

Competition alters tree growth responses to climate at individual and stand scales

Kevin R. Ford, Ian K. Breckheimer, Jerry F. Franklin, James A. Freund, Steve J. Kroiss, Andrew J. Larson, Elinore J. Theobald, and Janneke HilleRisLambers

Abstract: Understanding how climate affects tree growth is essential for assessing climate change impacts on forests but can be confounded by effects of competition, which strongly influences tree responses to climate. We characterized the joint influences of tree size, competition, and climate on diameter growth using hierarchical Bayesian methods applied to permanent sample plot data from the montane forests of Mount Rainier National Park, Washington State, USA, which are mostly comprised of *Abies amabilis* Douglas ex Forbes, *Tsuga heterophylla* (Raf.) Sarg., *Pseudotsuga menziesii* (Mirb.) Franco, and *Thuja plicata* Donn ex D. Don. Individual growth was sensitive to climate under low but not high competition, likely because tree ability to increase growth under more favorable climates (generally greater energy availability) was constrained by competition, with important variation among species. Thus, climate change will likely increase individual growth most in uncrowded stands with lower competition. However, crowded stands have more and (or) larger trees, conferring greater capacity for aggregate absolute growth increases. Due to these contrasting effects, our models predicted that climate change will lead to greater stand-scale growth increases in stands with medium compared with low crowding but similar increases in stands with medium and high crowding. Thus, competition will mediate the impacts of climate change on individual- and stand-scale growth in important but complex ways.

Key words: climate change, competition, Pacific Northwest, stand structure, water balance.

Résumé : Il est essentiel de comprendre comment le climat influence la croissance des arbres pour évaluer les impacts des changements climatiques sur la croissance des forêts, mais les effets du climat peuvent être confondus avec ceux de la compétition qui influence grandement la réaction des arbres au climat. Nous avons caractérisé l'influence conjointe de la taille des arbres, de la compétition et du climat sur la croissance en diamètre à l'aide de méthodes hiérarchiques bayésiennes appliquées à des données provenant de placettes échantillons permanentes dans les forêts montagnardes du parc national du mont Rainier dans l'État de Washington, aux États-Unis. Ces forêts sont surtout composées d'*Abies amabilis* Douglas ex Forbes, de *Tsuga heterophylla* (Raf.) Sarg., de *Pseudotsuga menziesii* (Mirb.) Franco et de *Thuja plicata* Donn ex D. Don. La croissance des arbres individuels était sensible au climat lorsque la compétition était faible mais pas lorsqu'elle était forte, probablement parce que la capacité des arbres à augmenter leur croissance sous des climats plus favorables (généralement plus de disponibilité d'énergie) était limitée par la compétition et la variation entre les espèces était importante. Ainsi, les changements climatiques augmenteront probablement davantage la croissance des arbres individuels dans les peuplements plus ouverts où la compétition est faible. Cependant, les peuplements denses comportent plus d'arbres ou des arbres plus gros, ce qui leur confère une plus grande capacité pour augmenter leur croissance totale absolue. À cause de ces effets contrastés, nos modèles prévoient une plus grande augmentation de la croissance due aux changements climatiques dans les peuplements de densité moyenne que de densité faible, mais des augmentations similaires dans les peuplements de densités moyenne et forte. Par conséquent, la compétition va conditionner les impacts des changements climatiques sur la croissance des arbres et des peuplements, et ce, de façon importante mais complexe. [Traduit par la Rédaction]

Mots-clés : changements climatiques, compétition, région du Nord-Ouest du Pacifique, structure des peuplements, bilan hydrique.

Introduction

Understanding the relationship between tree growth and climate is essential for assessing the impacts of climate change on forests, but it is confounded by the effects of competition on growth. While climate is a fundamental driver of growth (e.g., Chmura et al. 2011), other factors often have equal or greater influence (Ettinger and HilleRisLambers 2013; Zhang et al. 2015). Competition, as measured by the degree of crowding by neighboring trees, is one such factor that is an important determinant of individual- and stand-scale growth (Curtis 1970; Das 2012) and has the potential to alter

growth responses to differences in climate (Clark et al. 2011). Characterizing the joint influences of climate and competition on tree growth is critical because growth plays a key role in determining forest composition, structure, and function, both directly through physiological processes (e.g., biomass production) and indirectly through the influence of growth on survival and population dynamics (Moorcroft et al. 2001; Wyckoff and Clark 2002). Climate and competition have each been the focus of numerous tree growth studies, but their interacting effects on growth and other vital rates have received little attention relative to their importance for forest dynam-

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ics (Clark et al. 2014; but see Clark et al. 2011; Fernández-de-Uña et al. 2015; Linares et al. 2010).

Notably, the effects of climate on growth have not been explicitly incorporated into many empirical forest growth and yield models, which quantify the joint influences of site quality, competition, and tree attributes on individual-tree performance using measurements from forest stands. Often, growth and yield models characterize site quality using site index, a metric based on the observed height growth rates of dominant and co-dominant trees at a particular location (with greater height growth rates presumed to be indicative of greater productivity). Because site index is based on tree growth itself, it has the potential to successfully integrate the effects of many different environmental factors (i.e., both climatic and nonclimatic factors) and has been an effective measure of site quality in many situations (Weiskittel et al. 2011). However, the usefulness of site index for predicting stand dynamics in the future will likely be diminished as the magnitude of climate change increases and height growth rates under past climates become poorer indicators of performance under future climates. Similarly, models using a stand's latitude, longitude, and (or) elevation to characterize site quality will become less useful as future climates at a location become increasingly different from past climates. Explicitly modeling growth as a function of climate avoids this problem, yields more insight into the mechanisms behind patterns in growth, and can potentially provide more realistic projections of future growth.

In this study, we address these issues by extending a well-accepted growth modeling approach to characterize the interactive effects of climate and competition on tree diameter growth, a process that can ultimately provide forest managers with useful tools to prepare for climate change (Crookston et al. 2010). Specifically, we based our models on the diameter growth equation developed for ORGANON, which is an effective and widely used growth and yield model for tree species in the Pacific Northwest region of North America but does not explicitly include the effects of climate (Hann et al. 2006). In ORGANON, the diameter growth of an individual tree is a function of site index, symmetric competition (in which all neighboring trees have competitive impacts on the focal tree), asymmetric competition (in which only larger neighbors have competitive impacts), and tree-level attributes. The key conceptual change that we made was to use climate variables to characterize site quality instead of site index, thereby allowing for direct examination (and, ultimately, prediction) of the links between climate, competition, and growth.

