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An Annual basal area growth model with multiplicative climate modifier fitted to longitudinal data for shortleaf pine

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Understanding climatic influences on annual basal area growth (ABAG) rates of individual trees is necessary to predict future stand dynamics. We fitted nonlinear ABAG models for shortleaf pine (*Pinus echinata* Mill.) with climate variables linearly added to the arguments of logistic and exponential multiplicative functions of climate variables as climate modifiers to incorporate 14 growing seasons and 30 month-specific climate variables including standardized precipitation index. Data were collected from permanently established plots in Arkansas and Oklahoma. Six re-measurement events collected between 1985 and 2014 provided five growth periods (GPs) and ABAG models were fitted using a mixed-effects approach. Model performance was evaluated using likelihood ratio tests and fit statistics. Climate variables from GPs expressed as deviations from long-term means that performed better than other candidate variables included (1) month-specific: June mean maximum air temperature (°C) (DTMAX6), and September precipitation (mm) (DPPT9); and (2) growing seasons: mean maximum air temperature (°C) (DGTMAX) and precipitation (mm) (DGPPT). ABAG models fitted with multiplicative climate modifiers provided improved growth predictions compared with models fitted with climate variables linearly added to the argument of a logistic function. There was positive correlation with DGTMAX and negative correlation with DMPPT. In addition, 1°C increase in mean maximum temperature had a greater cumulative effect on ABAG rates of young versus old trees. Fitting ABAG models with climate modifiers are useful for assessing variations in productivity due to climate change in the future.

Introduction

Prediction of annual tree growth is often improved using climate variables in the model because they account for a significant portion of the variation in annual growth rate (Pokharel and Dech, 2012; Subedi and Sharma, 2013; Jiang *et al.*, 2015; Manso *et al.*, 2015). Such variation in an annual diameter growth or basal area growth (ABAG) rate over a period is usually studied using tree-ring analysis where significant correlations are often found with climate variables such as summer temperature, precipitation, and drought index (Graumlich, 1993; Biondi, 2000). For example, strong correlations exist between average summer temperature and tree diameter growth at high northern latitudes (Briffa *et al.*, 1998), and extended high temperatures during the growing season that induce drought stress affect radial growth (Barber *et al.*, 2000; Wilmking *et al.*, 2004; Anderegg *et al.*, 2013). As a result, climate variables such as precipitation and temperature are often regressed against annual tree ring growth rates in developing climate-based growth models (Biondi, 2000; Jump *et al.*, 2006; Chhin *et al.*, 2008; Duchesne *et al.*, 2012; Foster *et al.*, 2015) to explain variations in annual diameter or basal area increment responses for the period of study (Way and Oren, 2010).

Annual diameter increment responses may vary among tree species and tree size when exposed to climatic stressors (Callaway *et al.*, 1994; Hanson and Weltzin, 2000). The largest diameter trees in a forest stand provide the best insight into growth–climate relationships (Chhin *et al.*, 2008), but show highly variable growth rates (Hanson and Weltzin, 2000; Carrer and Urbinati, 2004), as mature trees are affected by severe drought stress and warmer temperatures (Hanson and Weltzin, 2000; Lloyd and Fastie, 2002; Jump *et al.*, 2006). These factors can also induce tree mortality. Regional conditions and site-specific limiting factors also affect the lengthened growing seasons in ways similar to the effects of variation in precipitation and temperature (Graumlich, 1993; Hanson and Weltzin, 2000; Boisvenue and Running, 2006). Therefore, monitoring and evaluating responses of trees from permanent plots to changes in climate is useful for understanding limiting factors of forest growth on particular sites (Boisvenue and Running, 2006; Moore *et al.*, 2006; Williams *et al.*, 2013).

Shortleaf pine (*Pinus echinata* Mill.) grows in more than 22 states in the USA and is second in volume among the southern pines to loblolly pine (*Pinus taeda* L.), but its abundance is declining due to replacement by plantations of other commercially viable southern pine species (Lawson, 1990). It is more

drought tolerant than loblolly pine and is found to grow well where total annual precipitation averages between 100 and 150 cm and average annual temperature ranges between 9 and 21°C (USDI Geological Survey, 1970). Studies focused on growth and yield of naturally grown shortleaf pine include Murphy *et al.* (1992), Lynch *et al.* (1991), Lynch *et al.* (1999), and Budhathoki *et al.* (2008), which are based on permanent plots established in even-aged naturally-occurring shortleaf pine forests in western Arkansas (Ozark and Ouachita National Forest) and south-eastern Oklahoma (Ouachita National Forest).

Most fitted climate-based tree diameter growth models use tree ring data which provides annual growth information. Climate data have been used less frequently for models fitted to periodic re-measurement data. Although national inventory or permanent plot data have frequently been used for modelling individual tree growth and developing growth simulation models (e.g. Wykoff *et al.* 1982; Pretzsch *et al.* 2002; Weiskittel *et al.*, 2011), individual tree growth models from such data have been rarely fitted with climate variables included. However, recently Zell (2018) used periodic re-measurement data from experimental forest management trials in Switzerland to study the impact of climate variables on individual tree growth. Saud *et al.* (2016) also used this type of data. Further, most studies have used climate variables as linearly added terms to the argument diameter growth or ABAG models and have shown modest improvement in model prediction. Although Saud *et al.* (2016) fitted ABAG model for shortleaf pine with climate variables (terms linearly added to the argument of a logistic function), investigation of the potential improvement from using climate variables and climate-based ABAG model sensitivity to climate change scenarios was lacking. Moreover, studies investigating the use of climate variables to show potential improvement in a climate-based growth model with re-measurement data to fit ABAG models are lacking as well. Therefore, this study aims to develop and compare the climate-based ABAG model by fitting climate variables as linearly added terms to the argument of a nonlinear growth model and in a multiplicative exponential function (multiplied by a base growth model) to show the potential influence of climate variables on ABAG of an individual tree. For this purpose, we used data from permanent plots measured six times over 25 years in naturally occurring even-aged shortleaf pine forests in Ozark and Ouachita National Forests, USA. Our specific study aims were: (1) to update the existing ABAG model with multilevel mixed-effects model including a variance function and an autocorrelation structure; (2) to develop a climate-based ABAG model with linear terms and multiplicative exponential functions of climate variable; (3) to show the correlation of climate variables with ABAG of an individual tree; and (4) to evaluate the sensitivity of prediction to different climate change scenarios in the climate-based ABAG model.

Methods

Tree data

Data were obtained from 208 permanent plots located in even-aged natural stands of shortleaf pine in the Ozark and Ouachita National Forests in western Arkansas and southeastern Oklahoma. The area ranged from north of Russellville, AR on the Ozark National Forest to east of Idabel, OK on the Ouachita National Forest (Latitudinal range: 33.801380 to 35.662309; longitudinal range: −92.959581 to −94.916550). In 1985–1987, the Department of Forestry (now, Department of Natural Resource Ecology and Management) at Oklahoma State University (OSU) and USDA Forest Service Southern Research Station (USFS) at Monticello, Arkansas jointly established these research plots to monitor long-term growth and yield performance of managed naturally occurring shortleaf pine stands (Lynch *et al.* 1991; Budhathoki *et al.*, 2008).

Permanent plots were circular in size with a radius of 16.06 m. At an interval of 4–6 calendar years, each plot was measured with the last (sixth) measurement made between 2012 and 2014. The dataset contains six measurements and five growth periods (GPs). At the time of plot establishment, diameter at breast height (dbh) ranged from 2.78 to 61.98 cm and the plot age ranged from 18 to 93 years. Diameters for individual trees on each plot were recorded at each measurement period. Using the ring count method, ages of dominant and codominant trees were determined and then averaged to obtain a stand age for each plot.

Most of the plots were thinned to their original basal area just after the third measurement (1995–1997) while a portion was left unthinned. Given that re-measurement periods were short and thinning effects are often time-lagged by 1–2 years with maximum effects occurring often 4–5 years later, we could have used the basal area at the beginning of the period. However, we deducted thinned basal area from the total stand basal area at the third measurement (for additional information see Saud *et al.* 2016) to account for the effect of reduced stand basal area on individual tree growth. In 2001, during the early phase of the fourth measurement, an ice storm damaged some of the plots. Individual trees recorded as having ice damage (crown damage) or otherwise not suitable (crown damage >25%) for growth calculation were not included in the growth model development process. Summary statistics of tree and stand level variables based on measurements are shown in Table 1. Summary statistics based on GPs are shown in Table 2.

Climate data

We used latitude and longitude coordinates of each plot to obtain climate information from 1980 to 2014 using four km resolution grids from Parameter-elevation Relationships on Independent Slopes Model (PRISM) (PRISM Climate Group, 2015). Climate attributes obtained over 34 years were air temperature (°C) [maximum (TMAX), mean (TMEAN), and minimum (TMIN)] and rainfall precipitation (PPT). To understand whether the variability in mean climate response exists among plot level or not, we grouped plots into 47 microclimate clusters based on similar climate means for plots in the first GP. On average, there were four plots per cluster. Unique climate identifiers (CLMID) were assigned to each microclimate cluster, and plots were assigned with the same CLMID in subsequent GPs, assuming that microclimate would not vary between plots of a climate cluster.

Variance in climate response among climate clusters was tested using one-way ANOVA. Results showed mean climate response variables: TMAX (df = 46, F = 15746. $P < 0.001$), TMEAN (df = 46, F = 80901, $P \leq 0.001$), TMIN (df = 46, F = 2026.6, $P < 0.001$), and PPT (df = 46, F = 586.5, $P < 0.001$) were significantly different among CLMIDs for GP1. Similarly, one-way ANOVA also showed that mean climate response was significantly different ($P < 0.0001$) for each CLMID among the remaining GPs. The above results supported our research efforts to : (1) use the climate variables to fit the models based on groups of plots with similar climate variability and (2) exhibit that the geographical spread of samples is large enough that the temporal variation within growth periods is not too strongly correlated across sites (plots).

The active growing season of shortleaf pine was presumed to be from April to September, which is the normal length for calculating the

Table 1 Summary statistics (mean and standard deviation) of tree and stand level variables measured six times (excluding ice damage) in naturally occurring even-aged shortleaf pine stands in Oklahoma and Arkansas, USA

Variables	Measurement (years)					
	M1 (85–87)[1] (*n* = 8290)	M2 (90–93) (*n* = 8088)	M3 (95–97) (*n* = 7587)	M4 (00–01) (*n* = 4722)	M5 (06–08) (*n* = 4403)	M6 (12–14) (4286)
Dbh (cm)	18.8 (9.9)	20.7 (9.9)	23.2 (10.1)	27.1[2] (9.7)	29.2[2] (10)	30.8[2] (10.4)
Basal area (m^2)	0.035 (0.35)	0.041 (0.038)	0.050 (0.042)	0.065[2] (0.045)	0.075[2] (0.05)	0.085[2] (0.055)
Plot age (years)	41.4 (19.6)	46.3 (19.67)	52.0 (19.8)	59.6 (20.1)	65.2 (20.0)	71.0 (20.1)
Site index[3] (m)	17.45 (2.89)	17.23 (2.98)	17.30 (3.01)	17.54 (3.04)	17.42 (3.02)	17.40 (3.0)
Stand basal area (m^2 ha^{-1})	21.31 (6.69)	25.75 (7.38)	29.72 (8.40)	25.36 (8.37)	27.95 (8.70)	30.20 (9.07)

[1]M with number refers to measurements; two-digit number in parentheses is corresponding year of measurement; dbh = diameter at breast height.
[2]Tree level estimate excludes ice-damaged trees.
[3]The base age for site index was 50 years.

