ECOSPHERE

Local differentiation in tree growth responses to climate

CHARLES D. CANHAM [iD],[1],† LORA MURPHY,[1] RACHEL RIEMANN,[2] RICHARD MCCULLOUGH,[3] AND ELIZABETH BURRILL[4]

[1]*Cary Institute of Ecosystem Studies, Millbrook, New York 12545 USA*
[2]*USDA Forest Service, Troy, New York 12180 USA*
[3]*USDA Forest Service, Newtown Square, Pennsylvania 19073 USA*
[4]*USDA Forest Service, Durham, New Hampshire 03824 USA*

Abstract. Many temperate tree species have extraordinarily broad distributions along gradients of temperature and precipitation. But it is not clear in most species whether this reflects very broad tolerance of climate conditions, or a high degree of genetic differentiation or phenotypic acclimation in their responses to local climate. Provenance trials and common garden experiments indicate that at least some tree species of the temperate forests of eastern North America show genetic differentiation in growth as a function of climate, although these studies have been largely limited to measurements on growth of seedlings and saplings. To test for evidence of either adaptation or acclimation in adult response to local climatic conditions, we used data from over 23,000 tree cores collected by the U.S. Forest Inventory and Analysis program in the 1980s for 14 tree species distributed in states from Maine to Ohio. We tested a suite of alternate models for interannual variation in radial growth as a function of (1) tree age, (2) size, (3) temperature, and (4) precipitation. The models included climate variables from both the current and previous year. The alternate models allowed us to test whether growth was best predicted from absolute values of the climate variables, or from deviation of current or previous year climate from long-term average at the location of an individual tree core. In all 14 species, models that used deviation from local, long-term mean climate were superior, indicating that all 14 species showed strong adaptation or acclimation to local climate. In most of the species, growth was highest in years that were cooler and wetter than long-term average at a location. The analysis does not allow us to distinguish between genetic differentiation and phenotypic acclimation responses. If the results are genetically based, trees within a given location could be much more sensitive to climate change than indicated by the very broad geographic distributions of these temperate tree species, but if the results are phenotypic, this would represent local acclimation that could help buffer species in the face of climate change.

Key words: acclimation; climate responses of tree growth; Forest Inventory and Analysis; local adaptation; tree ring analysis.

† **E-mail:** canhamc@caryinstitute.org

INTRODUCTION

Temperate tree species are notable for both their exceptionally broad climate niches (Manthey and Box 2007) and their tolerance of highly variable climatic conditions on diurnal to interannual time scales. Indeed, the tropical conservatism hypothesis proposes that lower tree species diversity in temperate vs. tropical climates reflects the ability of only a subset of

tropical lineages to adapt to the colder, drier temperate environments characterized by much greater fluctuations in temperature (Wiens and Donoghue 2004, Kerkhoff et al. 2014). Decades of research using provenance trials reveal considerable variation among temperate tree species in the degree of genetic adaptation to climatic conditions within local populations (Carter 1996, Alberto et al. 2013). There are also many mechanisms by which temperate trees can either simply tolerate or acclimate phenotypically to spatial and temporal variability in climate (Cunningham and Read 2003, Way and Oren 2010, Ostonen et al. 2013, Drake et al. 2015, Scafaro et al. 2017).

Both biogeography theory (Loehle 1998) and quantitative models of species and vegetation distribution (Schenk 1996, Smith et al. 2001) typically assume that there is a relationship between individual tree growth and population distribution and abundance across the climatic range of a species. That assumption is not necessarily supported by data (Canham and Murphy 2016*a*), and demographic models suggest that the successional dynamics and distribution of a tree species are more sensitive to the growth and survival of juvenile life history stages than to variation in adult tree growth (Pacala et al. 1996, Canham and Murphy 2016*b*, 2017). But primary productivity and the ecosystem services that flow from forest productivity, including nutrient retention and carbon sequestration, are clearly tied to variation in adult tree growth. Thus, understanding spatial and temporal variation in tree growth in response to variation to climate remains central to forecasting the responses of these ecosystems to climate change.

Provenance studies are generally limited to analyses of seedling and sapling responses. Tree ring studies offer a way to explicitly test whether adult trees also show local differentiation in response to climate (Hacket-Pain et al. 2016, Buechling et al. 2017, Latreille et al. 2017, McCullough et al. 2017). Typically, those studies identify geographically distinct populations and develop a standardized tree ring chronology which is then fitted to climate variables with separate models from each location. Differences in the nature of the climate responses in geographically distinct populations are then assumed to reflect either phenotypic acclimation or genetic adaption to local conditions (Latreille et al. 2017).

We take a different approach that can accommodate the availability of broadly distributed tree ring data, without the need to aggregate the data into discrete local populations. Specifically, we have used data from over 23,000 tree cores collected by the U.S. Forest Inventory and Analysis program in the 1980s for 14 eastern North American tree species distributed in states from Maine to Ohio. We tested a suite of alternate models for interannual variation in radial growth as a function of (1) tree age, (2) size, (3) temperature, and (4) precipitation. The models included climate variables from both the current and previous year. The alternate models allowed us to test whether growth across the entire range of the data for a given species was best predicted from absolute values of the climate variables (i.e., reflecting regional variation but no local differentiation), or whether growth was best predicted from both regional variation in response to average climate conditions at a location, plus local differentiation in response to deviation of current and/or previous year climate from the long-term average climate at the location of an individual tree core.