Climatic water balance variables are a potentially useful way to incorporate climate effects into growth and yield models. These variables are indicators of the availability of energy and water for plant growth, where energy availability is a function of temperature and insolation, and water availability is a function of water inputs to the soil from rain and snowmelt, the water holding capacity of the soil, and previous evapotranspiration. Thus, these variables integrate information on the values and seasonal dynamics of temperature, precipitation, insolation, snowpack, and soil moisture. While the annual and seasonal means of temperature and precipitation that are often used in climate-growth studies can be calculated more directly from data provided by climate stations or models, water balance variables are more physiologically meaningful and are often better predictors of plant growth and ecological processes across a wide range of climates (Littell et al. 2008; Rosenzweig 1968; Stephenson 1998). Also, because water balance variables integrate multiple environmental factors, they allow researchers to incorporate complex climatic effects into growth models that already have parameters for competition and tree attributes with few additional parameters. Thus, we used climatic water balance variables to characterize the climate trees experienced.

We conducted our study in mature and old-growth forests in the western Cascade Range of Washington State, USA (part of the Pacific Northwest region). These mid- to high-elevation forests

experience cool temperatures, abundant precipitation, and persistent snowpacks, and growth in these environments is thought to currently be limited mostly by the availability of energy (as well as stresses associated with low-energy environments such as frost and snow damage) and not water (Albright and Peterson 2013; Ettinger et al. 2011; Ettinger and HilleRisLambers 2013). Climate models suggest that the Pacific Northwest could experience substantially higher temperatures in the future, but projected changes in precipitation are uncertain (Mote et al. 2013). These forests provide valuable ecosystem services, including habitat for endangered species and exceptionally high levels of carbon storage (National Research Council (NRC) 2000; Smithwick et al. 2002), so it is important to understand how climate change might impact tree growth and the functioning of these ecosystems (Littell et al. 2013).

Abies amabilis Douglas ex Forbes (Pacific silver fir), *Tsuga heterophylla* (Raf.) Sarg. (western hemlock), *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir), and *Thuja plicata* Donn ex D. Don (western redcedar) are some of the most widespread and abundant species in these forests and play critical ecological and economic roles in the region (Franklin and Dyrness 1988). In the western Cascade Range, *A. amabilis* tends to be located at higher elevations with colder and wetter climates compared with the other focal species, which are most abundant at lower elevations with warmer and drier climates. All of these species are found on a wide variety of soils. *Pseudotsuga menziesii* tends to dominate young stands, with some individuals often persisting for over 1000 years, though recruitment in older stands is very low; the other species tend to be rare in young stands but become abundant or dominant as stands age (Franklin et al. 1988).

The objectives of our analyses were to (i) examine how climate, competition, and their interaction influence tree growth to assess how growth responses to climatic gradients differ based on the local competitive environment and how these effects might vary among tree species, (ii) project potential impacts of climate change on individual-tree growth across a range of local competitive environments, and (iii) assess how these impacts of climate change on growth at the individual scale will translate into impacts on aggregate tree growth at the stand scale in stands with differing levels of competition.

Methods

Study area

Our study plots were established in mature and old-growth forests in Mount Rainier National Park, which occupies a rugged mountainous landscape with large elevation, topographic, and climatic gradients, encompassing 95 354 ha of the western Cascade Range in Washington State, USA (Fig. 1). The region experiences a temperate, maritime climate with cool, wet winters and mild, relatively dry summers. Temperatures decrease with elevation, whereas precipitation increases. Precipitation is also lower on the eastern side of the Park due to rain shadow effects. Thus, the Park supports a wide range of climatic conditions that are representative of mountain climates west of the Cascade Crest in the Pacific Northwest region. The forests are also notable for their abundance of old stands with heterogeneous structure, so that tree species experience a wide range of competitive environments (Franklin et al. 1988).

Tree data

We surveyed trees at 15 permanent sample plots established at Mount Rainier in 1977 and 1978 as part of the Pacific Northwest Forest Permanent Sample Plot Network. These plots span an elevational range of 581 to 1452 m (Table 1; Fig. 1). Each 100 × 100 m (1 ha) square-shaped plot was divided into sixteen 25 × 25 m subplots. In each subplot, all trees with a diameter at breast height greater than 15 cm were marked with metal tags placed at breast height (1.37 m). In some subplots, we also marked all trees between 5 and 15 cm diameter. The surviving trees and any new trees

Fig. 1. Map of the study area — Mount Rainier National Park. [This figure is available in colour online.]

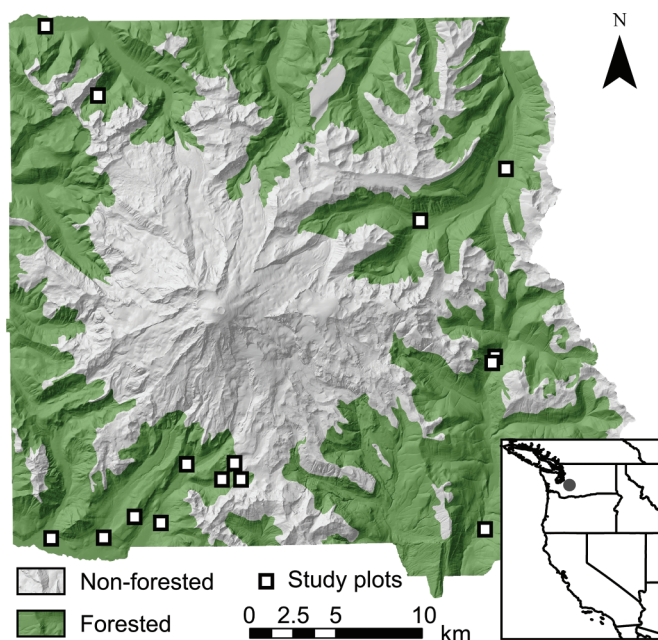


Table 1. Plot characteristics.

Plot	Elevation (m)	PET (mm)	AET (mm)	Deficit (mm)	Stand age (years)
TO11	581	497	425	73	550
TA01	647	554	413	141	250
TO04	659	514	416	98	750
TB13	825	516	418	99	150
AV02	857	441	332	109	1000
AO03	866	437	329	107	1000
AG05	925	493	404	89	650
AV06	1051	437	361	76	750
AB08	1061	439	318	121	750
AX15	1074	396	328	69	150
AV14	1101	323	296	27	1200
PP17	1147	391	298	94	550
AM16	1185	416	350	66	600
AE10	1449	338	300	39	300
AR07	1452	241	224	18	330

Note: PET, potential evapotranspiration; AET, actual evapotranspiration; Deficit, climatic water deficit. Stand age from Franklin et al. (1988).

that grew to become larger than the minimum diameter threshold (5 or 15 cm, depending on the subplot) were re-measured at the height of the tags using diameter tape about every 5 years through 2008 (Acker et al. 1998; Larson and Franklin 2010) (Table 2).