Table 2 Summary statistics (mean and standard deviation) of tree and stand level variables related to growth periods (GP) used for model development

Variables	Growth Periods (GPs)				
	GP1	GP2	GP3	GP4	GP5
ABAG (m^2/tree)/year	0.00121 (0.0001)	0.00135 (0.0011)	0.00150 (0.0011)	0.00153 (0.0011)	0.00138 (0.0011)
Mid dbh (cm)	19.9 (9.9)	21.4 (10.3)	26.3 (9.5)	28.2 (9.8)	29.7 (10.3)
Mid basal area (m^2)	0.039 (0.037)	0.044 (0.040)	0.061 (0.044)	0.070 (0.048)	0.078 (0.052)
Mid stand basal area (m^2 ha^{-1})	23.37 (6.87)	27.89 (7.79)	23.34 (7.80)	26.07 (3.31)	29.22 (8.87)
Mid ratio of QMD to dbh	1.12 (0.34)	1.16 (0.20)	1.09 (0.17)	1.06 (0.26)	1.08 (0.31)
Mid stand age (year)	44.2 (19.7)	49.2 (19.8)	54.0 (19.5)	62.0 (20.2)	64.0 (20.3)

ABAG = annual basal area growth; QMD = quadratic mean diameter; Mid = averages of the two consecutive measurements; *n* = individual tree observations.

standardized precipitation index (SPI). The SPI is a surrogate for the effects of both temperature and precipitation and can be used as an alternative to the Palmer drought index (Guttman, 1999). The SPI based on 6 months shows seasonal to medium-term trends for precipitation by comparing it with the precipitation of the same 6-month period for long-term data (20–30 years). The SPI index was estimated using the 'spei' package in R (Beguería *et al.*, 2013) and indicates wet and dry events using scales: ≤−2.0 (extremely dry), ≤−1.5 (moderately dry), ≤−1.0 (dry), <1.0 (neutral), <1.5 (wet), <2.0 (moderately wet) and >2 (extremely wet).

We constructed seven candidate climate variables for the GPs: (1) GPTMAX = average maximum temperature, (2) GPTMEAN = average mean temperature, (3) GPTMIN = average minimum temperature, (4) GPPPT = average monthly precipitation, (5) GPSPI = average standardized precipitation index, (6) GPTPPT = average total precipitation and (7) GPTSPI = average total standardized precipitation index. Additionally, we created 30 climate variables specific to calendar month of GP using TMAX, TMEAN, TMIN, PPT and SPI. Hereafter, the latter 30 climate variables are termed 'month specific climate variables' and labelled with a number to indicate the respective month.

Mean climate response variables over 34 years are shown in Figure 1. Over the period of 34 years, mean monthly climate response during the growing season were as follows: PPT of 111.36 ± 25.13 mm (mean ± standard deviation (SD)) with a range of 37.14–209 mm; TMAX of 28.95°C ± 1.20°C with a range of 25.84–33.43°C; TMEAN of 22.63 ± 0.88°C with a range of 20.18–26.25°C; and TMIN of 16.29 ± 0.85 with

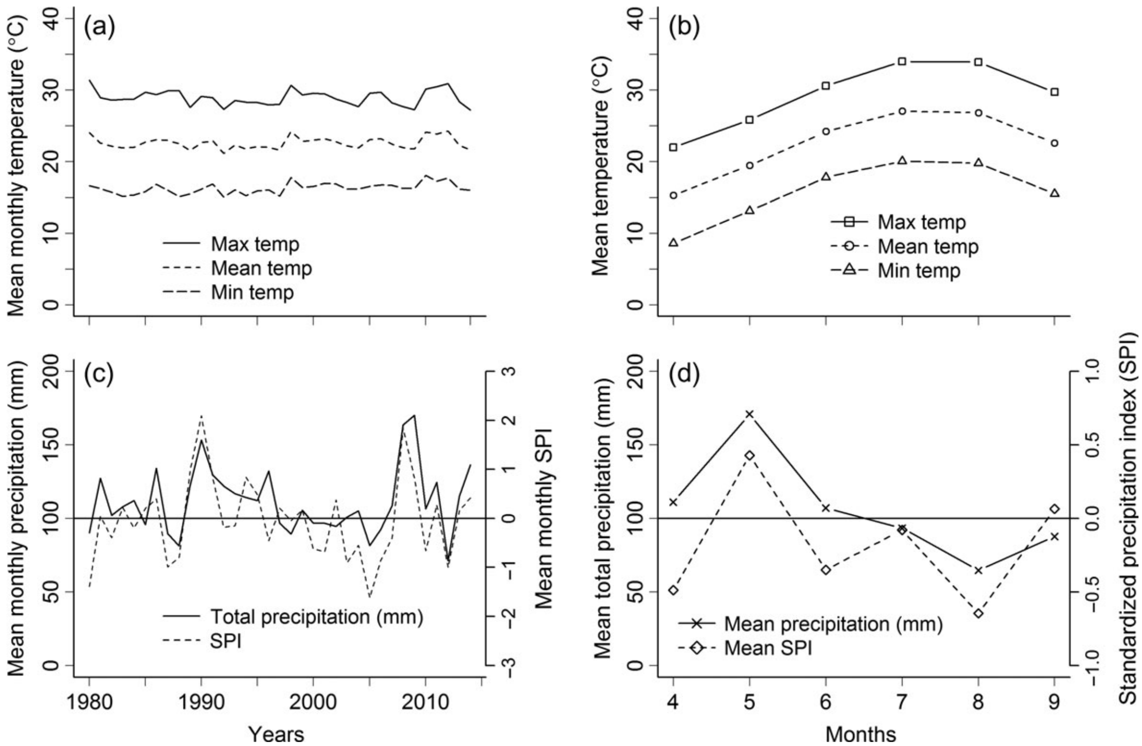

Figure 1 Temperature and precipitation distribution between 1980 and 2014: (a) mean maximum, minimum and mean air temperature during growing season; (b) mean growing season temperature over the length of the study period (1984–2014); (c) mean total monthly perception and monthly standardized perception index during growing season; (d) mean precipitation and standardized precipitation index of month of the growing seasons over the length of the study period (1984–2014). Months '4–9' represents April–September.

range of 14.00–19.55°C. In addition to these climate variables, we introduced new climate variables that represented the deviation in climate response from its long-term mean (over the study period). For example: DGTMAX = GPTMAX of GP minus mean of TMAX during growing season over the period of 34 years; DGPPT = GPPPT of GP minus mean of PPT during growing season over the period of 34 years; where the letter 'D' indicates the deviation or difference. One-way ANOVA results also showed mean deviation of climate: DGTMAX (F = 992.4, P < 0.0001), DGTMEAN (F = 329.5, P < 0.0001), DGTMIN (F = 922.4, P < 0.0001) and DGPPT (F = 2249.7, P < 0.0001) were significantly different among CLMIDs indicating that deviation of climate from normal for a given growth period was not similar between plots grouped in different CLMIDs.

Model formulations

(a) *Base model*. Annual basal area growth (ABAG) of an individual tree was estimated as the ratio of total basal area growth during a GP divided by the length of measurement interval in years. ABAG was predicted using the model given by Lynch *et al.* (1999) for shortleaf pine and that model was considered as the base ABAG model (Eq. (1)). This ABAG model is based on a potential-modifier framework, i.e. predicted growth equals to the growth function times potential growth modifier (e.g. Murphy and Shelton, 1996) and produces sigmoid shaped growth curves for individual trees. Eq. (1) is of the potential-modifier form in which a Chapman-Richards (Richards, 1959) curve constrained by maximum basal area (Shifley and Brand, 1984), which represents potential tree growth and is multiplied by a logistic modifier. Murphy and Shelton (1996) constrained the modifier function to take on value between zero and one so that it reduces potential growth based on the variables representing tree and stand attributes and site conditions. An example of this general type of individual-tree basal area growth model is used in TWIGS, a forest growth and yield simulation programme (e.g. Miner *et al.* 1989) for the north central states, although TWIGS uses a different modifier. The logistic function in our application is non-negative and restricted to be less than one and the denominator acts to reduce the maximum possible growth of a tree of a given basal area based on conditions on the plot. The base ABAG model (Model 1) given by Lynch *et al.* (1999) for shortleaf pine is shown below:

$$y_{ijk} = \frac{\beta_1 B_{ijk}^{\beta_2} - (\beta_1 B_{ijk}/B_{max}^{1-\beta_2})}{1 + \exp(\beta_3 + \beta_4 B_{s_{jk}} + \beta_5 A_{jk} + \beta_6 R_{ijk} k + \beta_7 B_{ijk})} + \varepsilon_{ijk} \quad (1)$$

where i, j, k are tree, plot, and GPs, y_{ijk} = average ABAG($m^2\,yr^{-1}$) of a tree; B_{ijk} = growth interval midpoint basal area (m^2) of tree; Bmax = 0.656683(m^2) (the maximum expected basal area for a shortleaf pine tree); B_{sjk} = stand basal area per hectare ($m^2\,ha^{-1}$) at the growth interval midpoint; A_{jk} = stand age (years) of plot at the growth interval midpoint; R_{ijk} = is the ratio of a tree i diameter to the quadratic mean diameter of plot at the growth interval midpoint; $\beta_1, \beta_2, \ldots, \beta_7$ are the fixed parameter estimates; and ε_{ijk} is within-plot error, residual for tree i in the plot j for the GPs k where $\varepsilon_{ijk} \sim N(0,\sigma^2)$. Values of variables at the growth interval midpoint were obtained by averaging initial and final values because we assumed that competition pressure during the growth interval should be a major influence on growth during that time. Alternatively the basal area at the beginning of the period can be used instead of midpoint values. Maximum basal area came from averaging the largest known Shortleaf pine and the maximum diameter at breast height in our data (see Lynch *et al.* 1999).