METHODS

Data compilation

We used radial growth data from tree cores collected by the USDA Forest Service Forest Inventory and Analysis (FIA) program in the late 1980s as part of research on air pollution effects on forests of the northeastern United States (Hornbeck et al. 1988, Smith et al. 1990). The cores were collected from 7010 plots distributed in six New England states (Maine, New Hampshire, Vermont, Massachusetts, Connecticut, and Rhode Island) and the states of Pennsylvania, West Virginia, and Ohio. Increment cores were taken at 1.37 m above the ground from "four healthy dominant or codominant trees representing major species" in the plot (Smith et al. 1990). The cored trees were located just outside the plot. Preparation of the cores, cross-dating, and ring width measurement methods are described in Hornbeck et al. (1988) and Smith et al. (1990). The dataset contains over 27,000 cores from 78 species, with sample sizes ranging from a single core of *Tsuga caroliniana* to 3,478 cores of *Acer rubrum*. We have analyzed the cores from 14 of

the 15 most common species in the dataset, representing 23,048 of the cores (Table 1). The fifteenth species (*Pinus virginiana*) was distributed in too narrow a range of climate conditions within the study area for us to test for local differentiation in response to climate.

To avoid uncertainty associated with competitive effects on growth of seedlings and saplings, we limited our analyses to ring widths for which age was greater than or equal to 10 yr old (at 1.37 m height) and cumulative diameter (at the beginning of that year of growth) was ≥5 cm. Cumulative diameter each year was determined by summing increments. According to Smith et al. (1990), some cores did not reach the pith. But the final cumulative diameter calculated from the sum of radial increment very closely matched the field measurement of dbh, so the error in estimated age is assumed to be negligible. Because one of our principal hypotheses was to test for the nature of growth responses to absolute vs. long-term mean climate conditions, we also limited our analyses to ring widths in years greater than or equal to 1940. Ring width data from the year a tree was cored were not used because the growth could have been incomplete that year. Fourteen ring width measurements (of the over 800,000 measurements in the dataset) were >50 mm and were treated as errors. For those cores, the ring width data sequence was truncated at that point because cumulative diameter could not be determined for

later years. Final sample sizes ranged from 20,902 ring width measurements for *Tsuga canadensis* to 122,981 measurements for *A. rubrum* (Table 1).

We obtained true plot locations under a security memorandum with the Forest Service. The plot locations were used to extract monthly climate data for the period from 1930 to 1990, using bilinear interpolation of the 800 m resolution PRISM climate dataset. Total annual precipitation and mean annual temperature were compiled from the monthly data, using the period from October of the previous year through September of the current year of a radial growth measurement as "current year" data, and from October of two years prior to September of the previous year as the "previous year" data for that ring width.

Data analysis

Dendro-climatological studies have traditionally used a variety of highly specialized standardization methods prior to fitting models to relate radial growth to climate. But these come at the expense of the ability of those methods to translate model results into predictions of the effects of climate on absolute (not standardized) growth, and at the ability to assess the relative impact of variation in climate vs. other biological processes that influence growth (particularly ontogeny and competition). Both our objectives and our statistical framework using likelihood

Table 1. Characteristics of the datasets for the 14 study species.

Species	No. of plots	No. of trees	No. of ring widths	Age (mean)	Age (5–95% quantile)	dbh (mean) (cm)	dbh (5–95% quantile)
Acer rubrum	907	3478	122,981	54	23–85	20.9	13.3–30.3
Acer saccharum	687	2396	94,640	63	32–97	22.4	14.0–32.4
Betula alleghaniensis	113	547	20,611	64	32–101	22.0	14.2–31.2
Betula papyrifera	146	809	27,550	53	26–84	19.4	12.9–26.9
Fagus grandifolia	160	723	28,803	73	36–113	20.9	12.8–30.4
Fraxinus americana	335	1372	45,070	50	22–89	21.9	13.4–31.9
Liriodendron tulipifera	652	2377	64,676	39	17–67	26.3	16.4–38.7
Picea rubens	541	1485	55,766	70	35–114	21.1	14.2–30.5
Pinus strobus	585	2747	82,254	44	20–78	24.7	15.9–35.2
Prunus serotina	223	812	24,453	42	18–72	22.9	14.6–32.9
Quercus alba	589	2195	95,456	72	36–124	22.6	14.4–32.2
Quercus prinus	450	1681	73,554	73	39–125	21.3	12.9–31.7
Quercus rubra	528	1929	73,663	58	29–88	22.0	13.8–32.8
Tsuga canadensis	153	497	20,902	71	32–111	23.8	14.4–34.4

Note: Age and dbh are from the year a tree was sampled.

estimation obviate the need for those procedures, and indeed, a number of recent dendro-ecological studies have abandoned traditional standardization methods in favor of more direct estimation of relationships between growth and climate (Rollinson et al. 2016, Buechling et al. 2017). Our approach is to fit nonlinear models to observed radial growth in a given year as a function of estimated average potential radial growth (PRG in mm), and scalar terms that characterize the effects of (1) tree age and (2) size (dbh in cm) at the beginning of the year, and current year and previous year (3) mean annual temperature and (4) precipitation (Eq. 1):

$$
\begin{aligned}
\text{Radial increment(mm)} = \ & \text{PRG} \times \text{age effect} \\
& \times \text{size effect} \\
& \times \text{temperature effect} \\
& \times \text{precipitation effect}
\end{aligned}
$$