We used these data to model the growth rates of all measured trees in the plots (controlling for differences in growth rate among species) and fit species-specific growth models for tree species that met the following criteria: (i) were present in plots that spanned an elevational range of at least 500 m (so they experienced a wide range of climates), (ii) had at least 15 individuals per plot in a minimum of six plots, and (iii) had a total of 100 individuals across all plots. Four of the 17 species in the plots met all criteria and represented 84% of all individuals in the study: *A. amabilis*, *T. heterophylla*, *P. menziesii*, and *T. plicata* (Table 2).

We used these tree diameter measurements to calculate tree size, growth rate, and competition metrics for each tree while it was alive and included in the surveys. For the analyses, we used the midpoint of the individual's diameter over the time that it was tracked in the study as our measure of tree size. We calculated the

Table 2. Tree measurement information.

Plot	Years measured	No. of surveys	Mean diameter (cm)	Number of trees				
				All	ABAM	TSHE	PSME	THPL
TO11	1978–2008	6	59.9	192	0	159	15	16
TA01	1977–2007	7	47.9	381	10	224	134	2
TO04	1978–2008	6	38.2	338	58	243	7	18
TB13	1978–2008	6	44.6	426	15	244	120	47
AV02	1977–2008	7	18.9	1223	1036	176	4	6
AO03	1977–2008	7	38.9	410	296	102	3	9
AG05	1978–2008	6	33.2	603	242	193	19	98
AV06	1978–2007	6	24.0	709	449	245	6	6
AB08	1978–2008	6	45.5	355	30	238	17	64
AX15	1978–2008	6	33.1	704	8	420	212	64
AV14	1978–2008	6	40.3	339	179	156	0	0
PP17	1978–2008	6	20.1	542	4	61	127	0
AM16	1978–2007	6	30.8	533	306	39	0	0
AE10	1978–2007	6	39.1	635	325	0	0	0
AR07	1978–2007	6	45.2	418	150	0	0	0
All			33.5	7808	3108	2500	664	330

Note: ABAM, *Abies amabilis*; TSHE, *Tsuga heterophylla*; PSME, *Pseudotsuga menziesii*; THPL, *Thuja plicata*.

mean annual diameter growth rate for each tree in the study as the change in diameter over the time that it was tracked, divided by the number of years in which it was tracked (thus, each data point in the analyses represented one tree from the study). We used this long-term mean value of growth, instead of the growth measurements from each survey, to reduce the effects of measurement error, which could potentially be large relative to the very small growth increments typically observed during the ~5-year measurement intervals. Over the single measurement intervals, the median diameter growth increment was 0.7 cm and the median relative growth increment was 2.4% of the tree's diameter; over the whole study, the median diameter growth increment was 2.8 cm and the median relative growth increment was 10.2% of the tree's diameter. For each tree, we defined basal area (BA) as the total basal area of all trees in the focal tree's 25 × 25 m subplot (our measure of symmetric competition) and defined basal area of larger trees (BAL) as the basal area of all trees in the subplot larger than the focal tree, based on diameter (our measure of asymmetric competition).

Climate data

We calculated three water balance variables to represent the climate that trees experienced at each plot for each year of the study (1977–2008): (i) potential evapotranspiration (PET), an indicator of the amount of energy available for growth, (ii) actual evapotranspiration (AET), an indicator of the simultaneous availability of energy and water for growth, and (iii) climatic water deficit (Deficit), an indicator of the magnitude of drought stress. To calculate these variables, we used a Thornthwaite-type water balance model following Lutz et al. (2010), an approach considered most appropriate when temperature and precipitation data are available but reliable measures of humidity and wind speed are not (Dingman 2002), as was the case in this study.

The model characterizes the water balance at a location on a monthly time step as follows. Water enters the system as precipitation, with the fraction falling as rain versus snow determined by temperature. The snow accumulates in a snowpack and melts at a rate determined by temperature. Water supply to the soil is the sum of rain and snowmelt, with the maximum amount of water held in the soil determined by the soil's water holding capacity, which we extracted from the Natural Resources Conservation Service (NRCS) SSURGO database (NRCS 2015). The model tracks water availability in the top 150 cm of the soil, the depth to which soil data were available. Water leaves the system through

evapotranspiration or through runoff or subsurface flow (surplus). PET is the amount of evapotranspiration that would occur at the location for a hypothetical standard vegetation cover with unlimited water and increases with air temperature and insolation (with the estimate of insolation being a function of day length, latitude, slope, and aspect). AET is the amount of evapotranspiration from that same hypothetical standard vegetation cover with the actual water availability and is equal to either PET or available water, whichever is lower. Deficit is the amount of PET not met by available water and is equal to PET minus AET.

We estimated monthly mean temperature and precipitation at each plot for each year of the study by combining information from recordings at the Longmire weather station located within Mount Rainier National Park at 842 m (www.ncdc.noaa.gov) and the 1971–2000 climatological normals from the 800 m PRISM climate map (Daly et al. 2008) following the methods in Ettinger et al. (2011). For each tree, we calculated the mean of the annual sums of monthly estimates of PET, AET, and Deficit over all of the years that the tree was included in the study (we used water years, which run from 1 October of the previous year to 30 September of the current year). In addition, we calculated annual water balance variables at the plots for future time periods under different climate change scenarios using the monthly temperature and precipitation estimates from ClimateWNA (Wang et al. 2012) based on the ensemble projections of climate models used for informing the 5th Assessment Report of the Intergovernmental Panel on Climate Change (IPCC 2013). We then used these values to estimate mean tree growth rates under possible future climates.

Data analysis

We fit a diameter growth model for all trees in the study that controlled for differences in growth rate among species (hereafter, the “all-trees” model), as well as species-specific growth models for each of the four focal species. The deterministic component of our model was based on the diameter growth equation from ORGANON (Hann et al. 2006) and was

$$(1) \quad \sqrt{\text{Growth}} = \sum_{i=0}^7 \beta_i x_i$$

where Growth is mean annual diameter growth rate ($\text{cm}\cdot\text{year}^{-1}$); $x_0 = 1$; $x_1 = \ln(\text{Diameter})$; $x_2 = \text{Diameter}$; $x_3 = \text{BAL}/\ln(\text{Diameter})$; $x_4 = \sqrt{\text{BA}}$; $x_5 = \sqrt{\text{PET}}$; $x_6 = \sqrt{\text{AET}}$; and $x_7 = \sqrt{\text{Deficit}}$.

