix S1; Canham and Thomas 2010). This suggests that other aspects of the demography of many of these species, including seed production and seedling recruitment, and survival at either seedling, sapling, or canopy tree stages, may respond more directly to precipitation (Benavides et al. 2013, Buechling et al. 2016, Canham and Murphy 2016).

Variation in growth along the temperature gradient was generally more pronounced than along the effective precipitation gradient. The most common pattern was for a roughly monotonic increase in growth across a limited range of the temperature gradient, but an effectively flat response across the remainder of a species current distribution. For a small set of species of cold climates, growth of either saplings or canopy trees declined in warmer climates (e.g., *Picea glauca* and *Pinus resinosa*; Appendix S1). The result for *Picea glauca* mirrors results obtained from a tree-ring study (D'Arrigo et al. 2004). An increase in growth with increasing temperature across at least some portion of the temperature gradient is certainly not unexpected given the underlying temperature dependence of photosynthesis (Saxe et al. 2001). In addition, dendroecological studies often show positive relationships between interannual variation in temperature and interannual variation in tree growth within a given location (Bunn et al. 2005, Way and Oren 2010), although there is evidence that those responses have weakened in the past 50 yr (D'Arrigo et al. 2008). Similarly, the lack of variation in diameter growth along some or most of a species' distribution along the temperature gradient is not unexpected given studies of local acclimation and/or adaptation to long-term mean growth temperatures (Carter 1996, Cunningham and Read 2003*a*, *b*).

Prunus serotina was the only one of the 50 species that showed a unimodal peak in growth of both saplings and adults that coincided roughly with the distribution of the species along the temperature gradient (Appendix S1). For two other species—*Ulmus americana* and *Picea glauca*—variation in growth of canopy trees but not saplings mirrored the current distributions of the species along the temperature gradient (Appendix S1). A mismatch between the temperature dependence of growth and a species' distribution along the temperature gradient is not unexpected, given that growth is just one of the components of demography that will vary along the temperature gradient and that many processes may create a divergence between the fundamental and realized climate niches of these temperate tree species. But it is worth noting that in a study that examined variation in growth of 14 of these 50 species along soil moisture and soil nutrient gradients within a given climate (Canham et al. 2006), maximum potential growth of adults of at least the shade-tolerant, successional dominant species coincided closely with the local environments in which those species were most abundant (as indicated by an ordination). Less shade-tolerant species, in contrast, showed some degree of displacement of their realized niches (defined in terms of abundance) away from their fundamental niches (defined in terms of growth in the absence of competition) (Canham et al. 2006).

Our most general conclusion regarding the climate responses of these temperate tree species is that there is an enormous range of species-specific variation in the relationship between growth and distribution along the climate gradients. Indeed, Vanderwel et al. (2013) concluded that recruitment and mortality were more important than variation in growth in explaining the distribution of forest types along climate gradients. Many empirical studies and models of forest response to climate change have dealt with this variability by grouping species into functional types (e.g., Way and Oren 2010, Vanderwel et al. 2013). We would simply note that the functional type groupings are often arbitrary and based on simple sets of readily observed traits (Iida et al. 2014, Simova et al. 2015). The integration of ecophysiological and demographic processes into dynamic models provides a way to quantitatively assess the sensitivity of population dynamics to variation in specific traits and combination of traits (Pacala et al. 1996, Vanderwel et al. 2013). Pacala et al. (1996) outlined a set of strategic trade-offs among a set of demographic traits of the nine species they studied and noted that coexistence of the species in the model required trait combinations that were distributed in a very limited portion of trait space. But it is still an open question whether species cluster into distinct functional types within those regions of trait space, or whether evolution and niche differentiation have led to more uniform distributions of individual species in trait space.

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