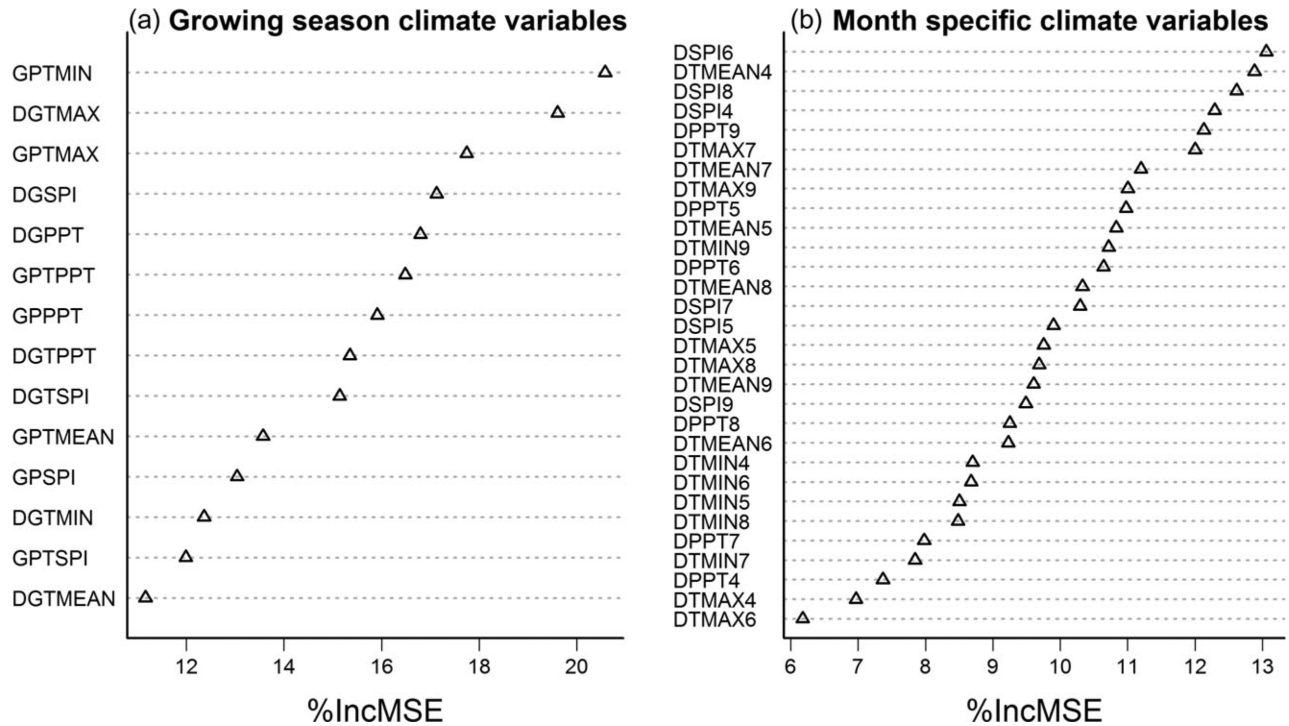

Figure 2 Random forest plots showing importance value of each growing season climate variable and month specific climate variable (from top to bottom in order) when used for predicting annual basal area growth. Variable importance is measured by %IncMSE, which refers to mean decrease in accuracy (i.e. the greater the value, the better the prediction); (a) growing season climate variables over growth period, and (b) month-specific climate variables, where numbers indicate the corresponding month of a calendar year such as 4–9 indicates April–September. TMIN = minimum temperature; TMAX = maximum temperature; TMEAN = mean temperature; PPT = precipitation; TPPT = total precipitation; and SPI = standardized precipitation index. 'D' as initial letter indicates difference between mean responses of a climate variable during growth period from their mean response over 34 years; GP = Growth periods; DG = Deviation in climate during growth period.

(b) *Climate-based model*. Candidate climate variables were selected using randomForests (RF) in R (Liaw and Wiener, 2002). RF reports variable importance scores by the percentage increases in mean square errors (%incMSE) of the model computed for not permuted versus randomly permuted predictors (Liaw and Wiener, 2002; Jiang *et al*., 2015). Variables with higher %incMSE are the most promising predicting variables as linear predictors in terms of reducing the model mean square error. Because the randomForests fits the variables in a linear regression framework (Liaw and Wiener, 2002), the selected predictors not be completely reliable for nonlinear models. However, the variables with higher %incMSE of deviation in growing season climate variables (Figure 2a) and month specific climate variables (Figure 2b) were considered reasonable candidate variables for use in a climate modifier.

All possible candidate climate variables with %IncMSE (Figure 2) were tested in the ABAG model as terms linearly added to the argument of the exponential multiplicative function to Eq. (1). The combination of climatic variables that produced the best fit were selected. Hereafter, we called the model with climatic variables as the 'climate-based ABAG model.' Two different sets of climatic variables (growing season and month specific) were fitted to the base model as linearly added terms to the arguments of logistic portion of Eq. (1) and as variables in an exponential multiplicative function. Climate variables added as linear terms that represent deviation in seasonal climate variables resulted in Model 2 and deviation in month specific climate variables resulted in Model 3. Hereafter 'linearly added' means the climate variables added to the argument of the logistic function in the denominator of the model (e.g. Eqs. (2 and 3) below).

Similarly, a climate-based ABAG model fitted with an exponential multiplicative function of deviation in seasonal climate variables resulted in Model 4 and a model with month specific climate variables resulted in Model 5. We also fitted all potential climate variables as variables in a multiplicative exponential function and found that the best fit was obtained with climate variables similar to those fitted to the logistic function. Hereafter, a climate-based ABAG model with an exponential function is called a 'climate modifier' (Eqs. (4 and 5) below). The climate modifier is designed to be equal to one when the GP means are equal to the long-term climate means otherwise the weight of the climate modifier will be greater than or less than one.

$$y_{ijk} = \frac{\beta_1 B_{ijk}^{\beta_2} - (\beta_1 B_{ijk}/B_{\max}^{1-\beta_2})}{1 + \exp(\beta_3 + \beta_4 Bs_{jk} + \beta_5 A_{jk} + \beta_6 R_{ijk} + \beta_7 B_{ijk} + \beta_8 DGTMAX_{jk} + \beta_9 DGPPT_{jk})} + \varepsilon_{ijk} \tag{2}$$

$$y_{ijk} = \frac{\beta_1 B_{ijk}^{\beta_2} - (\beta_1 B_{ijk}/B_{\max}^{1-\beta_2})}{1 + \exp(\beta_3 + \beta_4 Bs_{jk} + \beta_5 A_{jk} + \beta_6 R_{ijk} + \beta_7 B_{ijk} + \beta_8 DTMAX6_{jk} + \beta_9 DPPT9_{jk})} + \varepsilon_{ijk} \tag{3}$$

$$y_{ijk} = \frac{\beta_1 B_{ijk}^{\beta_2} - (\beta_1 B_{ijk}\,/\,B_{\max}^{1-\beta_2})}{1 + \exp(\beta_3 + \beta_4 Bs_{jk} + \beta_5 A_{jk} + \beta_6 R_{ijk} + \beta_7 B_{ijk})} * (\exp(\beta_8 DGTMAX_{jk} + \beta_9 DGPPT_{jk})) + \varepsilon_{ijk} \tag{4}$$

$$y_{ijk} = \frac{\beta_1 B_{ijk}^{\beta_2} - (\beta_1 B_{ijk} / B_{max}^{1-\beta_2})}{1 + \exp(\beta_3 + \beta_4 Bs_{jk} + \beta_5 A_{jk} + \beta_6 R_{ijk} + \beta_7 B_{ijk})} * (\exp(\beta_8 DTMAX6_{jk} + \beta_9 DPPT9_{jk})) + \varepsilon_{ijk} \quad (5)$$

where β_8, and β_9 are the parameters to be estimated corresponding to climate variables. The remaining terms are described as above.

$DTMAX6_{jk}$ is the difference between the average maximum temperatures of June (*MTMAX6*) for the plot *j* during the GP *k* minus the mean maximum temperature of June (*TMAX6*) for the plot *j* over the period of 34 years. $DPPT9_{jk}$ is average precipitation of September (MPPT9) of the plot *j* during the GP *k* minus the mean precipitation of September (PPT9) for the plot *j* over the period of 34 years.

Model 4 and 5 in which climate effects are contained in a multiplicative term might have promise as a method for updating legacy, already existing basal area growth models. The climate multiplier could be fitted with a smaller ancillary dataset by using a two-stage process in which the climate factor is multiplied by the prediction from an already existing legacy basal area growth prediction model. This might provide a way to introduce climate effects into already existing individual tree growth and yield simulation programmes.

Note that for climate equal to the average during the 34-year period, the difference in climate variables are equal to zero so that Eqs. (2–5) reduce to the form of the base model of Eq. (1) in that case.

Mixed-effects model

The issue of autocorrelation between measurements for individual trees was evaluated using the first order of autoregressive (AR (1)) structure with the residuals of Model 1 suggest no serious correlation issue between errors with individual tree observations. The homoscedasticity assumption of residuals was evaluated by plotting standardized residuals against predicted ABAG. Additionally, we also fitted power variance functions with all models as suggested by Pinheiro and Bates (2000, p. 391) to address the issue of heteroscedasticity of errors. The error variance was modelled with the covariate, individual tree basal area (*B*) because this covariate was associated with smaller AIC values than alternatives and there were convergence issues with alternative variance function structures. Also, non-constant variances for regressions between individual tree attributes have often been observed to be associated with individual tree size in previous studies (e.g. Budhathoki *et al.* 2008). The power variance function is defined as $\sigma^2(v) = |v|^{2\Theta}$, where Θ is the variance function coefficient and $\sigma^2(v)$ is variance function evaluated at covariate v.

We used a mixed-effects approach to fit two different models, i.e. (1) base-ABAG model and (2) the best climate-based ABAG model. Because we wanted to provide optimal estimates that can be easily applicable in the absence of climate variables, we fitted Model 1 with mixed-effects approach. For the climate-based ABAG model, Model 5 with exponential form was fitted with mixed-effects approach because of better-fit statistics than Model 4.

The random-effect (u_7) associated with the fixed-effect (β_7) performed better than fitting random effects with other variables. Because we are using a plot level random effect, we need to associate the random effect with a variable that is not constant for all trees within a plot, so we cannot use stand level covariates, which might be confounded with the stand level random effect. For example, site index age and basal area per hectare are the same for all trees within a given plot, but the tree diameters and hence individual tree basal areas of course vary from tree to tree within a plot. For all mixed-models we studied, we associated the random effect with individual tree basal area. The resultant mixed-effects models for the base ABAG is Model 6 and for the climate-based ABAG is Model 7 are:

$$y_{ijk} = \frac{\beta_1 B_{ijk}^{\beta_2} - (\beta_1 B_{ijk} / B_{max}^{1-\beta_2})}{1 + \exp(\beta_3 + \beta_4 B_{s_{jk}} + \beta_5 A_{jk} + \beta_6 R_{ijk} + (\beta_7 + u_{7jk}) B_{ijk})} + \varepsilon_{ijk} \quad (6)$$

$$y_{ijk} = \frac{\beta_1 B_{ijk}^{\beta_2} - (\beta_1 B_{ijk} / B_{max}^{1-\beta_2})}{1 + \exp(\beta_3 + \beta_4 Bs_{jk} + \beta_5 A_{jk} + \beta_6 R_{ijk} + (\beta_7 + u_{7jk}) B_{ijk})} * (\exp(\beta_8 DTMAX6_{jk} + \beta_9 DPPT9_{jk})) + \varepsilon_{ijk} \quad (7)$$

where u_{7jk} is the random parameters specific to *j*th plot associated with the mid-tree basal area fixed effect coefficient β_7, and the rest of the terms are described as above for Model 1. It is assumed that $u_{7jk} \sim N(0, \sigma_u^2)$, $\varepsilon_{ijk} \sim (N, \sigma^2)$ and cov (μ_{7jk}, ε_{ijk}) = 0. The variances are an indication of the spread of the random coefficients and we would usually be interested in estimates of the variance of (μ_{7jk}), i.e. $\hat{\sigma}_u^2$.