Equation 1 represents the full range of explanatory variables considered. We fit the models with hierarchical Bayesian methods and used model selection based on the deviance information criterion (DIC) to help determine which set of explanatory variables to include in the final model. DIC was developed to evaluate competing models fit to the same data set using Bayesian methods (Spiegelhalter et al. 2002). Models with lower deviance and lower number of effective parameters have better (lower) DIC values.

We included normally distributed random effects of subplots (nested within plots) on the intercept of the model (β_0) to account for variability among locations in unmeasured factors that could influence site quality. For the all-trees model, we also included normally distributed random effects of species on β_0 to account for variability in growth rates among species. We used a normal error distribution and found that using square-root-transformed growth values led to normally distributed residuals, while other transformations and the untransformed values did not. The square-root transformation required us to exclude negative growth values. However, this exclusion affected only a small portion of the dataset (2.9%). We also tried fitting nonlinear versions of the model (as in ORGANON), but those did not converge.

Because variance in growth often increases with tree size, we allowed the standard deviation of square-root-transformed growth

to vary by tree diameter. To determine how to best characterize this relationship for each focal species and the all-trees analysis, we fit candidate models in which the standard deviation of transformed growth either did not vary with diameter, varied with x_1 , varied with x_2 , or varied with both x_1 and x_2 . In each of these candidate models, transformed growth was a function of both x_1 and x_2 . We calculated DIC for each candidate model to select the best model and used that model’s standard deviation component in all subsequent modeling.

Next, for each focal species and the all-trees analysis, we fit additional candidate models that differed by which combination of competitive environment (x_3, x_4) and climatic water balance explanatory variables (x_5, x_6, x_7) were included. We calculated DIC for each candidate model to aid in climate and competition variable selection. After selecting the final set of explanatory variables, we added parameters for interactions between the selected climate and competition variables (regardless of whether the interaction parameters improved model fit) to ensure that we realistically characterized the interactive effects of climate and competition on growth and to avoid spurious interaction effects that could be artifacts of model form. For example, the equation for the final model in the all-trees analysis was

$$(2) \quad \sqrt{\text{Growth}} = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_5 x_5 + \beta_{\text{int}} x_3 x_5$$

where β_{int} is the parameter for the interaction between x_3 and x_5 (the terms that include the BAL competition variable and the PET climate variable, respectively).

We fit the models using Markov chain Monte Carlo (MCMC) simulation techniques implemented in JAGS using the rjags package and GLM module (Plummer 2014) in R version 3.1.2 (R Core Team 2014). We used the normalized values of all terms in the model (x_i) and assigned non-informative prior distributions to all parameters. For standard deviation parameters, we assigned uniform prior distributions on the interval 0–10. For intercepts and coefficients (β_i), we assigned flat normal prior distributions with a mean of 0 and a standard deviation of 100. We ran the models with three MCMC chains and a burn-in of 1000 iterations and continued each MCMC run for 1000 more iterations (the GLM module in JAGS can allow chains to converge with relatively few iterations). We confirmed that the chains had converged using the Gelman–Rubin statistic and visual inspection of the chains and posterior parameter distributions.

We then used the final model for each species (and the all-trees analysis) to assess how mean individual growth rate varied across different combinations of climatic and competitive conditions and to project the impact of climate change on individual growth under different levels of competition. Our goal was to apply our models to real populations of trees with representative distributions of individual sizes, while avoiding any confounding effects that variation in tree size among plots and subplots could have on characterizing the relationship between growth and climate or competition. To do this, we used the fitted growth models to calculate the mean expected growth rate for each species (or all trees) under different combinations of climatic and competitive conditions based on the data for all measured individuals across all study plots during the survey closest to the midpoint of the study (i.e., we calculated the mean expected growth rate for the same set of trees under different combinations of climate and competition).

We also used the all-trees model to calculate how total growth at the stand scale varies with climate and competitive environment to assess the impacts of climate change on stand-scale growth rates. First, we considered the trees observed at each of the 240 subplots during the survey closest to the midpoint of the study to be a sampling of stands that covered a range of competitive environments, each with a particular distribution of tree sizes and degree of crowding. We then estimated the annual diameter growth of each tree greater than 15 cm diameter in each of these 240 subplots under

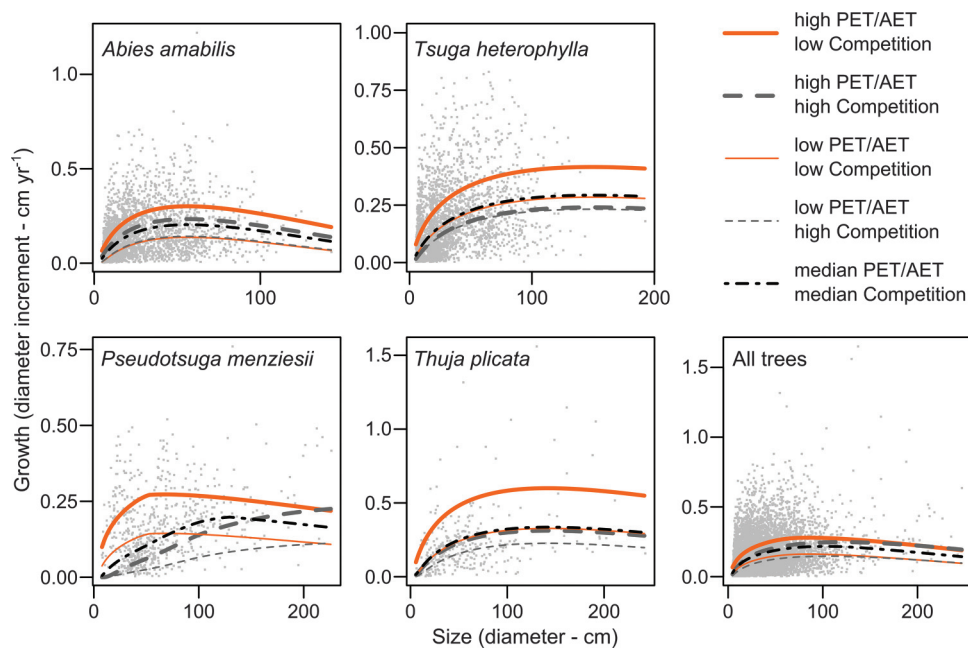
Table 3. Best estimates for model parameters (β_i) with 95% credible intervals in parentheses.

