

# *Pinus taeda* forest growth predictions in the 21st century vary with site mean annual temperature and site quality

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## Abstract

Climate projections from 20 downscaled global climate models (GCMs) were used with the 3-PG model to predict the future productivity and water use of planted loblolly pine (*Pinus taeda*) growing across the southeastern United States. Predictions were made using Representative Concentration Pathways (RCP) 4.5 and 8.5. These represent scenarios in which total radiative forcing stabilizes before 2100 (RCP 4.5) or continues increasing throughout the century (RCP 8.5). Thirty-six sites evenly distributed across the native range of the species were used in the analysis. These sites represent a range in current mean annual temperature (14.9–21.6°C) and precipitation (1,120–1,680 mm/year). The site index of each site, which is a measure of growth potential, was varied to represent different levels of management. The 3-PG model predicted that aboveground biomass growth and net primary productivity will increase by 10%–40% in many parts of the region in the future. At cooler sites, the relative growth increase was greater than at warmer sites. By running the model with the baseline [CO<sub>2</sub>] or the anticipated elevated [CO<sub>2</sub>], the effect of CO<sub>2</sub> on growth was separated from that of other climate factors. The growth increase at warmer sites was due almost entirely to elevated [CO<sub>2</sub>]. The growth increase at cooler sites was due to a combination of elevated [CO<sub>2</sub>] and increased air temperature. Low site index stands had a greater relative increase in growth under the climate change scenarios than those with a high site index. Water use increased in proportion to increases in leaf area and productivity but precipitation was still adequate, based on the downscaled GCM climate projections. We conclude that an increase in productivity can be expected for a large majority of the planted loblolly pine stands in the southeastern United States during this century.

## KEYWORDS

aboveground biomass, forest productivity, global climate model, leaf area index, loblolly pine, net primary productivity, process model, representative concentration pathway, transpiration

## 1 | INTRODUCTION

There is wide recognition that temperature and precipitation are key environmental factors regulating primary productivity of terrestrial ecosystems, including forests. Using data collected in the

International Biome Program, Lieth (1973) demonstrated that net primary productivity (NPP) in ecosystems ranging from the tundra to the tropics increased with increasing site mean annual temperature with a slight sigmoidal pattern over a range from –12°C to 29°C. He also demonstrated that the same sites could be arrayed along a

gradient of precipitation, with NPP increasing rapidly, and nearly linearly, as precipitation increased from approximately 150 mm/year to >1,700 mm/year. Net primary productivity appeared to approach an asymptote at sites with precipitation more than 1,800 mm/year, but there were few sites in the analysis with precipitation >2,000 mm/year.

The relationships between NPP and temperature and precipitation are relevant to the present time because air temperature and precipitation are changing globally and are expected to continue to do so throughout the 21st Century. There have been several retrospective analyses that have indicated that forest growth has already been responding to recent changes in temperature and precipitation. Charru, Seynave, Hervé, and Bontemps (2014) reported that stand basal area growth of Norway spruce (*Picea abies*) increased over the period of 1980–2005 in three mountainous areas in western Europe. The average increase ranged from 79% in the Massif Central area to 19% in the Alps. Charru et al. (2014) concluded that an increase in temperature contributed to the increase in growth in both areas, but the smaller increase in growth in the Alps was due to lower soil water availability. Bosela, Štefančík, Patrás, and Vacek (2016) reported that aboveground productivity of European beech (*Fagus sylvatica*) in the western Carpathian Mountains in Eastern Europe was 5%–40% higher in recent years compared to growth in the 1960s. That growth increase was correlated with increased temperature—which did not result in an increase in water deficits—although the increase in atmospheric [CO<sub>2</sub>], a decrease in sulfur dioxide, and changes in forest management practices over that time could also have been contributing factors. Schaphoff, Reyer, Schepaschenko, Gerten, and Shvidenko (2016) reviewed studies of the patterns of forest productivity in Russian forests and concluded that temperature increases are lengthening the growing season in the boreal zone and increasing forest productivity. They also concluded that there is evidence that increased [CO<sub>2</sub>] and precipitation have increased tree growth in some parts of Russia. However, the positive growth response to increased [CO<sub>2</sub>] depended on sufficient soil water availability.

Drought stress has also substantially decreased NPP in some forested regions. Mekonnen, Grant, and Schwalm (2016) modeled gross primary productivity (GPP) of ecosystems in North America and concluded that over the last three decades GPP had increased by 7% in eastern deciduous forests and 22% in northern forests from 1980 to 2010 due to increasing temperature and adequate precipitation. However, in western North America, Mekonnen et al. (2016) found that many ecosystems have experienced a decrease in GPP over that time period, which was associated mainly with a decrease in precipitation.