Model evaluation

All models were fitted as a generalized nonlinear regression model using nlme package (Pinheiro *et al.*, 2018) of R (R Core Team, 2018) and models were compared goodness of fit statistics primarily using the likelihood ratio test (LR). We also reported the Akaike Information Criteria (AIC) value for each model. Another criterion for model selection was the growth prediction accuracy of each model, which was evaluated fit index (pseudo R^2), root mean square error (RSE), and bias. Fit index estimation is based on observed and predicted growth by nonlinear models and by mixed-effects models without random effects, so that both models have equal numbers of parameters involved in model prediction comparison criteria. We have also reported fit index based on mixed effect model fit. The AIC of a mixed-effects model can be improved by the use of estimated random parameters. However, unless the mixed model is calibrated by estimating random parameters for applications, only the fixed effects can be used in prediction. Some authors (Temensgen *et al.*, 2008; Saud *et al.* 2016) have argued that nonlinear least squares models can be superior for prediction unless it is possible to calibrate mixed model alternatives.

We also used Spearman rank (rho) correlation to show the relationship between the deviation in climate response with ABAG over the study period and during each growth period. The correlation is shown using head scatter plot based on a two-dimensional kernel density estimation.

Predictions under different climatic scenarios

To demonstrate possible variability in the ABAG prediction by two different forms of fitted climate-based ABAG models, we simulated ABAG of an individual tree for fifty years under four different climate scenarios. We selected Model 2 & 4 instead of Model 3 & 5 because the projected climate values by general circulation Model (GCM) were available as year specific to characterize decade's midpoint not as month-specific climate variables. Future climate predicted by GCMs model are based on several development scenarios, or storylines formulated by the IPCC (2007).

For the first two scenarios, we used climate values of mean (μ) and upper quartile (UQ) with SD of the growing season between 1980 and 2014. The value at μ, UQ, and SD were 28.95, 29.77 and 3.29°C for temperature and 111.36, 126.39 and 25.13 mm for precipitation, respectively. The latter two-scenarios represent GCM prediction models storylines of two extreme future climate change scenarios. CGCM3-A1B (Canadian Center for Climate Modeling and Analysis with storyline A1B) projects future climate under the secenario of global rapid economic growth with balanced energy fossil fuel and non-fossil fuel technology. HADCM3-B2 (Hadley Center/World Data Center with storyline B2) projects future climate under the secenario of local envorinment sutainablity with different patterns in demographic, social, economic, technological and environmental development worldwide. We obtained

the future climate data at the year 2060 for a sample plot location from Moscow Forestry Sciences Laboratory (2015) under these GCM model scenarios. Mean precipitation was of 103.8 ± 32.5 and 89.1 ± 25.7 mm and mean maximum temperature was of 31.6 ± 4.5 and 32.5 ± 4.9°C for the respective scenarios.

Individual tree growth was simulated for 50 years using values of tree variables measured during the final (i.e. 6th) re-measurement event. We simulated individual tree growth rather than growth of entire plots because a climate-based survival function to simulate plot or stand growth was not available for shortleaf pine. We selected an individual tree that represented the lower quantile (25 per cent) and upper quantile (75 per cent) of stand age distribution of 38-years and 78-years, respectively. Both the 38-year old tree (dbh = 20.2 cm) and the 78-year old tree (dbh = 32.9 cm) were grown for the next 50 years with an annual average increment of all covariates in the model assuring that simulated growth would follow biological expectation within range of the existing dataset. The values of the input variables for the 38 year old tree were: B_i = 0.0321 m^2, B_{sj} = 14.7543 $m^2\,ha^{-1}$, R_{ij} = 0.5788, and for the 78 year old tree were: B_i = 0.0851 m^2, B_{sj} = 11.7767 $m^2\,ha^{-1}$, R_{ij} = 0.5825.

In the simulation process, both climate variables were randomly generated using SD of the data over the period of 34 years, and subtracted from the μ of the corresponding climate variable. The simulation of each scenario was conducted with five different cases (levels): (1) with multiplicative climate modifier (Eq. (4)); (2) with linearly added term (Eq. (2)); (3) Model 1 without climate variables (Eq. (1)); (4) climate modifier equation but without using estimates of climate (Eq. (4)) with multiplier set to (1); and (5) climate variables linearly added to equation argument but without using estimates of climate (Eq. (2) with climate variables set to zero). The latter cases 4 and 5 were used to demonstrate how well the climate based-ABAG model in the absence of climate coefficients predicts with base ABAG model. These four different climate sensitivity scenarios on ABAG were simulated for 10 000 runs with the five different cases.

Results

Annual basal area growth

Average annual basal growth rate of individual shortleaf pine trees was 0.001395 $m^2\,yr^{-1}$ over the period of 25 years. The periodic mean ABAG rate of individual shortleaf pine trees was 0.00121, 0.00135, 0.00150, 0.00153 and 0.00138 $m^2\,yr^{-1}$ respectively for GP1, GP2, GP3, GP4 and GP5 (Table 2). Comparison of all periodic mean ABAG rate with the mean ABAG of GP1 showed positive difference in the growth rate was of 11.6, 24, 26.4 and 14 per cent for the consecutive GPs, respectively.

ABAG models

According to the likelihood ratio test, the goodness of fit indicated that fitted climate-based ABAG models (Model 2–5) were significantly different from the base ABAG Model 1 (Table 3). However, climate-based ABAG models fitted with either variables based on growing season climate (Model 2 & 4) or variables based on month specific climate (Model 3 & 5) were not significantly different from each other according to the likelihood ratio test (Table 3). Although the climate-based ABAG models (Model 2–5) were not significantly different, the fit-statistics (Table 4) of the ABAG models fitted with climate modifier (Model 4 & 5) were slightly better than ABAG fitted with terms of climate variable linearly added to the equation argument (Model 2 & 3). Models 4 & 5 fitted with climate modifier showed improved ABAG prediction by showing increased in fit indices of 1.1 and 2.5 per cent, respectively, for ABAG prediction over the Model 1. Similarly, increased fit indices were 1.0 and 2.1 per cent for linearly added climate-based ABAG Model 2 and Model 3, respectively when compared with the fit index of Model 1. Although all models are practically equivalent, the improved ABAG prediction and reduced bias percentage of both Model 3 and 5 indicated that deviation in month specific climate variables performed slightly better than deviation in growing season climate variables for modelling the effect of climate on ABAG of individual trees using re-measurement data from the long-term study.

The parameter estimates of Models 1–5 were highly significant (Table 5) and were similar to each other for the variables which all the models had in common. The mean growth (coefficient β_3) was higher for the ABAG Models 2 & 3 with linearly added terms of climate as compared with ABAG Models 4 & 5 with climate modifier (Table 4). Models 4 & 5 showed a negative parameter estimate for temperature and a positive parameter estimate for precipitation, while Models 2 & 3 showed the opposite parameter signs due the differences in mathematical form, although the effect on predictions was similar. The difference in sign of parameters was due to the fact that climate variables were in the denominator of Models 2 & 3 compared with Models 4 & 5. Moreover, climate-based models fitted with month specific climate variables (Models 3 & 5) had a lower standard error associated with climate variables than the ABAG models fitted with growing season climate variables (Table 4). Standardized residual distribution patterns were similar between the base ABAG model (Figure 3a) and climate-based ABAG models (Figure 3b, c) and the climate-based model fitted with

Table 3 Matrix of likelihood ratio test statistics of the fitted ABAG models for shortleaf pine

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7
Model 1	–	891.6	1041.4	1081.3	1203.8	3297.7	4970.9
Model 2		–	NS	NS	NS	2256.3	4079.3
Model 3			–	NS	NS	2256.3	3929.5
Model 4				–	NS	2216.4	3889.6
Model 5					–	2093.9	3767.1
Model 6						–	1673.2
Model 7							–

NS indicates non-significant likelihood ratio test between fitted ABAG models otherwise significant (P < 0.0001).

Table 4 Summary of fit-statistics with and without climate variables of fitted basal area growth models for shortleaf pine

Model	AIC[1]	Bias	Bias (%)	RMSE[2]	RMSE (%)	Fit indices (%)
1	−328136	-1.252976×10^{-5}	0.922	0.003406	48.56	63.18
2	−329024	1.548767×10^{-5}	1.140	0.003359	48.14	63.81
3	−329173	1.479791×10^{-5}	1.089	0.003249	47.66	64.52
4	329 213	1.549838×10^{-5}	1.140	0.003381	48.08	63.89
5	−329336	1.348799×10^{-5}	0.993	0.003248	47.49	64.77
6	−331432	-3.246186×10^{-5}	−0.239	0.002990	50.10	60.80
7	−333101	3.563285×10^{-5}	2.623	0.002829	49.35	61.98

Fit-statistics for mixed-effects models are based on parameter estimates with random-effects set to zero to make comparable with other models.
[1]AIC = Akaike Information Criteria.
[2]RMSE = Root mean square error.

mixed-effect approach (Figure 3d). No serious issues in the homogeneity of residuals were displayed with the corresponding ABAG models fitted respectively and all ABAG models had a similar power variance function.

ABAG models with mixed-effects

The LR statistics showed that climate-based ABAG models fitted with the mixed-effects approach (Model 6–7) were significantly different from all other fitted models (Table 3). Both mixed-effects models had a lower AIC value than the models fitted without mixed-effects (Table 4). Results showed (Tables 4 and 5) increases in fit indices and decreases in both bias (%) and RMSE (%) in the model based fit statistics for mixed-effects models. The model based fit indices for Model 6 & **7** were 69.1 per cent and 71.1 per cent respectively, which was an increase of 9.4 per cent and 9.7 per cent in fit indices to the corresponding model without mixed-effects (Model 1 and 5). However, the mixed-effects models showed increases in bias and RMSE (percentage) and decreases in fit-indices (Table 4) when fit statistics were computed setting the random effects set to zero to make models comparable with the models that did not contain random effects.

The parameter estimates of all mixed-effects models were highly significant and are shown in Table 6. Results showed a reduced constant effect on growth (coefficient β_3) and midpoint basal area (coefficient β_7), but increased effect of individual tree status (coefficient β_6) in predicting ABAG. Model 7 showed more negative effect of temperature than models without mixed-effects (Model 5) in ABAG; however, the positive effect of precipitation was similar between Model 5 (Table 5) and Model 7 (Table 6). Variability in ABAG prediction attributed to the random effects associated with plot was high in the Model 6 than in the Model 7 (Table 6). The performances of the climate-based ABAGs Model 5 without the mixed-effects approach and Model 7 with the mixed-effects approach were judged better than other models because of better fit-statistics (Table 4, refer to fit indices).