β_i^*	All trees	<i>Abies amabilis</i>	<i>Tsuga heterophylla</i>	<i>Pseudotsuga menziesii</i>	<i>Thuja plicata</i>
β_0	0.35 (0.33, 0.38)	0.33 (0.32, 0.35)	0.39 (0.38, 0.41)	0.39 (0.37, 0.41)	0.45 (0.42, 0.48)
β_1	0.093 (0.083, 0.103)	0.15 (0.14, 0.17)	0.11 (0.10, 0.13)	0.030 (-0.007, 0.070)	0.14 (0.10, 0.19)
β_2	-0.037 (-0.045, -0.029)	-0.071 (-0.084, -0.059)	-0.025 (-0.042, -0.009)	-0.029 (-0.065, 0.006)	-0.062 (-0.119, -0.007)
β_3	-0.026 (-0.034, -0.017)	—	—	-0.066 (-0.083, -0.049)	—
β_4	—	-0.010 (-0.023, 0.0015)	-0.043 (-0.057, -0.029)	—	-0.055 (-0.087, -0.023)
β_5	0.040 (0.029, 0.051)	0.048 (0.037, 0.060)	0.017 (0.003, 0.032)	0.042 (0.014, 0.069)	—
β_6	—	—	—	—	0.038 (0.006, 0.068)
β_{int}	-0.0054 (-0.0091, -0.0015)	-0.0087 (-0.022, 0.0040)	-0.011 (-0.024, 0.002)	-0.0033 (-0.0155, 0.0087)	-0.014 (-0.045, 0.016)
r^2	0.40	0.45	0.46	0.56	0.70

Note: We used the normalized values of the terms (x_i in eq. 1) for model fitting. The r^2 value for each model indicates the correlation between predicted and observed growth values.

*The terms associated with each parameter (β_i) are as follows: β_0 (the intercept, 1; β_1 , $\ln(\text{Diameter})$; β_2 , Diameter; β_3 , BAL/ $\ln(\text{Diameter})$; β_4 , $\sqrt{\text{BA}}$; β_5 , $\sqrt{\text{PET}}$; β_6 , $\sqrt{\text{AET}}$; β_{int} , the interaction effect for the terms related to competition (x_3 or x_4 , the terms with BAL and BA, respectively) and climate (x_5 or x_6 , the terms with PET and AET, respectively). See eq. 1.

Fig. 2. The relationship between growth and size (diameter) varies by climate and competitive environment. The measure of climate was AET (simultaneous availability of energy and water for growth) for *Thuja plicata* and PET (availability of energy for growth) for the rest. The measure of competition was BAL (asymmetric competition) for *Pseudotsuga menziesii* and the all-trees model and BA (symmetric competition) for the rest. To illustrate how the growth–size relationship varies under different climatic and competitive conditions, we show the curves for the expected growth rates when climate or competition variables are high (90th percentile), low (10th percentile), or at the median. For model fitting, we used the square-root-transformed growth values but show model predictions on the untransformed scale in these plots. [This figure is available in colour online.]



different climate conditions (current and future) given the subplot's competitive environment (based on all trees greater than 15 cm diameter). Finally, we converted our estimates of diameter growth to estimates of aboveground biomass accrual (a more appropriate measure of stand-scale growth) using taxon-specific allometric equations (Jenkins et al. 2003) and summed these individual biomass accrual values to estimate aggregate growth at the stand scale under current and future climate conditions.

Results

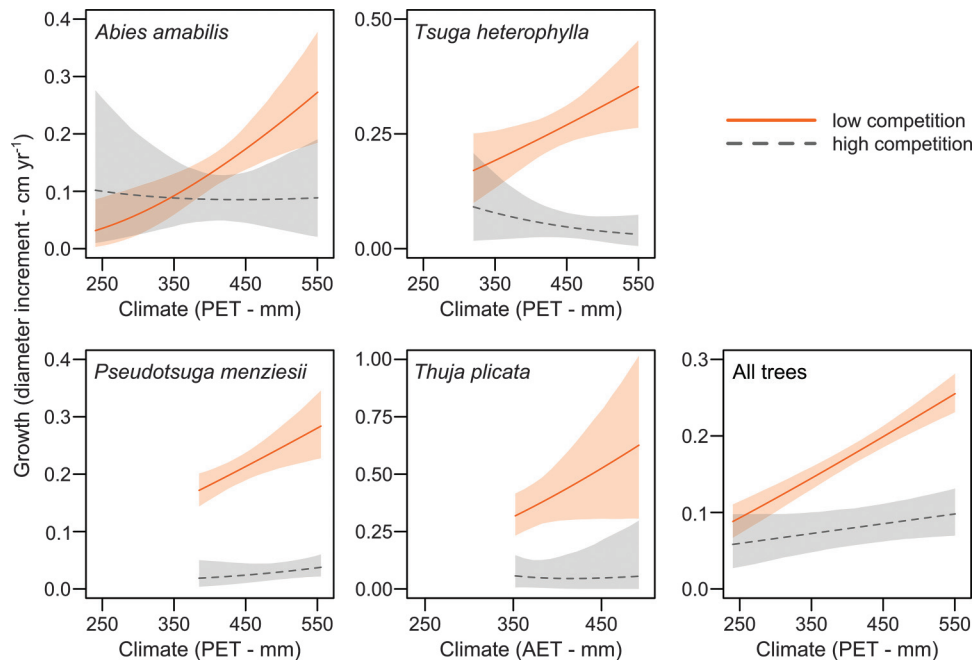
Tree size, competition, and climate all had important impacts on growth. Individual growth varied nonlinearly with size, and this relationship differed by species, competitive environment, and climate (Table 3; Fig. 2). Variance in growth also tended to increase nonlin-

early with greater size. The residuals of the growth models met the assumption of normality (Supplementary Fig. S1¹) and were not biased with respect to competition (Supplementary Fig. S2¹) or climate (Supplementary Fig. S3¹). The plots of predicted versus observed growth values also showed no clear biases (Supplementary Fig. S4¹).

Individual growth was typically greater in less competitive environments (Fig. 3), but species differed in whether the symmetric (BA) or asymmetric (BAL) measure of competition led to lower DIC values (indicating better fit) (Table 3). Growth also tended to increase with greater energy availability. Other than the *T. plicata* analysis, the candidate model with the lowest DIC value included a positive effect of PET as the only climatic effect (*P. menziesii*), implying that greater energy availability was associated with higher growth rates or included a positive effect of Deficit (*A. amabilis*,

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2016-0188>.