(1)

The age, size, temperature, and precipitation terms are scalars ranging from 0 to 1 to reduce parameter trade-offs in the model. Analyses of tree growth typically use either age or size (dbh) to account for ontogenetic variation in growth. We tested models using either one of these two terms alone, but models including both terms were highly superior in terms of Akaike's information criterion (AIC) and goodness of fit. In practice, the age term accounts for ontogenetic variation, and the size term (i.e., variation in dbh for a given age) helps account for variation in competitive status (i.e., dominant vs. subordinate status of large vs. small trees relative to age). We used a flexible three-parameter lognormal shape for both the age and size terms (Eq. 2):

$$
\text{age or size effect} = e^{-0.5\left(\frac{\ln((X+x_p)/x_0)}{x_b}\right)^2}
$$

(2)

where X was age or diameter (cm) at the beginning of the year, and x_p, x_0, and x_b are estimated parameters. The x_p parameter shifts the lognormal to the left to allow non-zero intercepts at zero age or diameter.

Climate effects were fit with a flexible four-parameter asymmetric exponential function (Eq. 3 and Fig. 1C):

$$
\text{temperature or precipitation effect} = a \times \mathbf{b}^{(X-c)^2}
$$

(3)

where X is either current or previous year temperature (°C) or precipitation (m). The estimated parameter a determines the maximum value of the effect, the parameter c determines the value of X at which the effect is maximum, and $\mathbf{b}$ is a vector of two parameters that determine the decline in the effect when X is less than or greater than c (Fig. 1C). Separate sets of a, $\mathbf{b}$, and c parameters were estimated for current and previous year climate effects. Current and previous year temperature and precipitation effects were assumed to be additive, that is:

$$
\begin{aligned}
\text{temperature effect} = & (\text{current year temperature} \\
& \text{effect} + \text{previous year} \\
& \text{temperature effect}).
\end{aligned}
$$

(4)

The values of the estimated parameters for the two terms (i.e., a, c, and $\mathbf{b}$ for current vs. previous year variables) determine the relative influence of current vs. previous year temperature and precipitation. We tested simpler models using only current year climate effects, but models using both current and previous year climate terms were superior (lower AIC) for all 14 species.

The model for our null hypothesis of no local differentiation in response to climate was fitted using the absolute values of the climate variables at the location of a sampled tree. In effect, this model assumes that all trees across the range of the samples for a given species show similar responses to interannual variation in the climate variables (Fig. 1A). The alternative hypothesis assumes that there could be predictable differentiation in growth in response to local climate variation from the long-term mean. This hypothesis (Fig. 1B) was tested by fitting a model in which the climate variable was instead the deviation of the annual climate variable from the long-term mean value of that variable at the location of a sampled tree during the 40-yr period from 1941 to 1980, that is,

$$
\begin{aligned}
X = & \text{current or previous temperature or} \\
& \text{precipitation} - \text{long-term mean} \\
& \text{temperature or precipitation.}
\end{aligned}
$$

(5)

In this model, the c parameter provides an estimate of the degree to which peak growth is
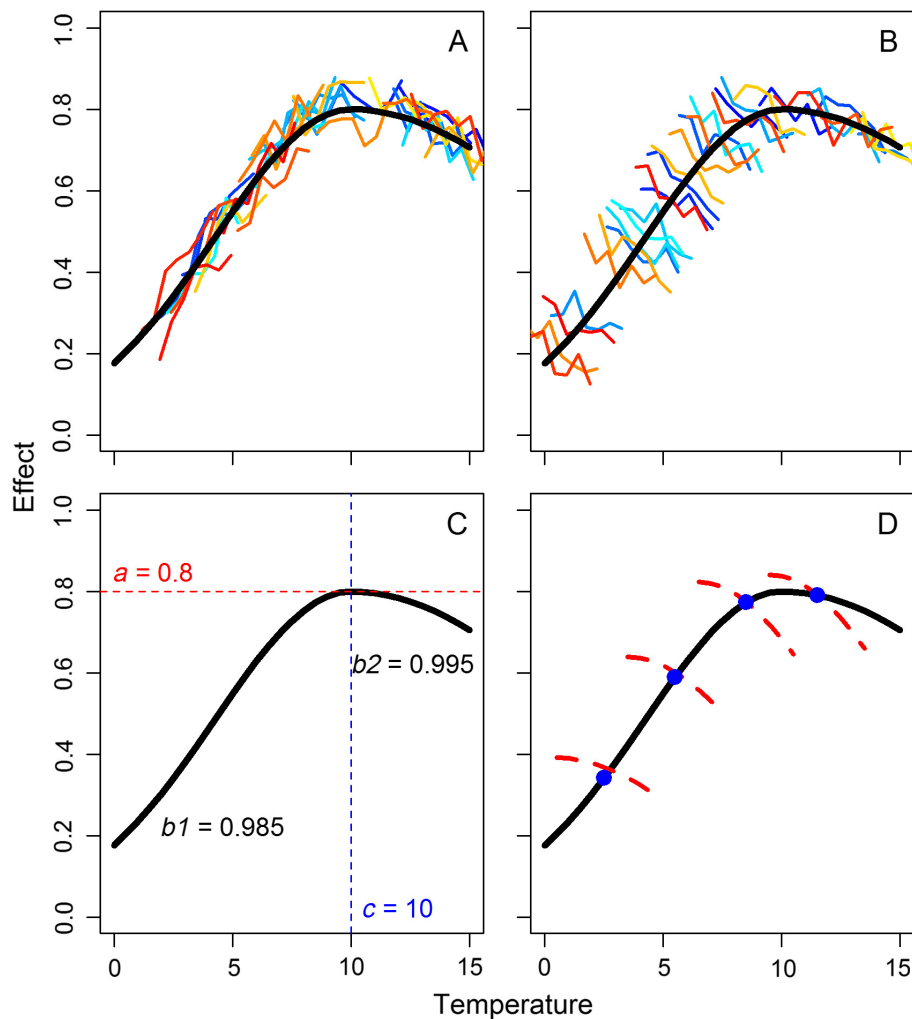
Fig. 1. Hypothetical responses of radial growth to variation in mean annual temperature. "Effect" is the fraction of potential radial growth observed at a given temperature. The solid black line is fitted across the entire range of a dataset consisting of many individual tree cores (colored lines). In (A), the cores show random variation around the overall pattern reflecting regional variation but no local differentiation. In (B), the cores show both regional variation across the climate gradient, and a different local response to interannual variation around the regional mean pattern. (C) The four-parameter exponential function used to characterize climate responses. (D) The function fitted to the hypothetical data in (B), the solid black line is the predicted variation in growth in years when the temperature equals the long-term mean at a given location. The four dashed red lines show the predicted pattern of growth in response to interannual variation in growth for four hypothetical locations with long-term mean temperatures indicated by the blue dots.