ABAG and climate correlation

Over 25 years, the Spearman rank (rho) correlation between ABAG and deviation in climate response was significant (*P*-value <0.0001) but small in magnitude. The correlation was positive to DGTMAX (0.02), and negative to DGPPT (−0.06). In contrast, the correlation and its significance vary for each GP (Figure 4). The correlation was positive between ABAG and DGTMAX, when all observations were around the mean (zero) or lower than the mean (−ve DGTMAX) level, though statistically not significant (Figure 4). GP5 showed increase in DGTMAX had a significant but negative correlation with ABAG (Figure 4e) and increases in DGPPT had a significant positive correlation with ABAG (Figure 4e).

ABAG sensitivity with climate change

The simulation study of ABAG sensitivity showed similar growth patterns under four different climate change scenarios for climate-based ABAG Model 2 fitted with the linearly added term and Model 4 fitted with climate modifier (Figure 5). Although ABAG prediction under the long-term mean temperature scenario by both models was close to the ABAG predicted by Model 1 (base model), the simulated ABAG curves for both stand ages by Model 2 (Figure 5a and c) were slightly higher than those of Model 4 (Figure 5b and c). This result was also supported by Wilcox matched-pairs signed rank test indicating significant differences in ABAG predicted between Model 2 and Model 4 (V = 61, P-value < 0.0001) and also with Model 1 (V = 1275, P-value < 0.0001). In the remaining three scenarios, the simulated ABAG curve for both stand ages by Model 4 was slightly higher than that for Model 2, and Wilcox matched-pairs signed rank test also indicated a significant difference in ABAG predicted between models for the similar stand ages under the respective climate sensitivity scenarios.

Differences in ABAG simulation of both stand ages between the beginning and the end of the 50-year period was high for Model 2, but it was low in the Model 4 when compared with Model 1 (Table 7). Similarly, the largest difference in ABAG rate was observed in the simulation scenario of long-term mean temperature change, while the smallest difference in ABAG was in the HADCM3-B2 scenario for both models. In all scenarios, differences in ABAG at the end of 50 years was less with Model 4 than with Model 2 when compared with Model 1 (Table 7). At the end of 50 years, under the long-term mean temperature change scenario, a positive gain in ABAG rate was higher for Model 2 than for Model 4 for both stand ages, and it was a

Table 5 Parameter estimates (EST) and standard errors (SE) of fitted base annual basal area growth (ABAG) prediction model (Model 1) of shortleaf pine with long-term deviation in growing season climate (Model 2 & 4) and in month specific climate (Model 3 & 5) as linearly added terms (Model 2, 3) and multiplicative exponential (climate modifier) (Model 4 & 5)

Parameters	Base	Linear		Multiplicative exponential	
	Model 1	Model 2	Model 3	Model 4	Model 5
	Est (SE)	Est (SE)	Est (SE)	Est (SE)	Est (SE)
β_1	0.045333	0.056660	0.044311	0.044651	0.031282
	(0.002431)	(0.003258)	(0.002312)	(0.002376)	(0.001493)
β_2	0.626412	0.651761	0.610007	0.638146	0.572312
	(0.010777)	(0.011049)	(0.011142)	(0.010844)	(0.010762)
β_3	−3.011162	−2.595969	−2.765213	−3.109814	−3.235068
	(0.107396)	(0.104662)	(0.100223)	(0.101859)	(0.095199)
β_4	0.136035	0.133542	0.141733	0.144687	0.151407
	(0.002816)	(0.002709)	(0.002757)	(0.002827)	(0.002736)
β_5	0.024693	0.023009	0.023859	0.025087	0.025548
	(0.000675)	(0.000622)	(0.000642)	(0.000668)	(0.000669)
β_6	2.398520	2.205123	2.329420	2.354085	2.476926
	(0.051204)	(0.047482)	(0.047237)	(0.048762)	(0.047639)
β_7	−9.938124	−9.137884	−10.053112	−10.473871	−11.848415
	(0.362780)	(0.323247)	(0.344926)	(0.368203)	(0.390949)
β_8	–	0.170810	0.202255	−0.102785	−0.128153
		(0.013407)	(0.009719)	(0.007964)	(0.005619)
β_9	–	−0.008197	−0.007730	0.006275	0.005144
		(0.000582)	(0.000285)	(0.000348)	(0.000145)
θ	0.562496	0.563268	0.554116	0.566401	0.554924

θ is power in $\sigma^2(v) = v_2\theta$ power variance function.

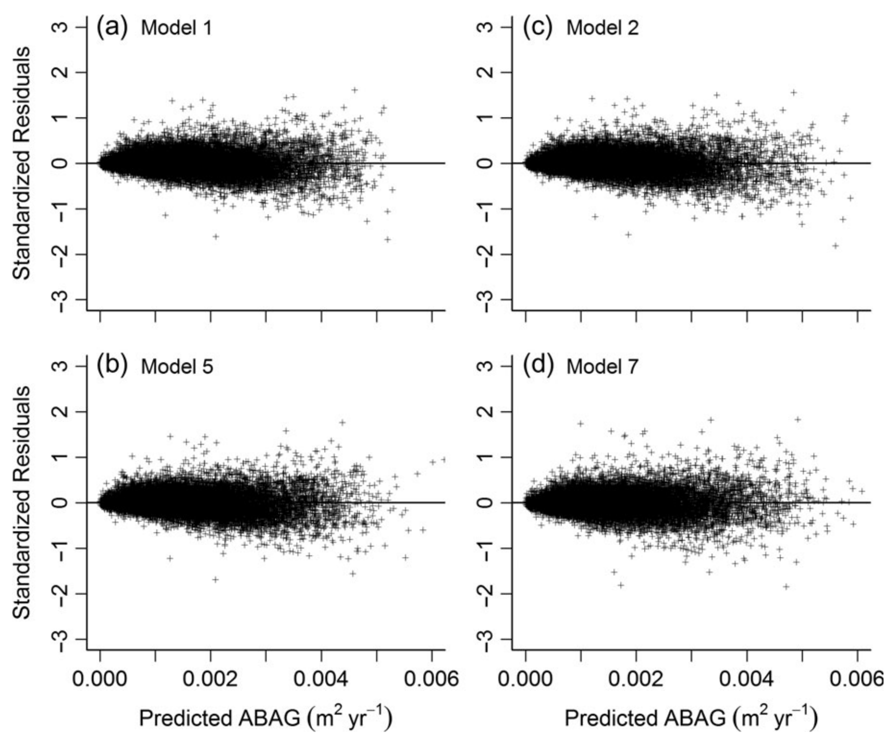

Figure 3 Standardized residuals of fitted annual basal area growth (ABAG) models for shortleaf pine: (a) Model 1: base model; (b) Model 2: linearly added deviation in growing season climate variables to the arguments of the logistic function; (c) Model 5: climate modifier with deviation in month specific climate variables; (d) Model 7: mixed-effects model using climate modifier with deviation in month specific climate variables.

Table 6 Parameter estimates (Est) and standard errors (SE) of fitted mixed-effect models of base model (Model 6) and climate based annual basal area growth (ABAG) prediction model (Model 7) for shortleaf pine. Model 7 is the mixed-effect model form that uses long-term deviation in month specific climate as multiplicative exponential function (climate modifier)

Parameters	Model 6 Est (SE)	Model 7 Est (SE)
β_1	0.028657 (0.001524)	0.026210 (0.001483)
β_2	0.538394 (0.013301)	0.516379 (0.013705)
β_3	−3.616600 (0.091737)	−3.365396 (0.090125)
β_4	0.153460 (0.002988)	0.178038 (0.002985)
β_5	0.010896 (0.000801)	0.010049 (0.000757)
β_6	3.485150 (0.060986)	3.129876 (0.057617)
β_7	−4.455328 (0.661377)	−4.627350 (0.583578)
β_8	–	−0.152973 (0.005292)
β_9	–	0.006302 (0.000157)
$\sigma^2(u_{7jk})$	6.894065	5.810658
ε_{ijk}	0.002990	0.002829
θ	0.546061	0.538699
Fit Indices (%)	69.11	71.08
Bias (%)	0.307	0.466
RMSE (%)	44.48	43.03

ε = error; u_7 = plot level random effect; i = tree; j = plot & k = growth period; θ is power in σ^2 $(v) = v_{2\theta}$.

substantial positive gain for stand age 78 years grown under similar climatic conditions. Likewise, differences in total ABAG at the end of 50 years, when compared with Model 1, was also higher for Model 2 than for Model 4 under simulation scenario for long-term mean temperature (Table 7).

Except the long-term mean temperature scenario, all other climate sensitivity scenarios showed negative differences in ABAG values at the end of 50 years and in total ABAG at the end of 50 years. The smallest negative difference was observed with long-term upper quartile temperature indicating that one-degree centigrade (°C) increment in long-term mean temperature could significantly (V = 0, P-value < 0.0001) reduce ABAG over the period. Other climate sensitivity scenarios such as HADCM3-B2 and CGCM3-A1B showed the most substantial negative differences indicating a more stressed growth rate in young trees with an increase in temperature and decrease in precipitation than compared with older trees grown in similar climatic conditions (Table 7). It should also be noted that differences in basal area and social status influenced the growth rate. Therefore, variability in ABAG rate within different climate sensitivity scenarios was higher for the younger stand than for the older aged stand at the end of a prolonged period of climate change.

Discussion

ABAG models

Improved AIC values and large LR statistics indicated that the mixed-effects model was a reasonable choice for modelling ABAG using repeated measurements compared with models fitted by OLS. Mixed-effects models in association of both an AR (1) structure and variance power function are often used to address the problems of heteroscedasticity of errors and correlated measurements (Subedi and Sharma, 2013; Saud *et al.*, 2016). We used variance power function to address the homoscedasticity issue of residuals in the ABAG model, but the smaller autocorrelation of residuals and similar residual distributions of all fitted models indicated it was not necessary to model repeated measurement correlation issue among individual tree in addition to mixed-effect modelling techniques. All climate based models behave in a very similar manner, however the model precision was somewhat better with a multiplicative climate modifier (Eq. (4 and 5)).

Unless the mixed-effects model is calibrated by estimating random parameters for applications, only the fixed effects can be used in prediction. Some authors (Temensgen *et al.*, 2008; Saud *et al.* 2016) have argued that nonlinear least squares models can be superior for prediction unless it is possible to calibrate mixed model alternatives. It is true that predictions produced by using the fixed effect estimates from nonlinear mixed-models (i.e. marginal predictions) may be biased. However this can be corrected by weighing a set of conditional predictions by the distribution of the random effects (Fortin, 2013). If the random effects are predicted and used, the growth prediction will improve, but it may be difficult to predict the random effect associated with a new site, new tree or especially a new interval measurement. In that case, only the marginal but corrected prediction (Fortin, 2013) would be expected to be better than uncorrected prediction.