Fig. 3. The relationship between expected mean individual growth and climate under low and high competition. The increase in growth with higher PET (availability of energy for growth) or AET (simultaneous availability of energy and water for growth) tended to be greater under low competition. The low/high competition curves show expected growth rates in the subplots with the lowest/highest basal area values observed for the given species (or all trees), which were as follows (in $\text{m}^2 \cdot \text{ha}^{-1}$): *Abies amabilis*, 14.2/301.8; *Tsuga heterophylla*, 11.8/301.8; *Pseudotsuga menziesii*, 10.4/184.6; *Thuja plicata*, 25.8/301.8; all trees, 10.4/301.8. Shading shows 95% credible intervals. The measure of competition was BAL (asymmetric competition) for *Pseudotsuga menziesii* and the all-trees model and BA (symmetric competition) for the rest. For the all-trees model, the random effects of species on growth were weighted by the relative abundance of the species in the study. For model fitting, we used the square-root-transformed growth values but show model predictions on the untransformed scale in these plots. [This figure is available in colour online.]

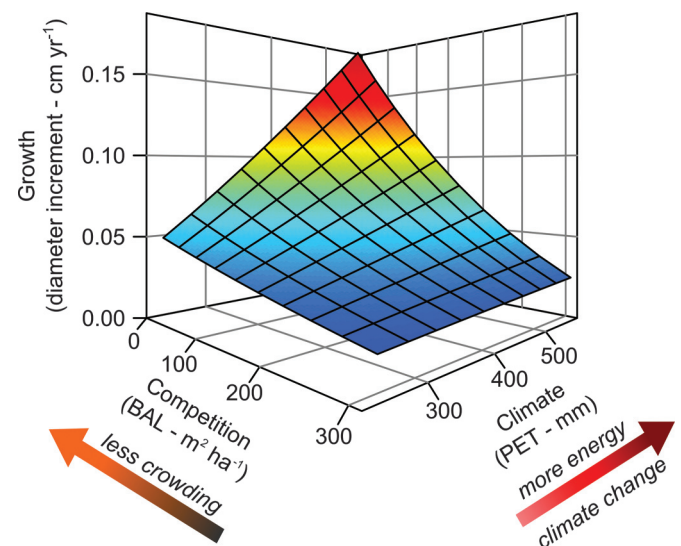


T. heterophylla, and the all-trees analysis), implying that drought stress was associated with higher growth rates (a biologically implausible causal relationship). Whenever Deficit was in the lowest DIC model, the model with PET as the only climate variable had the next lowest DIC value. In these situations, we used the more biologically plausible model that showed a positive effect of PET, as opposed to the model showing a positive effect of Deficit, which was likely an artifact of collinearities between Deficit and PET ($r^2 = 0.67$) and between Deficit and other unmeasured climatic variables. Using PET in place of Deficit when Deficit was in the lowest DIC model did not qualitatively change our conclusions about the effects of climate, competition, and their interaction on growth and had little effect on the accuracy of the predictions (using PET in place of Deficit never decreased the r^2 value for the correlation between predicted and observed values by more than 0.0037 or increased the root mean squared error (RMSE) by more than 0.0009 cm) (Appendix A). Thus, in our final models, higher PET was generally associated with greater growth (Table 3; Fig. 3). For *T. plicata*, the lowest DIC model included a positive effect of AET and no other climatic effects (Table 3), suggesting that growth in this species was limited by the simultaneous availability of energy and water (Fig. 3).

Growth tended to increase with more favorable climatic conditions (higher PET or AET) where competition (BA or BAL) was low but was mostly insensitive to climate under high competition (Figs. 3 and 4). These results are unlikely to be due to collinearity of the climate and competition variables because the correlations between these variables were weak (Supplementary Fig. S5¹). However, the strength of the growth responses to climate, competition, and their interaction varied by species (Table 3; Fig. 3).

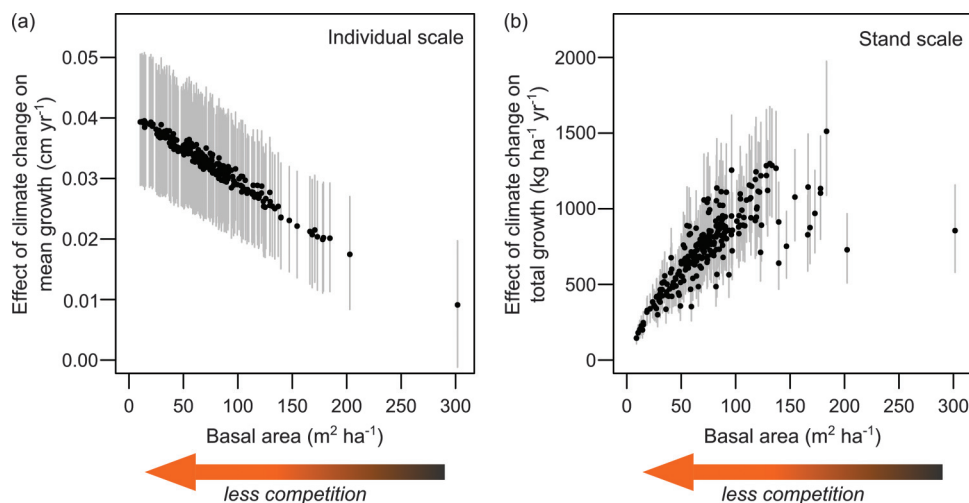
The all-trees model predicted that climate change would lead to higher growth rates in the 2041–2070 time period under the RCP4.5 climate change scenario (a medium warming scenario) compared with the study time period (1977–2008) because higher temperatures lead to higher PET but that the magnitude of growth enhancement

Fig. 4. The joint effects of climate and competition on growth. Modeled growth increased with greater energy availability and increased more sharply when competition was lower (less crowding). Viewed another way, growth increased under reduced competition, and this increase was greater where there was more energy availability. The surface shows the expected growth rates for a smaller sized tree (15 cm diameter at breast height) based on the all-trees model. [This figure is available in colour online.]



would vary with competitive environment at both individual and stand scales (Fig. 5). Using other scenarios or time periods led to different magnitudes of projected growth changes but the same patterns (results not shown).

Fig. 5. Effects of climate change on (a) expected mean diameter growth at the individual scale and (b) total aboveground biomass growth at the stand scale in different competitive environments (based on the all-trees model). Data points show expected changes in growth due to the change in climate between the study period (1977–2008) and a future time period (2041–2070). Bars show the 95% credible intervals. Within each time period (study period or future), we used the mean PET value across all plots to predict growth in each competitive environment to compare growth responses in different competitive environments with the same change in climate. Future climate data were from the RCP4.5 climate change scenario (a medium warming scenario) and the ensemble model projections used in the 5th Assessment Report of the Intergovernmental Panel on Climate Change (IPCC 2013). [This figure is available in colour online.]