displaced above (positive) or below (negative) the long-term mean temperature or precipitation at a plot location. In addition, the height of the local climate response (*a*) was assumed to vary with the absolute value of the climate variable (Fig. 1D). We also tested two variants of the "local differentiation" model in which either temperature or precipitation alone showed local differentiation.

In effect, the model testing for local differentiation fits a whole family of curves (as in Fig. 1B), with one curve for each core centered around the

long-term mean climate for that core, but with the curve centered around the growth predicted by the parameters that determine expected growth when climate in a given year is equal to the long-term mean climate at that location. For simplicity, Fig. 1D and the figures in the *Results* section show just a small sample of the expected local responses. The important distinction is that while most previous studies of local differentiation in tree growth response to climate have required arbitrarily dividing the range of a species up into discrete sub-regions, our approach allows an integrated analysis of all of the available data across the range of climates present in the dataset.

The ring width data were normally distributed, but with variance proportional to the predicted mean, so for the likelihood function the standard deviation (SD) was a power function of the mean, with two estimated parameters (α and β):

$$SD = \alpha \hat{X}^{\beta} \qquad (6)$$

Maximum likelihood values of the parameters in the models were estimated using global optimization in the likelihood package in R (R Core Team 2014). Alternate models were compared using AIC. Goodness of fit was assessed with R^2, and potential bias measured using the slope of regression (through the intercept) of observed vs. predicted radial growth. Two-unit support intervals were calculated as measures of uncertainty in the parameter estimates.

RESULTS

Models with local differentiation in climate responses were clearly superior in all 14 species to the null model of no differentiation (Table 2). The best model for one species—*Betula alleghaniensis*—had local differentiation in temperature effects but not precipitation effects. The remaining 13 species showed clear local differentiation in response to interannual variation in both temperature and precipitation (Table 2, Figs. 2 and 3; Appendix S1). The models were unbiased (slopes of regression of observed on predicted ranged from 0.996 to 1.006), and the best models explained 11–40% of the variation in radial growth (mean = 25% across the 14 species; Table 2).

Regional responses to long-term mean temperature vs. local responses to interannual variation

The fourteen species show a wide range of patterns of regional variation in growth during years when temperature equals the long-term mean at a site, and a great deal of variability in the relative importance of current vs. previous year temperature (Fig. 2; Appendix S1). In particular, there were a number of species where there was a strong contrast between the importance of current vs. previous year temperature (i.e., *Acer saccharum*, *B. alleghaniensis*, *Fagus grandifolia*, *Fraxinus americana*, *Pinus strobus*, *Prunus serotina*, *Quercus prinus*, and *Tsuga canadensis*). In six of these eight species (all except *Q. prinus* and *B. alleghaniensis*), previous year temperature was vastly more important to growth than current year temperature when the species was within the warmer parts of a species' climatic distribution. But the additive net effects of current and previous year temperatures were counter-balancing in all eight of those species, and minimized regional variation in growth as a function of average long-term climate at a site (Fig. 2). Only two of the species (*Acer rubrum* and *Q. alba*) showed net positive responses to

Table 2. Model comparison (ΔAIC) for the four alternate models.