Climate based ABAG models

Previously, modellers have formulated climate-based growth models by introducing climate variables linearly within the argument of existing growth models. This might be because most of the studies have been formulated either on tree-ring chronologies or on annual measurement data where climate variables are regressed against annual growth (Biondi, 2000; Jump *et al.*, 2006; Chhin *et al.*, 2008; Duchesne *et al.*, 2012; Foster *et al.*, 2015). However, Zell (2018) has recently investigated the effects of climate on growth from multi-year periodic measurements of forests in Switzerland. Additionally, the growth models in some of these studies are already linear in form of their arguments (Subedi and Sharma, 2013; Manso *et al.*, 2015) and added climate variables performed better than was the case with our nonlinear model. The model reported by Saud *et al.* (2015) was a nonlinear model with linearly added climate variables to the argument of the model for shortleaf pine. However, in this study linearly added climate variables did not perform quite as well as the climate modifier did in our growth model.

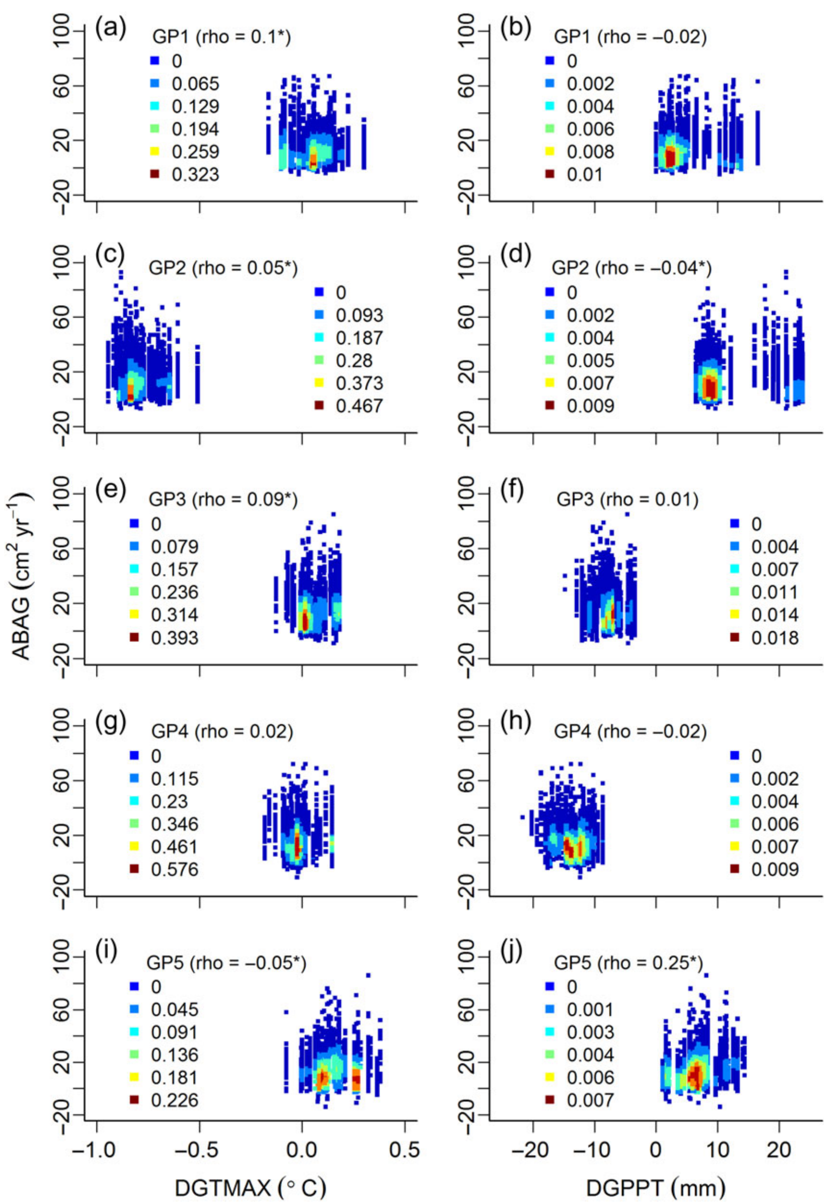

Figure 4 Heat scatter plots showing non-parametric Spearman rank (rho) correlation and Kernel density (values associated with six different colour gradient densities) of annual basal area growth (ABAG) of an individual tree with deviation from the long-term mean temperature (DGTMAX; zero is no deviation) (left) and the precipitation (DGPPT) (right) for each growth period (GP). DGTMAX usually has positive effect on ABAG unless it has large positive deviation (GP5). However, correlation of DGPPT with ABAG varies depending upon response of DGTMAX. Used 10 000 as division factor to convert $cm^2\ yr^{-1}$ to $m^2\ yr^{-1}$. *Significant correlation at $\alpha = 0.05$ level.

Using the climate modifier has a major advantage over the linearly added term in that its weight was adjusted to greater or less than one depending on deviations from long-term climate and becomes equal to one if there is no deviation so that it behaves as Model 1. An additional property of the multiplicative climate modifier structure (Eq. (4 and 5)) is that it might be used in future studies to add climate sensitivity to legacy individual tree diameter and basal area functions which are already embedded in forest growth prediction systems and software. One could collect ancillary diameter growth and climate data, possibly from increment cores, and then parametrize a climate modifier using a two-stage estimation process, where the parameter estimates for legacy diameter increment functions are the first stage and the parameters of the climate modifier are the second stage:

$$y_i = \widehat{y_L} \times \exp(\beta_1 x_1 \cdots \beta_n x_n) + \varepsilon_i$$

where y_i is individual tree basal area or diameter increment measured from ancillary data $\widehat{y_L}$ is the basal area or diameter increment prediction from a previously existing legacy prediction equation and x_i are climate variables with corresponding

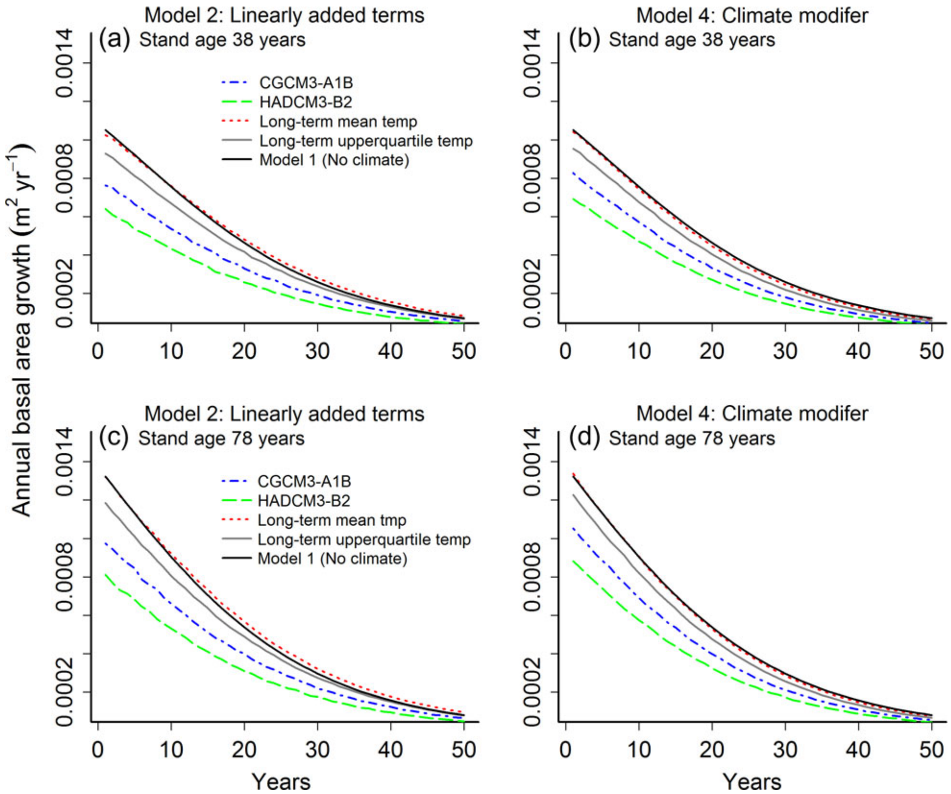

Figure 5 Simulated (10 000-runs) climate sensitivity scenarios of climate-based ABAG models fitted with linearly added term of climate variables to the logistic function (Model 2) and multiplicative exponential function of climate variables as climate modifier (Model 4) for stand age 38 (a & b) and 78 (c & d) years for the next 50 years. Climate sensitivity on the predicted ABAG were compared with base model (Mode 1) and four different climate scenarios deviating from long-term (1980–2014) mean climate response; temperature (°C) and precipitation (mm). The climate scenarios are: (1) long-term mean temperature (temp: $\mu = 28.94$, $\sigma = 2.42$; ppt: $\mu = 111.36$, $\sigma = 25.13$); (2) long-term upper quartile temperature (temp: $\mu = 29.77$, $\sigma = 2.42$; ppt: $\mu = 111.36$, $\sigma = 25.13$); (3) CGCM3 A1B scenario (temp: $\mu = 31.6$, $\sigma = 4.5$; ppt: $\mu = 103.8$, $\sigma = 32.5$); and HADCM3-B2 scenario (temp: $\mu = 32.5$, $\sigma = 4.9$; ppt: $\mu = 89.1$, $\sigma = 25.7$).

Table 7 Percentage difference (%) based on annual basal area growth (ABAG) rate of an individual tree at stand age 38 and 78 years at the end of 50 years under four different climate sensitivity scenarios using Model 2 (linearly added climate variables) and Model 4 (climate modifier) as compared to Model 1 without climate effects

Percentage (%) difference in ABAG	Stand age 38 years				Stand age 78 years			
	Model 2: Linearly added climate [*Model 4: Climate modifier*]				Model 2: Linearly added climate [*Model 4: Climate modifier*]			
	CGCM3-A1B	HADCM3-B2	Long-term mean temp	Long-term upper quartile temp	CGCM3-A1B	HADCM3-B2	Long-term mean temp	Long-term upper quartile temp
Between beginning and end of 50 years	92.61 [*94.39*]	93.43 [*94.59*]	91.89 [*93.19*]	92.57 [*93.97*]	93.32 [*94.83*]	94.00 [95.04]	92.93 [*94.42*]	93.29 [*94.58*]
At end of 50 years compared to Model 1	−23.78 [*−42.50*]	−51.85 [*−62.59*]	14.90 [*−9.65*]	−3.54 [*−21.74*]	−21.38 [*−38.78*]	−49.44 [*−59.14*]	14.78 [*−7.67*]	−1.43 [*−19.25*]
Total ABAG at end of 50 years compared to Model 1	−32.05 [*−30.25*]	−53.98 [*−48.88*]	2.58 [*−2.74*]	−11.23 [*−12.69*]	−29.81 [*−27.93*]	−51.47 [*−46.41*]	3.86 [*−1.25*]	−9.81 [*−10.90*]

Note: CGCM3-A1B = Canadian Center for Climate Modeling and Analysis with storyline A1B for future climate scenario (IPCC, 2007); HADCM3-B2 = Hadley Center/World Data Center with storyline B2 for future climate scenario (IPCC, 2007); Long-term mean and upper quartile temperature scenario represents climate of 1980–2014.

parameters β_i. Two stage regression techniques are frequently applied in econometrics and have been used in forestry applications. Furnival and Wilson (1971) and Borders and Bailey (1986) have proposed use to two-stage and three-stage regression for forest growth modelling. Recently Zhao *et al.* (2019) modelled biomass components for slash pine (*Pinus elliottii*) using a two-stage component ratio approach in which predicted total biomass was multiplied by a ratio function fitted with Dirichlet regression. However, this proposal does differ from classical two-stage regression applications in that the ancillary dataset could be a completely different dataset than the dataset used to fit the legacy increment model.