Discussion

We found that competition altered tree growth responses to climate at individual and stand scales, suggesting that the effects of climate change on growth will vary based on the local competitive environment (also see Clark et al. 2011; Fernández-de-Uña et al. 2015; Linares et al. 2010). At the individual scale, growth tended to increase sharply with higher PET or AET under low competition but showed little response under higher competition, reflecting the negative effects of crowding on the ability of trees to respond to more favorable climates with increased growth (Figs. 3 and 4). Climate change will likely increase individual growth in these forests by increasing energy availability, and these enhancements will likely be most prevalent in stands with low basal area where there is little competition (Fig. 5a). However, there were some important species-specific variations on this theme, suggesting that growth responses to climate change under different competitive environments will be similar yet distinct among species (Figs. 2 and 3). At the stand scale, the response of aggregate growth to climate change will be determined by changes in individual growth rates and the density and sizes of those individuals. Our results suggest that stand-scale increases in biomass growth due to climate change will be greater at medium basal area than at low basal area, due to greater capacity for biomass increases with greater basal area, but similar at high and medium basal areas, due to greater competition counteracting the effects of further gains in capacity for biomass increases (Fig. 5b). Thus, competition will likely mediate the impacts of climate change on tree growth in important but complex ways at individual and stand scales.

Effects of climate on individual growth

Our analyses suggest that tree growth at Mount Rainier is primarily energy-limited under current conditions. During the study, there were periods of modeled climatic water deficit in the top 150 cm of soil, suggesting the trees did experience some drought stress, but these values tended to be low (Table 1). Including Deficit in the growth models often led to lower DIC values (implying better fit), but in these situations, Deficit had a biologically implausible positive effect on growth. However, PET and Deficit are tightly linked (Deficit = PET – AET) and showed a strong positive correlation with each other ($r^2 = 0.67$), so the positive effect of Deficit in some models might

be an indication of the positive effect of energy availability on growth despite (and not because of) the resulting increase in drought stress. Deficit may also be correlated with other variables about which we did not have reliable information at the spatial scale of the plots, so the positive effects of Deficit might reflect the influence of those variables (e.g., Deficit may have been associated with reduced cloudiness, which led to increased growth). Thus, it appears that these established trees (≥ 5 cm diameter) were well buffered from the modest drought stress at Mount Rainier, potentially because they used water obtained from deeper layers and spread throughout the soil profile by hydraulic redistribution (Unsworth et al. 2004; Warren et al. 2005). Instead, growth appeared to be primarily limited by energy availability, as shown by the positive effects of PET in most models (Table 3). We therefore used PET as the climatic explanatory variable instead of Deficit in situations where Deficit led to better fit but showed a positive effect of drought stress on growth to select biologically plausible models that are more likely to produce robust predictions under novel conditions (such as those created by climate change) (for discussions of the importance of considering model plausibility in addition to measures of fit and parsimony, see Spiegelhalter et al. (2002) and Weiskittel et al. (2011)).

Because our models imply that tree growth at Mount Rainier is primarily limited by energy availability under current conditions, climate change will likely lead to enhanced growth at most locations in these forests in the near future. However, as climate change progresses and drought stress becomes more severe, water limitation will likely become an increasingly important determinant of growth, so further climate change that leads to substantial reductions in water availability in the warm part of the year could produce declines in growth (Chmura et al. 2011; Littell et al. 2013). In addition, our analyses are based on long-term averages of growth and climate (typically around 30 years), so growth responses to short-term climate fluctuations could differ from what our model would suggest.

Effects of competition on individual growth

Our growth models suggest that the trees in our study generally responded to reductions in crowding with increased growth, but that species could differ in their sensitivities to asymmetric versus symmetric competition. The all-trees analysis suggests that asym-

metric competition was generally a more important determinant of growth than symmetric competition, because models with BAL (our measure of asymmetric competition) performed better than models with BA (our measure of symmetric competition), or BAL and BA together. However, for *A. amabilis*, *T. heterophylla*, and *T. plicata*, the model with BA (as the only competition variable) performed best, while for *P. menziesii*, the model with BAL was better. This difference might be due to the shade tolerances of the species. *Pseudotsuga menziesii* is not shade-tolerant and is likely to be relatively sensitive to shading from larger trees (one manifestation of asymmetric competition) (Franklin and Dyrness 1988). The other focal species are shade-tolerant (Franklin and Dyrness 1988) and therefore might be relatively insensitive to shading by larger trees, but still sensitive to competition for other resources that might be more symmetric (e.g., competition for nutrients in the top soil layers) (Schwinning and Weiner 1998). Though our analyses were able to detect clear impacts of competition, our competition metrics were susceptible to edge effects because trees on the edges of subplots were surely affected by competition from neighboring trees adjacent to the subplot, but those effects were not reflected in the competition metrics. Thus, analyses with distance-dependent competition metrics may lead to further improvement in our understanding of how competition mediates the relationship between climate and growth in these forests.

Joint effects of climate and competition on individual-scale growth

At the individual scale, growth rates were often highly sensitive to differences in climate under low competition but mostly insensitive under high competition (Figs. 3 and 4), likely because the ability of trees to respond to more favorable climatic conditions (in this study, that was generally greater energy availability) is constrained by competition for resources (Carnwath et al. 2012; Gómez-Aparicio et al. 2011; Prior and Bowman 2014). Thus, we expect the greater energy availability brought by climate change to generally produce higher individual growth rates and for this growth increase to be greatest in the least competitive stands (Fig. 5a). The interactive effect of climate and competition on growth also implies that as warming leads to a generally more favorable climate in these forest types, competition effects will become increasingly important and differences in crowding will be associated with greater differences in individual growth rates.

Our results also suggest that the effects of climate change on the relative abundances of tree species within forest communities may differ based on competitive environment (also see Dobrowski et al. 2015). First, changes in community structure might be most rapid in low-competition environments because growth and the sensitivity of growth to climate are highest in these locations, potentially allowing thermophilic species to increase in abundance more quickly (HilleRisLambers et al. 2015). Second, species responses to climate change are likely to be individualistic and vary by competitive environment due to variability among species in the effects of climate, competition, and their interaction on growth (Fig. 3). These idiosyncratic responses could lead to a wide range of demographic trajectories and the formation of communities different from those found today (Davis 1986).

However, changes in tree populations will also depend on the impacts of climate and competition on mortality and recruitment (Kroiss and HilleRisLambers 2015; Larson et al. 2015). For example, large changes in climate would likely produce more intense droughts in the region, which could lead to increased mortality even in forests that are not generally considered water-limited (Allen et al. 2010). These mortality responses might be more severe in high-competition stands where trees are currently under greater stress (Luo and Chen 2013). Thus, while changes in individual growth might be greatest in low-competition stands, changes in individual mortality might be greatest in high-competition stands.