Species	ΔAIC				R^2 (%)
	LPT	LP	LT	RPT	
Acer rubrum	0	2908	2783	4914	23.1
Acer saccharum	0	1697	441	1670	16.8
Betula alleghaniensis	34	352	0	297	19.1
Betula papyrifera	0	71	76	126	39.9
Fagus grandifolia	0	289	9	730	11.2
Fraxinus americana	0	564	1235	1462	38.5
Liriodendron tulipifera	0	875	3778	4904	33.6
Picea rubens	0	559	473	598	20.4
Pinus strobus	0	920	845	726	29.2
Prunus serotina	0	491	224	806	31.2
Quercus alba	0	533	803	1101	18.8
Quercus prinus	0	283	274	94	24.8
Quercus rubra	0	238	777	935	31.1
Tsuga canadensis	0	287	342	255	14.6

Notes: Model RPT fits regional responses to the absolute value of the current and previous years' precipitation and temperature, while models LPT, LP, and LT fit responses to current and previous year climate relative to the long-term mean precipitation (*P*) and/or temperature (*T*) at the site where a tree was sampled. Also reported is the R^2 of the best model (ΔAIC = 0). AIC, Akaike's information criterion.
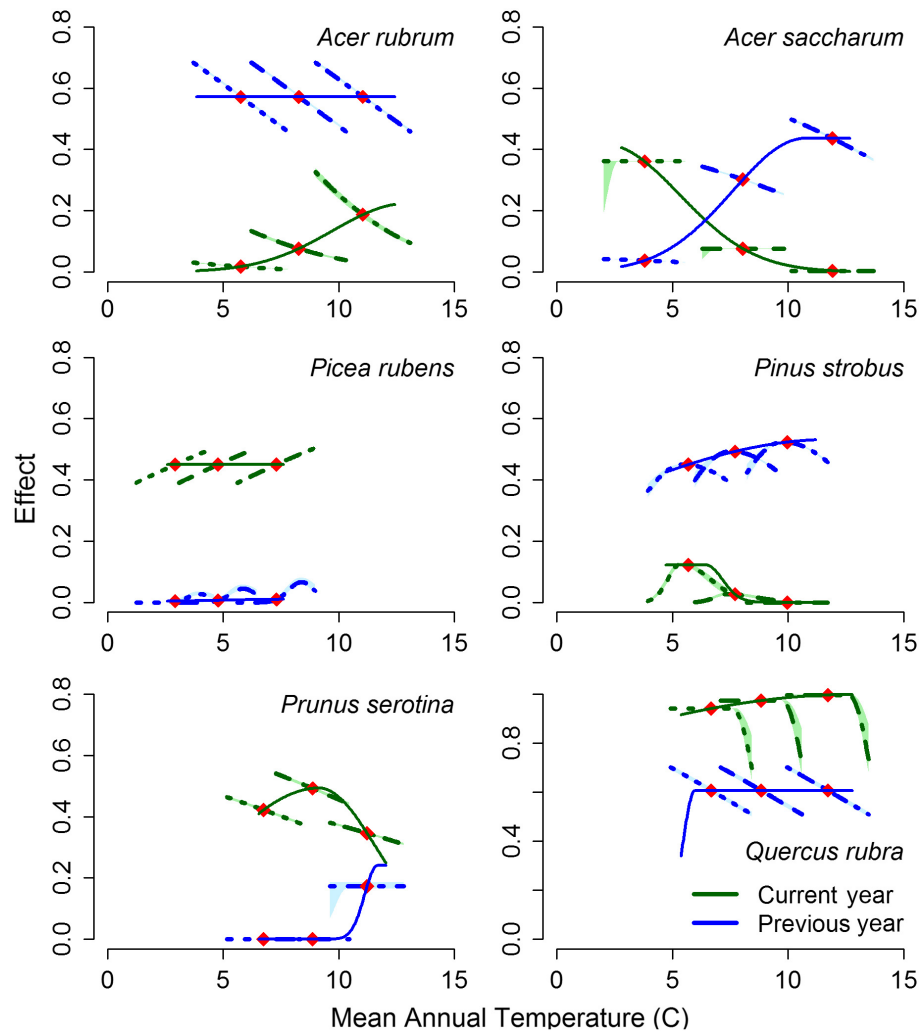
Fig. 2. Predicted effect on growth of variation in mean annual temperature of the current (green) and previous year (blue) for six representative tree species. "Effect" is the fraction of potential radial growth observed at a given temperature, given other terms in the model. Predicted responses for the full dataset consisting of 14 species are shown in Appendix S1. The solid lines are the predicted effect of temperature on growth when temperature equals the long-term (1940–1980) mean temperature at a location (i.e., the regional response). The dashed lines illustrate response to interannual variation for cores sampled at locations corresponding to the minimum, mean, and maximum long-term average temperature in the dataset for a given species (red diamonds). Note that the model predicts a whole family of such curves with the predicted growth for a given curve centered at the long-term mean temperature at the location of a given core. The shaded regions are two-unit support intervals around the predicted patterns of local differentiation. The cumulative effects of current and previous year temperature are additive in these models.

warmer regional average climates, and only one species—a birch with a northern distribution (*Betula papyrifera*)—had a net negative response to a warmer regional average climate (Fig. 2; Appendix S1).