Climate-based growth models may perform differently for different tree species. For example, Subedi and Sharma (2013) reported 0.34 per cent and 1.56 per cent reductions in RSE of annual diameter growth model of jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* [Mill.] B.S.P.) respectively in boreal Ontario, Canada. However, Manso *et al.* (2015) reported substantial reduction (15 per cent) in the AIC value in an annual diameter increment model of beech (Fagus spp.) and oak (Quercus spp.) even-aged stands across France. Saud *et al.* (2015) reported 3.4 per cent improvement in the fit index of the climate-based growth model with the addition of climate variables for shortleaf pine. The variation in results could be influenced by the nature of climate variables used for modelling. Differences in the performance among climate based ABAG model indicates the choice of climate variables and climate variables fitting approach can greatly affect degree of model improvement. It may be possible to achieve greater reductions in RMSE using tree ring data and climate data associated with growth rings than with periodic re-measurement data such as used here, because within a growth period, variations due to climate tend to be 'averaged out' during a 5-year or similar growth period. However, much if not most of the data available worldwide for tree and forest growth models comes from periodically remeasured plots, with period lengths longer than one year. Therefore, it is crucial to explore integration of climate effects in these models if they are to be responsive to future climate change scenarios. As indicated in the test scenarios above, even rather small climate effects on annual growth can have a substantial cumulative effect over a period of several years or decades.

The above discussion suggests improvement in climate-based growth models not only depends on characteristics of tree species growth rate but also the nature of climate variables used. For example, precipitation and temperature, which are dictated by regional conditions (altitudinal and latitudinal range) and site-specific factors (microclimate), limits forest productivity (Hanson and Weltzin, 2000; Boisvenue and Running, 2006; Williams *et al.*, 2013). Because of this, climate variables that are often expected to be influential including mean temperature, maximum temperature, and total annual precipitation (Subedi and Sharma, 2013; Manso *et al.*, 2015), did not always perform well in climate-based growth models. However, the interacting effects of climate variables on the tree growth are largely influenced by the individual tree status, stand level competition and site quality while interpreting the biological growth (Zell, 2018). In our study also, change in the coefficient magnitudes for individual tree status, stand age, and stand level competition indicates that climate variables also influence the biological growth pattern of this species.

Influence of climate variables

The reason for fitting climate-based ABAG model with the month specific climate variables was to avoid over parameterization of the model and to illustrate the influence of the month specific climate variation on ABAG since such influences have not been evaluated with repeated measurement permanent plot data. Our results indicated that deviation in month specific climate variables were better for improving statistics of fit than deviation in growing season climate for climate-based growth models. This may be because air temperature in warmer areas during the growing season is stable and greater which limits plant productivity by inducing water stress (Lloyd and Fastie, 2002; Way and Oren, 2010). However, if there is a drop in high temperature (i.e. maximum air temperature during the growing season) it may show a significant effect on plant growth. However, for ABAG sensitivity with climate change scenarios, deviations in growing seasonal climate variables are preferred in order to be consistent with the data structures associated with those climate change scenarios.

Month specific climate variables have also been found to be important predictors of tree growth by Carrer and Urbinati (2004). Month specific climate variables are commonly used in tree ring data study because of greater tree ages used for tree ring studies that increase the total number of observations for the month specific climate variables and reduce variability. Additionally, month specific climate variables would be useful for addressing early and latewood tree growth.

Shortleaf pine, which is more drought resistance than other southern pines (Lawson, 1990), had an annual growth rate that responded well to month specific climate variables (i.e. DTMAX6 and DPPT9). These variables indicated moderate temperature and rainfall later in the growing season favour growth, which also corresponds to the period of latewood formation in tree rings. It also indicated moderate water stress conditions during the growth season. The interrelationship between temperature and precipitation is probably ecologically significant with respect to shortleaf pine because annual average temperature varies widely across the natural range of this species from 7°C to 23°C than average annual rainfall throughout its range (Guldin, 1986). In the northeastern part of its range, temperature varies considerably with the seasons, but rainfall is more-or-less uniformly distributed throughout year while in the southwestern part of the range, temperatures are warmer and less variable and precipitation is more sporadic (Guldin, 1986). Thus, this species could be very sensitive to a large reduction in precipitation during key months for ring development but not as sensitive to monthly temperature; the temperature playing a more long-term role. These climate patterns not only define shortleaf's physiological environment, but also could affect its ability to compete with other species. Studies have shown that warmer growing season or an extended growing season, and either spring warm up or late fall warmup favours growth of drought resistant tree species. For examples, jack pine in boreal forest of Ontario, Canada (Subedi and Sharma, 2013) and rocky mountain juniper (*Juniperus scopulorum* Sarg.) on the volcanic badlands of western New Mexico, USA (Spond *et al.*, 2014). Biondi (2000) also indicated Douglas fir (*Pseudotsuga menziesii* [Mirb.]) in Idaho, USA grown on an arid site had moisture stress during the growth period because annual growth had a negative

response to summer temperature and a positive response to late spring/early summer precipitation.

ABAG and climate relationship

The correlation between climate variables and growth based on periodic measurement data was small but studies with tree-ring chronologies often show strong correlation between annual growth rate and climate variables; however, the magnitude varies with tree species and location (Biondi, 2000; Spond *et al.*, 2014). Usually, the correlation of annual growth rate with mean temperature and precipitation during the growth season is positive for some tree species at higher northern latitudes (Briffa *et al.*, 1998), Alaskan region (Barber *et al.*, 2000) and midwestern USA (Biondi, 2000); France (Manso *et al.*, 2015). However, sometimes this correlation can be negative in response to temperature and positive to precipitation, for example tree species of southern European regions (Jump *et al.*, 2006) and the southern Rocky Mountains, USA (Chhin *et al.*, 2008). The contrasting effect of climate variables on climate-based ABAG models could be the resultant effect of both geographical distribution of this species and the use of different approaches of fitting climate variables in a model. In our study, the negative correlation of DGPPT with ABAG during the GP was partially governed by DGTMAX indicating the possibility of an interaction effect.

Although the correlation between climate variables and ABAG is small, tree growth is a cumulative process so that modest effects may have a more substantial cumulative effect over numerous years as was indicated by the simulation results reported above. The noticeable differences between individual tree growth rates of different ages due to use of different climate variable fitting approaches and variability in climate variables accounted by those models. The deviation in maximum temperature influenced the basal area growth rate more than deviation in precipitation. As a result, the simulation showed decreased annual growth rate compared with Model 1 due more to increased temperature than to increased precipitation (Figure 5), and a slight change in temperature-affected growth of the young-aged tree more than old trees (Table 7) in combination with basal area and age.

Studies have shown that older stand age or larger diameter stands are more responsive to climate variation than younger stands (Callaway *et al.* 1994; Hanson and Weltzin 2000; Carrer and Urbinati, 2004; Chhin *et al.*, 2008). However, young stands exposed to changing climate scenarios (increased temperature and deceased precipitation) could have more negative growth responses than older stand ages. The negative growth difference from Model 1 represented a stressed response in annual growth rate due to the positive deviation from long-term mean maximum temperature and the negative growth difference represents vice versa. ABAG growth response could be significantly reduced by an increase in temperature of one-degree centigrade. Simulation results also suggested that the decrease in ABAG rate is associated with a combination of decreased precipitation and increased temperature during the growing season, which was also discussed by Barber *et al.* (2000), Jump *et al.* (2006) and Anderegg *et al.* (2013). In the changing climate scenario, that predicts warmer temperature with variable and intense precipitation (Mitchell *et al.* 2014), the ability of shortleaf pine to withstand drought should allow it to thrive in these changing conditions (Guyette *et al.*, 2007; Campbell, 2015). Under several global climate models and two emissions scenarios, it is expected that shortleaf pine will increases its current range and expand northward (Landscape Change Research Group, 2014) which indicates, as our finding suggests, that reduced temperature and higher precipitation would increase its productivity with the appropriate ecological and silviculture management. Although it is difficult to establish the effects of changing climate on growth conclusively, Boisvenue and Running (2006) demonstrated positive impacts on forest productivity if water was not limiting. Hence, the climate simulations indicated that the cumulative effects of climate over a rather long period of years could lead to important effects in tree growth even though gain in fit statistics on annual basal area growth is not very large.

Conclusions

Although the climate-based ABAG model showed modest improvements in RSE, this improvement could play a significant role in understanding the dynamics of growth change in response to climate variability. The month specific climate variables can be used as a proxy for seasonal climate variables while establishing annual growth relationships with climate change for repeated measurement data. It is expected that the level of accuracy and precision of climate-based growth models would increase if measurement data were reconstructed to annual growth or were obtained from dendrochronology. However, it is assumed the developed climate-modifier can be easily replicated with tree ring width data that may be more useful in providing estimates of future forest growth response. Although annual growth measurements may be optimal for correlation with climate variables, annual growth data are rarely available for development of comprehensive forest growth and yield models, which are usually based on periodic measurements similar to our dataset. Therefore, the approach used here may be helpful for incorporating climate variation in forest growth and yield models. The climate-based ABAG model with climate modifier provides a somewhat better estimate of future growth response than linearly added climate terms in the model argument showing a negative effect of increased temperature and a positive effect of precipitation on growth. We believe such climate-based ABAG modelling approach should be helpful to improve our understanding of stand structure changes over the time under different climate change scenarios.

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Conflict of interest statement

None declared.

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References

Anderegg, W.R.L., Kane, J.M. and Anderegg, L.D.L. 2013 Consequences of widespread tree mortality triggered by drought and temperature stress. *Nat. Clim. Chang.* **3** (1), 30–36.

Barber, V.A., Juday, G.P. and Finney, B.P. 2000 Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature* **405** (6787), 668–673.

Beguería, S., Vicente-Serrano, S.M. and Beguería, M.S. 2013 Package 'SPEI'.

Biondi, F. 2000 Are climate-tree growth relationships changing in North-Central Idaho, U.S.A.? *Arct. Antarc. Alp. Res* **32** (2), 111–116.

Boisvenue, C. and Running, S.W. 2006 Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century. *Glob. Chang. Biol.* **12** (5), 862–882.

Borders, B.E. and Bailey, R.L. 1986 A compatible system of growth and yield equations for slash pine fitted with restricted three-stage least squares. *For. Sci.* **32** (1), 185–201.