Joint effects of climate and competition on stand-scale growth

Projected growth responses to climate change at the stand scale varied nonlinearly with basal area due to the contrasting effects of basal area on the intensity of competition among individuals and the capacity of stands to increase growth in response to more favorable climate, highlighting the importance of individual-scale interactions for stand-scale dynamics (Moorcroft et al. 2001). While individuals in crowded stands (high basal area) will likely have reduced growth responses to climate change relative to individuals in uncrowded stands due to greater competition, there are more and (or) larger trees in crowded stands, conferring a greater capacity for aggregate absolute increases in stand-scale growth. Our results suggest that the positive effects of greater basal area on stand-scale growth responses to climate change predominate in low to medium basal area stands but are balanced by the negative effects of competition at higher basal area values (Fig. 5b). Thus, increases in growth brought by climate change will likely be greatest in medium to high basal area stands. These results also imply that while population- and community-level responses to climate change via increased individual growth might be greatest in less crowded stands, ecosystem-level responses via enhanced biomass production might be greatest in more crowded stands.

Implications for future research and management

This study highlights the importance of assessing the impacts of climate change on tree growth in the context of the competitive environment that trees experience. Permanent sample plots provide valuable data for these types of assessments because they allow researchers to study growth responses to climate for trees that differ greatly in size and in the degree of competition that they face. Our finding that growth responses to climate depend on the tree's local competitive environment implies that forest managers should expect climate change effects on tree growth to be heterogeneous across the landscape and to vary based on stand structure. These types of inferences cannot be made directly with growth models that do not explicitly include climate such as those that base site quality on site index. However, our study shows that the interactive effects of climate and competition on growth can be characterized in meaningful ways by incorporating physiologically relevant climate variables such as climatic water balance variables into well-established growth models such as ORGANON. This approach can enable researchers to adapt proven but climatically static models for use in modeling climate change impacts on forests and evaluating potential management responses to new climatic regimes.

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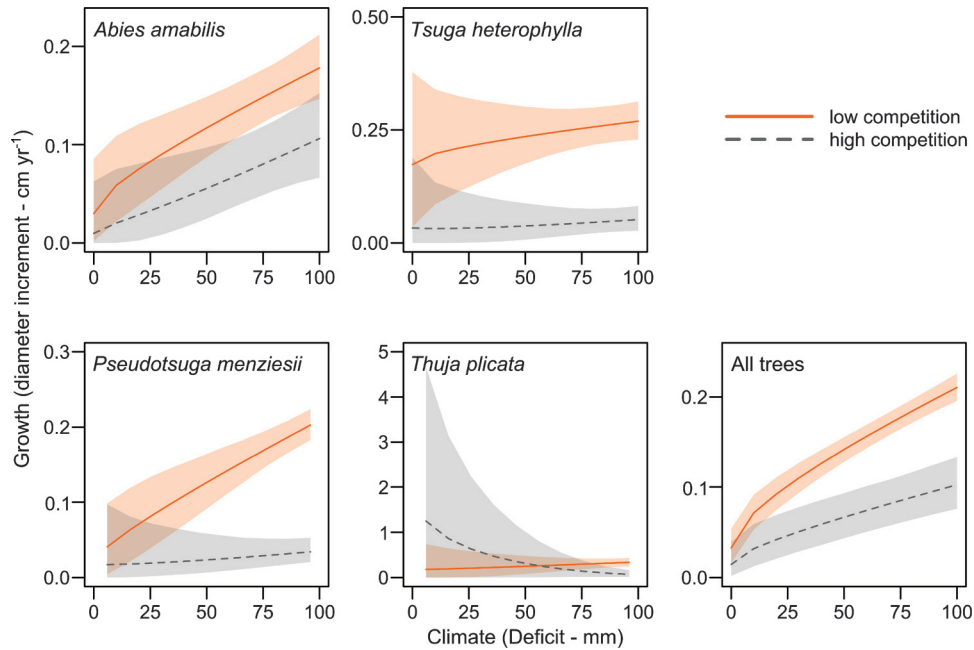
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Appendix A. Using Deficit in the growth models

Using Deficit in our growth models instead of PET or AET led to qualitatively similar relationships between growth and the joint

Fig. A1. The relationship between expected mean individual growth and Deficit under low and high competition. The low/high competition curves show expected growth values for the lowest/highest basal area values observed for the given focal species (or all trees), which were as follows (in $\text{m}^2\text{-ha}^{-1}$): *Abies amabilis*, 14.2/301.8; *Tsuga heterophylla*, 11.8/301.8; *Pseudotsuga menziesii*, 10.4/184.6; *Thuja plicata*, 25.8/301.8; all trees, 10.4/301.8. Shading shows 95% credible intervals. The measure of competition was BAL for *Pseudotsuga menziesii* and the all-trees model and BA for the rest. For the all-trees model, the random effects of species on growth were weighted by the relative abundance of the species in the study. [This figure is available in colour online.]



effects of climate and competition, with the exception of *T. plicata*. The qualitatively similar relationships were that growth tended to be higher in less competitive environments and that growth tended to increase with greater PET and Deficit and to show a more pronounced increase under low competition (Fig. A1, compare with Fig. 3). The similarity in the effects of PET and Deficit was likely due, in part, to their strong positive correlation ($r^2 = 0.67$). However, for *T. plicata*, using Deficit produced very different and poorly constrained results. But for this species, the lowest DIC model included AET, not PET or Deficit. In addition, the lowest DIC model for *P. menziesii* included PET and no other climate variables. For the other three analyses (*A. amabilis*, *T. heterophylla*, and the all-trees analyses), the model with Deficit had the lowest DIC value, and while the differences in DIC between the models with PET versus Deficit could be substantial, the differences in the accuracy of the predicted values were minimal (as shown by the very similar r^2 and RMSE values for comparisons of predicted

Table A1. Model assessments for the growth models with PET or Deficit for analyses in which the model with Deficit had a lower DIC value.

Analysis	Δ DIC	r^2		RMSE (cm)	
		PET	Deficit	PET	Deficit
All trees	88	0.3964	0.4001	0.1030	0.1027
<i>Abies amabilis</i>	16	0.4471	0.4439	0.0898	0.0889
<i>Tsuga heterophylla</i>	6	0.4635	0.4326	0.1086	0.1114

Note: The Δ DIC values indicate the difference in DIC between the models with PET versus Deficit. The r^2 values show the correlation between predicted and observed growth values. The RMSE values show the root mean squared errors of the predicted compared with the observed growth values.

and observed values; Table A1). In some of these cases, the r^2 or RMSE values were actually better for the PET model. Thus, these differences in DIC were likely due primarily to large sample sizes (Table 2) and not large differences in model predictions.