In all 14 species, local responses to interannual variation in temperature relative to long-term mean at a site differed dramatically from the regional patterns of response to mean temperatures (Fig. 2; Appendix S1). For simplicity, Fig. 2
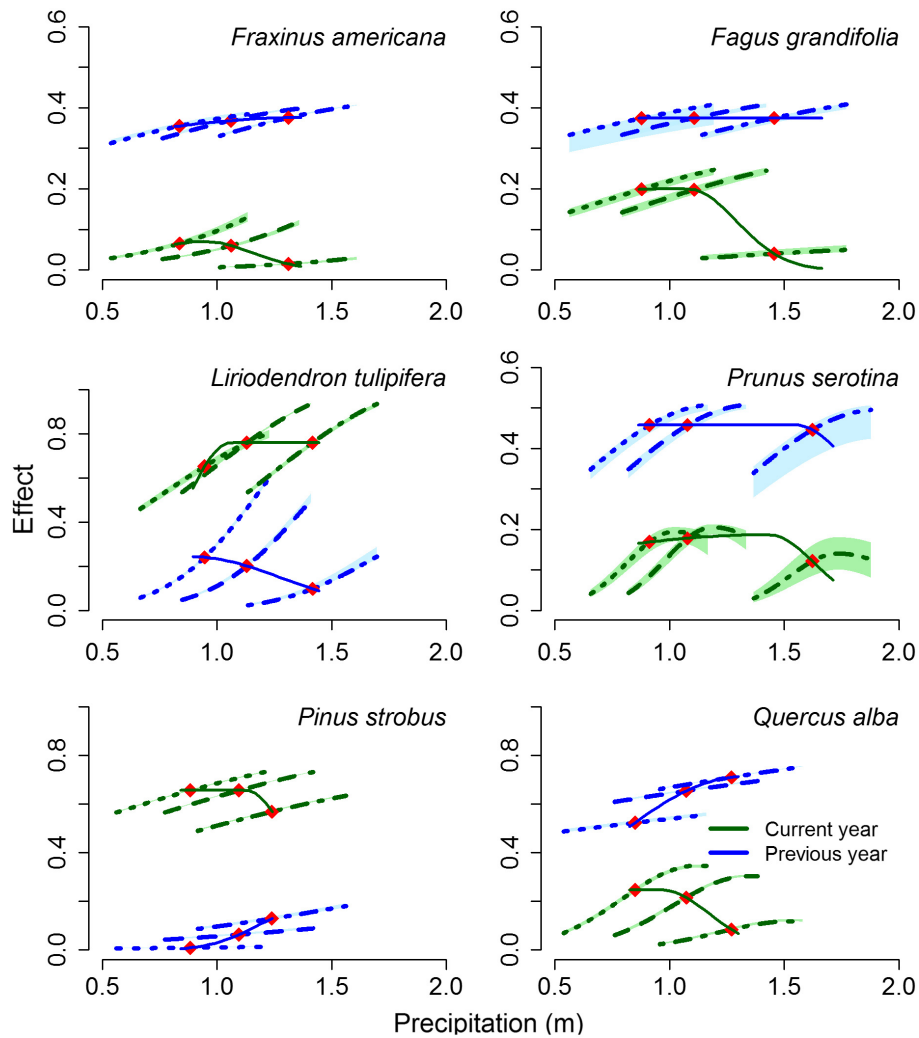
Fig. 3. Predicted effect on growth of variation in total annual precipitation for the current (green) and previous year (blue) for six representative tree species. "Effect" is the fraction of potential radial growth observed at a given precipitation, given other terms in the model. Predicted responses for the full dataset consisting of 14 species are shown in Appendix S1. The solid lines are the predicted effect of precipitation on growth when precipitation equals the long-term (1940–1980) mean precipitation at a location (i.e., the regional response). The dashed lines illustrate response to interannual variation for cores sampled at locations corresponding to the minimum, mean, and maximum long-term average precipitation in the dataset for a given species (red diamonds). Note that the model predicts a whole family of such curves with the predicted growth for a given curve centered at the long-term mean precipitation at the location of a given core. The shaded regions are two-unit support intervals around the predicted patterns of local differentiation. The cumulative effects of current and previous year precipitation are additive in these models.

shows the expected local responses (dashed lines) for cores with the minimum, mean, and maximum long-term temperature in the dataset for a given species (red diamonds in Fig. 2). But the model predicts a whole family of such curves

with the predicted growth for a given curve centered at the long-term mean temperature at the location of a given core. The most consistent pattern was for highest growth when current and/or previous years were cooler than the long-term

mean at a site (*A. rubrum, A. saccharum, F. grandifolia, L. tulipifera, F. americana, P. serotina*, and *Q. rubra*). In the two birch species (*B. alleghaniensis* and *B. papyrifera*), growth declined when current and/or previous year temperatures were warmer than the long-term mean, but did not increase in cooler years. Only two species (*Picea rubens* and *Q. prinus*) had positive responses to interannual variation in temperature relative to the long-term mean. Eastern hemlock (*T. canadensis*) was distinctive in showing effectively no response to interannual variation in temperature relative to the long-term mean. And finally, only white pine (*P. strobus*) showed optimal growth in years that matched the long-term mean temperature at a site (Fig. 2; Appendix S1).

Regional responses to long-term average precipitation vs. local responses to interannual variation

Responses of growth to both regional variation in long-term mean precipitation and interannual variation in precipitation at a given site were much more consistent across the 14 species than was the case for temperature. There was only very modest regional variation in growth as a function of long-term average precipitation, in many cases because of counter-balancing effects of current year vs. previous year precipitation (Fig. 3; Appendix S1). In contrast, there was much stronger response to interannual variation in precipitation relative to the long-term mean at a site. As in Fig. 2, Fig. 3 shows the expected local responses (dashed lines) for cores with the minimum, mean, and maximum long-term precipitation in the dataset for a given species (with the long-term mean indicated by the red diamonds in Fig. 3). But the model predicts a whole family of such curves with the predicted growth for a given curve centered at the long-term mean precipitation at the location of a given core. For 11 of the 14 species, peak growth occurred when either the current or previous year had precipitation above the long-term mean. The three exceptions were (1) *P. rubens*, in which there was very modest response to interannual average precipitation, but with peak growth under conditions very similar to the long-term mean, (2) *B. papyrifera*, in which growth declined in years that were drier than long-term mean but did not respond to wetter

years, and (3) *B. alleghaniensis*, for which there was no statistical support for response to interannual variation in precipitation relative to the long-term mean (Appendix S1).