Briffa, K.R., Schweingruber, F.H., Jones, P.D., Osborn, T.J., Shiyatov, S.G. and Vaganov, E.A. 1998 Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. *Nature* **391** (6668), 678–682.

Budhathoki, C.B., Lynch, T.B. and Guldin, J.M. 2008 Nonlinear mixed modeling of basal area growth for shortleaf pine. *For. Ecol. Manage.* **255** (8–9), 3440–3446.

Callaway, R.M., DeLucia, E.H. and Schlesinger, W.H. 1994 Biomass allocation of montane and desert ponderosa pine: an analog for response to climate change. *Ecology* **75** (5), 1474–1481.

Campbell, H. 2015. Ecological and societal history of shortleaf pine www.shortleafpine.net.

Carrer, M. and Urbinati, C. 2004 Age-dependent tree-ring growth responses to climate in Larix decidua and *Pinus cembra*. *Ecology* **85** (3), 730–740.

Chhin, S., Hogg, E.H., Lieffers, V.J. and Huang, S. 2008 Potential effects of climate change on the growth of lodgepole pine across diameter size classes and ecological regions. *For. Ecol. Manage.* **256** (10), 1692–1703.

Duchesne, L., Houle, D. and D'Orangeville, L. 2012 Influence of climate on seasonal patterns of stem increment of balsam fir in a boreal forest of Québec, Canada. *Agric. For. Meteorol.* **162–163**, 108–114.

Forest Range and Experiment Station. Ogden, UT 84401. GTR-Int-133.

Fortin, M. 2013 Population-averaged predictions with generalized linear mixed effects models in forestry: an estimator based on Gauss-Hermite quadrature. *Can. J. For. Res.* **43**, 129–138.

Foster, T., Schmalzer, P. and Fox, G. 2015 Seasonal climate and its differential impact on growth of co-occurring species. *Eur. J. For. Res.* **134** (3), 497–510.

Furnival, G.M. and Wilson, R.W. 1971 Systems of equations for predicting forest growth and yield. In *Statistical Ecology*, **Vol. 3**. Patil G.P., Pielou E.C. and Waters W.E. (eds). Pennsylvania State University Press, pp. 43–55.

Graumlich, L.J. 1993 Response of tree growth to climatic variation in the mixed conifer and deciduous forests of the upper Great Lakes region. *Can. J. For. Res.* **23** (2), 133–143.

Guldin, J.M. 1986 Ecology of shortleaf pine. In *Proceedings of Symposium on the Shortleaf Pine Ecosystem*. P.A. Murphy (ed.). 1986 March 31–April 2; Little Rock, AR. Monticello, AR: Arkansas Cooperative Extension Service, pp. 25–40.

Guttman, N.B. 1999 Accepting the standardized precipitation index: a calculation algorithm. *J. Am. Water Resour. Assoc* **35** (2), 311–322.

Guyette, R.P., Muzika, R.-M. and Voelker, S.L. 2007 The historical ecology of fire, climate, and the decline of shortleaf pine in the Missouri Ozarks. In *Shortleaf Pine Restoration and Ecology in the Ozarks: Proceedings of a Symposium*. J.M. Kabrick, D.C. Dey, D. Gwaze (eds.). 2006 November 7–9; Springfield, MO. Gen. Tech. Rep. NRS-P-15. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station, pp. 8–18.

Hanson, P.J. and Weltzin, J.F. 2000 Drought disturbance from climate change: response of United States forests. *Sci. Total Environ.* **262** (3), 205–220.

Intergovernmental Panel on Climate Change (IPCC) 2007 Climate change 2007: Mitigation. In *Contribution of Working Group III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Metz B., Davidson O.R., Bosch P.R., Dave R. and Meyer L.A. (eds). Cambridge University Press, pp. 7–231.

Jiang, H., Radtke, P.J., Weiskittel, A.R., Coulston, J.W. and Guertin, P.J. 2015 Climate-and soil-based models of site productivity in eastern US tree species. *Can. J. For. Res.* **45** (3), 325–342.

Jump, A.S., Hunt, J.M. and PeÑUelas, J. 2006 Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Glob.Chang. Biol.* **12** (11), 2163–2174.

Landscape Change Research Group 2014 *Climate Change Atlas*. Northern Research Station, U.S. Forest Service, http://www.nrs.fs.fed.us/atlas.

Lawson, E.R. 1990 *Pinus echninata* Mill. Shortleaf Pine. In Silvics of North America; Volume 1, Conifers: 316–326. Burns RM, Honkala BH, technical coordinators. U.S. Department of Agriculture, Forest Service Handbook 654. Washington, DC.

Liaw, A. and Wiener, M. 2002 Classification and regression by randomForest. *R News* **2** (3), 18–22.

Lloyd, A. and Fastie, C. 2002 Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Clim. Chang.* **52** (4), 481–509.

Lynch, T.B., Hitch, K.L., Huebschmann, M.M. and Murphy, P.A. 1999 An individual-tree growth and yield prediction system for even-aged natural shortleaf pine forests. *South. J. Appl. For.* **23** (4), 203–211.

Lynch, T.B., Murphy, P.A. and Lawson, E.R. 1991 Stand volume equations for managed natural even-aged shortleaf pine in eastern Oklahoma and western Arkansas. Research report P-921 Oklahoma Agricultural Experiment Station. 12p.

Manso, R., Morneau, F., Ningre, F. and Fortin, M. 2015 Effect of climate and intra- and inter-specific competition on diameter increment in beech and oak stands. *Forestry* **88** (5), 540–551.

Miner, C.L., Walters, N.R. and Belli, M.L., 1989 A Technical Guide to TWIGS for the North Central United Sates. General Technical Report NC-125. St. Paul, MN: U.S. Dept. of Agriculture, Forest Service, North Central Forest Experiment Station. 105 p.

Mitchell, R.J., Liu, Y., O'Brien, J.J., Elliott, K.J., Starr, G., Miniat, C.F., *et al* 2014 Future climate and fire interactions in the southeastern region of the United States. *For. Ecol. Manage.* **327**, 316–326.

Moore, D.J.P., Aref, S., Ho, R.M., Pippen, J.S., Hamilton, J.G. and De Lucia, E.H. 2006 Annual basal area increment and growth duration of *Pinus taeda* in response to eight years of free-air carbon dioxide enrichment. *Glob. Chang. Biol.* **12** (8), 1367–1377.

Moscow Forestry Sciences Laboratory. 2015 Custom Climate Data Requests. Available from http://forest.moscowfsl.wsu.edu/climate/customData/index.php [accessed 4 Aug 2015].

Murphy, P.A., Lawson, E.R. and Lynch, T.B. 1992 Basal area and volume development of natural even-aged shortleaf pine stands in the Ouachita Mountains. *South. J. Appl. For.* **16** (1), 30–34.

Murphy, P.A. and Shelton, M.G. 1996 An individual-tree basal area growth model for loblolly pine stands. *Can. J. For. Res.* **26**, 327–331.

Pinheiro, J. and Bates, D. 2000 *Mixed-effects Models in S and S-PLUS*. Springer Science & Business Media, p. 391.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. and Core Team, R. 2018 Linear and Nonlinear Mixed Effects Models, R package version 3.1.-137.

Pokharel, B. and Dech, J.P. 2012 Mixed-effects basal area increment models for tree species in the boreal forest of Ontario, Canada using an ecological land classification approach to incorporate site effects. *Forestry* **85** (2), 255–270.

Pretzsch, H., Biber, P. and Dursky, J. 2002 The single tree-based stand simulator SILVA: construction, application and evaluation. *For. Ecol. Manage.* **162** (1), 3–21.

PRISM Climate Group. 2015 Parameter-elevation regression on independent slopes model, http://www.prism.oregonstate.edu/explorer/created 14 June, 2015.

R Core Team 2018 *R: a language and environment for statistical computing*. R Foundation for Statistical Computing. ISBN 3-900051-07-0, http://www.R-project.org/.

Richards, F.J. 1959 A flexible growth function for empirical use. *J. Exp. Bot.* **10** (29), 290–300.

Saud, P., Lynch, T.B., Anup, K.C. and Guldin, J.M. 2016 Using quadratic mean diameter and relative spacing index to enhance height–diameter and crown ratio models fitted to longitudinal data. *Forestry* **89** (2), 215–229.

Saud, P., Lynch, T.B., Wilson, D.S., Stewart, J., Guldin, J.M., Heinemann, B., *et al* 2015 Influence of weather and climate variables on the basal area growth of individual shortleaf pine trees. In *Proceedings of the 17th Biennial Southern Silvicultural Research Conference. e-Gen. Tech. Rep. SRS-203*. Holley A.G., Connor K.F. and Haywood J.D. (eds). U.S. Department of Agriculture, Forest Service, Southern Research Station, pp. 406–408.

Shifley, S.R. and Brand, G.J. 1984 Chapman-Richards growth function constrained for maximum tree size. *For. Sci.* **30**, 1066–1070.

Spond, M.D., van de Gevel, S.L. and Grissino-Mayer, H.D. 2014 Climate-growth relationships for Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) on the volcanic badlands of western New Mexico, USA. *Dendrochronologia* **32** (2), 137–143.

Subedi, N. and Sharma, M. 2013 Climate-diameter growth relationships of black spruce and jack pine trees in boreal Ontario, Canada. *Glob. Chang. Biol.* **19** (2), 505–516.

Temensgen, H., Monleon, V.J. and Hann, D.W. 2008 Analysis and comparison of nonlinear tree height prediction strategies for Douglas-fir forests. *Can. J. For. Res.* **38** (3), 553–565.

U.S. Department of Interior, Geological Survey 1970 *The National Atlas of the United States of America*. U.S. Department of Interior, Geological Survey, p. 97.

Way, D.A. and Oren, R. 2010 Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. *Tree Physiol.* **30** (6), 669–688.

Weiskittel, A.R., Hann, D.W., Kershaw, J.A. and Vanclay, J.K. 2011 *Forest Growth and Yield Modelling*. Wiley-Blackwell & Sons Ltd.

Williams, A.P., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M., *et al* 2013 Temperature as a potent driver of regional forest drought stress and tree mortality. *Nat. Clim. Chang.* **3** (3), 292–297.

Wilmking, M., Juday, G.P., Barber, V.A. and Zald, H.S.J. 2004 Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. *Glob. Chang. Biol.* **10** (10), 1724–1736.

Wykoff, W.R., Crookston, N.L. and Stage, A.R. 1982 User's Guide to the Stand Prognosis Model. USDA Forest Service, Intermountain Forest Range and Experiment Station. Ogden, VT 84401, GTR-Int-133.

Zell, J. 2018 Climate sensitive tree growth functions and the role of transformations. *Forests* **9**, 382. doi:10.3390/f9070382.

Zhao, D., Westfall, J., Coulston, J., Lynch, T.B., Bullock, B. and Montes, C. 2019 Additive biomass equations for slash pine trees: comparing three modeling approaches. *Can. J. For. Res.* **49** (1), 27–40.