Size and age effects

The age and size terms in the model account for effects of ontogeny (age) and the competitive status of a tree in a stand (size relative to age). As expected, the individual terms have opposite patterns: Growth declines with age and increases with size (Appendix S2). But the age effects are strong enough that growth generally declines with size given the mean age of a species at that size. While the age effects were quite consistent regardless of size at a given age, there was much greater variability in growth as a function of size depending on the age of a stem relative to that size (Appendix S2).

Discussion

Our results indicate that—at least in terms of adult tree growth—either local genetic adaptation or phenotypic acclimation to long-term mean climate is ubiquitous in the most common tree species in forests of eastern North America. Our results also suggest that local responses to interannual variation in climate can be very different than, and in many cases opposite to, regional-scale variation in responses to mean climate. Spatial analyses of variation in tree growth using FIA plot data show very modest regional variation in response to temperature for most eastern U.S. tree species (Canham and Murphy 2016a). But within a site, our results mirror other recent studies that suggest that warmer and drier than average years are typically associated with lower than average growth (Ashiq and Anand 2016, Hacket-Pain et al. 2016, Tei et al. 2017). The effects of this combination of climate conditions on soil water deficits, vapor pressure deficits, and drought stress provide one likely mechanism for the observed response to variation in precipitation, even in the generally mesic, cool temperate climate of the northeastern United States (Noormets et al. 2008, Knutzen et al. 2017).

Our analyses do not allow us to discriminate between genetic adaptation vs. phenotypic acclimation, and those two possible mechanisms are

not mutually exclusive. It is worth noting that unlike many tree species of western North America in which strongly disjunct populations have clear genetic differentiation in their climate responses (Rehfeldt et al. 1999, Buechling et al. 2017), eastern North American tree species tend to have much more continuous geographic distributions. Despite this, there is ample evidence of genetic differentiation within even widely and continuously distributed temperate tree species (Aitken et al. 2008, Alberto et al. 2013). Nonetheless, we consider phenotypic acclimation an alternative and potentially more parsimonious explanation for the patterns we have observed. For example, the ability of adult trees to maximize growth in unusually wet and cool years could reflect long-term investment in construction of a root system that optimizes water uptake in those years, but with high maintenance costs in warmer, drier years.

There are clearly other functional forms for the climate responses that could be tested with these data. For example, in the interests of parsimony we have assumed a common shape to the response to interannual variability across the entire range of a species. For the most common species such as red maple, the models could be extended to test whether the shapes of the local responses themselves varied as a function of long-term mean climate. And many dendro-climatology studies test a large candidate set of climate variables, often representing different months and seasons. But even with datasets as large as the ones we use here, the very strong collinearity among those sub-annual temporal scale climate variables creates a strong potential for model selection uncertainty and idiosyncrasy in the selection of explanatory variables. Model comparison using likelihood and information theory (AIC) has become ubiquitous as a form of hypothesis testing in ecology, but without a strong mechanistic basis for the selection of alternate models, our analyses remain phenomenological. It seems abundantly clear that the nature of climate effects on metabolic relationships at the cellular and leaf scale cannot be simply scaled up and applied to measures of whole plant growth, particularly for a component of growth such as stem diameter increment that represents just one potential allocation of net photosynthesis.

Ultimately, it will be critical to understand whether the patterns we have observed represent genetic adaptation or phenotypic acclimation, or some combination of the two. The consequences for responses of these tree species to climate change could be very different depending on that balance. If the results are genetically based, trees within a given location could be much more sensitive to climate change than indicated by the very broad geographic distributions of these temperate tree species. But if the results are phenotypic, this would represent local acclimation that could help buffer species in the face of climate change. Adult tree growth is a dominant term in interannual variation in forest productivity and the attendant ecosystem properties associated with primary productivity, including carbon sequestration and nutrient retention. But from a demographic perspective, adult tree growth is much less important to the geographic distribution and successional dynamics of these temperate tree species than are other life history stages, particularly seedling recruitment and survival, and adult tree mortality (Pacala et al. 1996, Canham and Murphy 2016a, b, 2017). It remains an open question whether the ubiquitous local adaptation to long-term climate conditions we have documented for adult tree growth in these temperate tree species is present in those other critical life history stages.

Acknowledgments

Literature Cited

Aitken, S. N., S. Yeaman, J. A. Holliday, T. Wang, and S. Curtis-McLane. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications 1:95–111.

Alberto, F. J., et al. 2013. Potential for evolutionary responses to climate change evidence from tree populations. Global Change Biology 19:1645–1661.

Ashiq, M. W., and M. Anand. 2016. Spatial and temporal variability in dendroclimatic growth response of red pine (*Pinus resinosa* Ait.) to climate in northern Ontario, Canada. Forest Ecology and Management 372:109–119.

Buechling, A., P. H. Martin, and C. D. Canham. 2017. Climate and competition effects on tree growth in Rocky Mountain forests. Journal of Ecology 105:1636–1647.

Canham, C. D., and L. Murphy. 2016*a*. The demography of tree species response to climate: sapling and canopy tree growth. Ecosphere 7(10):e01474.

Canham, C. D., and L. Murphy. 2016*b*. The demography of tree species response to climate: seedling recruitment and survival. Ecosphere 7(8): e01424.

Canham, C. D., and L. Murphy. 2017. The demography of tree species response to climate: sapling and canopy tree survival. Ecosphere 8(2):e01701.

Carter, K. K. 1996. Provenance tests as indicators of growth response to climate change in 10 north temperate tree species. Canadian Journal of Forest Research 26:1089–1095.

Cunningham, S. C., and J. Read. 2003. Do temperate rainforest trees have a greater ability to acclimate to changing temperatures than tropical rainforest trees? New Phytologist 157:55–64.

Drake, J. E., M. J. Aspinwall, S. Pfautsch, P. D. Rymer, P. B. Reich, R. A. Smith, K. Y. Crous, D. T. Tissue, O. Ghannoum, and M. G. Tjoelker. 2015. The capacity to cope with climate warming declines from temperate to tropical latitudes in two widely distributed *Eucalyptus* species. Global Change Biology 21:459–472.

Hacket-Pain, A. J., L. Cavin, A. D. Friend, and A. S. Jump. 2016. Consistent limitation of growth by high temperature and low precipitation from range core to southern edge of European beech indicates widespread vulnerability to changing climate. European Journal of Forest Research 135:897–909.

Hornbeck, J. W., R. B. Smith, and C. A. Federer. 1988. Growth trends in 10 species of trees in New England, 1950–80. Canadian Journal of Forest Research 18:1337–1340.

Kerkhoff, A. J., P. E. Moriarty, and M. D. Weiser. 2014. The latitudinal species richness gradient in New World woody angiosperms is consistent with the tropical conservatism hypothesis. Proceedings of the National Academy of Sciences USA 111:8125–8130.

Knutzen, F., C. Dulamsuren, I. C. Meier, and C. Leuschner. 2017. Recent climate warming-related growth decline impairs European beech in the center of its distribution range. Ecosystems 20:1494–1511.

Latreille, A., H. Davi, F. Huard, and C. Pichot. 2017. Variability of climate-radial growth relationship among *Abies alba* trees and populations along altitudinal gradients. Forest Ecology and Management 396:150–159.

Loehle, C. 1998. Height growth rate tradeoffs determine northern and southern range limits for trees. Journal of Biogeography 25:735–742.

Manthey, M., and E. O. Box. 2007. Realized climatic niches of deciduous trees: comparing western Eurasia and eastern North America. Journal of Biogeography 34:1028–1040.

McCullough, I. M., F. W. Davis, and A. P. Williams. 2017. A range of possibilities: assessing geographic variation in climate sensitivity of Ponderosa pine using tree rings. Forest Ecology and Management 402:223–233.

Noormets, A., S. G. McNulty, J. L. DeForest, G. Sun, Q. Li, and J. Chen. 2008. Drought during canopy development has lasting effect on annual carbon balance in a deciduous temperate forest. New Phytologist 179:818–828.

Ostonen, I., K. Rosenvald, H. S. Helmisaari, D. Godbold, K. Parts, V. Uri, and K. Lohmus. 2013. Morphological plasticity of ectomycorrhizal short roots in *Betula* sp and *Picea abies* forests across climate and forest succession gradients: its role in changing environments. Frontiers in Plant Science 4:355. http://doi.org/10.3389/fpls.2013.00335

Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander Jr., R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: II. Estimation, error analysis and dynamics. Ecological Monographs 66:1–43.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rehfeldt, G. E., C. C. Ying, D. L. Spittlehouse, and D. A. Hamilton. 1999. Genetic responses to climate in *Pinus contorta*: niche breadth, climate change, and reforestation. Ecological Monographs 69:375–407.

Rollinson, C. R., M. W. Kaye, and C. D. Canham. 2016. Interspecific variation in growth responses to climate and competition in five eastern tree species. Ecology 97:1003–1011.

Scafaro, A. P., S. Xiang, B. M. Long, N. H. A. Bahar, L. K. Weerasinghe, D. Creek, J. R. Evans, P. B. Reich, and O. K. Atkin. 2017. Strong thermal acclimation of photosynthesis in tropical and temperate wet-forest tree species: the importance of altered Rubisco content. Global Change Biology 23:2783–2800.

Schenk, H. J. 1996. Modeling the effects of temperature on growth and persistence of tree species: a critical review of tree population models. Ecological Modelling 92:1–32.

Smith, R. B., J. W. Hornbeck, C. A. Federer, and P. J. Krusic Jr.. 1990. Regionally averaged diameter growth in New England forests. Research Paper NE-637. USDA Forest Service, Northeastern Forest Experiment Station, Radnor, Pennsylvania, USA.

Smith, B., I. C. Prentice, and M. T. Sykes. 2001. Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. Global Ecology and Biogeography 10:621–637.

Tei, S., A. Sugimoto, H. Yonenobu, Y. Matsuura, A. Osawa, H. Sato, J. Fujinuma, and T. Maximov. 2017. Tree-ring analysis and modeling approaches yield contrary response of circumboreal forest productivity to climate change. Global Change Biology 23:5179–5188.

Way, D. A., and R. Oren. 2010. Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. Tree Physiology 30:669–688.

Wiens, J. J., and M. J. Donoghue. 2004. Historical biogeography, ecology and species richness. Trends in Ecology and Evolution 19:639–644.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2368/full