In addition to estimating how changes in the climate are affecting current forest growth, estimates of forest growth in the future are needed to provide an assessment of potential changes in wood and fiber supply, as well as ecosystem services, such as carbon sequestration and water yield. Reyer et al. (2014) modeled forest NPP at 132 sites with a variety of tree species across Europe using the process model 4C (Forest Ecosystems in a Changing

Environment) using downscaled regional climate projections from three global climate models (GCMs). Carbon dioxide was either held constant at 350  $\mu\text{mol/mol}$ , or allowed to vary according to the A1B scenario (CO<sub>2</sub> emissions increase until mid-century then decline) or the B1 scenario (little change in CO<sub>2</sub> emissions until mid-century followed by a substantial decline; IPCC 2007). With a constant [CO<sub>2</sub>], modeled NPP generally increased at northern sites, decreased at southern sites and either increased or decreased at mid-latitude sites, compared to NPP predictions in the present time. When [CO<sub>2</sub>] was allowed to increase (A1B or B1 scenarios), the response of NPP was substantial; mean NPP was higher in the future than at the present time at all sites. Peters, Wythers, Shang, Bradford, and Reich (2013) used the PnET-CN model to estimate future forest productivity in the Great Lakes region of the United States. That model predicted that productivity of the six forest types in the region would increase in this century, due almost entirely to an increase in carbon gain by the trees in response to elevated [CO<sub>2</sub>]. The findings of both of those studies indicate the need for accurate representations in process models of the response of different tree species to elevated [CO<sub>2</sub>].

In this study, we used the hybrid process model 3-PG (Physiological Processes Predicting Growth; Landsberg & Waring, 1997) to predict the growth of planted even-aged loblolly pine (*Pinus taeda*) stands across the southeastern United States. Loblolly pine is native to the southeastern United States and is extensively planted in the region and managed for wood production. There are approximately 25 million hectares of planted trees in the United States (US) at the present time, of which loblolly pine represents 10 million hectares, making it the most planted tree species in the country (Robertson, Gaulke, McWilliams, LaPlante, & Guldin, 2011). Planted forests account for 22% of all forested area in the southeastern United States, and they play a large role in meeting the nation's wood and fiber demand.

The version of the 3-PG model we used, which was optimized for loblolly pine, was shown to produce very accurate estimates of loblolly pine growth and productivity across the entire native range of the species under present climatic conditions (Gonzalez-Benecke et al., 2016). We incorporated the species' response to elevated CO<sub>2</sub> based on results from the Duke forest free air CO<sub>2</sub> enrichment (FACE) study conducted in a planted loblolly pine stand (Oren et al., 2001). Downscaled climate projections (Abatzoglou & Brown, 2012) from 20 GCMs, under Representative Concentration Pathway (RCP) 4.5 and 8.5 scenarios (Meinshausen et al., 2011) were used to predict productivity and water use of loblolly pine stands planted across the region at the middle and end of the century. An overarching issue addressed in this study was the effect forest management would have on the response of managed forests to climate change across a species range. Thirty-six plantations, arrayed across the loblolly pine range, were used to develop these predictions. At each location five levels of management from almost no management other than planting to highly intensive management (optimal fertilization, weed control, superior genotypes) were represented in model simulations. Our specific objectives were: (1) to determine how growth and water use

of managed loblolly pine stands will respond to projected changes in regional climate, and (2) to evaluate how the species' response to climate change might differ across the region due to local differences in climate and management intensity. We hypothesized that: (1) stands in cooler areas would have relatively greater increases in growth than those in warmer areas, (2) stands with low growth rates would respond relatively more to changes in climate than stands with high growth rates, and (3) growth rates, NPP, and stand evapotranspiration (ET) will increase in both mid- and late-century time periods under both the RCP 4.5 and 8.5 scenarios.

## 2 | MATERIALS AND METHODS

To estimate loblolly pine stand growth under different climatic scenarios, we used the forest simulation model 3-PG (Physiological Processes Predicting Growth; Landsberg & Waring, 1997). 3-PG is a stand-level model that uses monthly weather data (e.g., global radiation, rainfall, number of frost days, and mean minimum and maximum temperatures) and simple site characteristics such as soil texture class, upper and lower limits of available soil water (mm), initial tree age, stocking (trees per ha), and biomass (Mg/ha) in roots, foliage, and stem (stemwood + bark + branches) to predict growth of even-aged, mono-specific stands. The model was parametrized and validated for loblolly pine forests growing across a wide range of ages and stand characteristics in the southern United States (Gonzalez-Benecke et al., 2016). For this analysis, we further modified the model to include the effects of increasing atmospheric CO<sub>2</sub> on stand productivity. We describe the major model assumptions in the Supplemental Material section and a detailed description of the model can be found in Landsberg and Waring (1997) and Landsberg and Sands (2011).

We ran the model under different climate and stand productivity scenarios for 36 loblolly pine plantations distributed across the range of the species (Figure 1; Table S1). The 36 sites used in this study were well distributed geographically and climatically across the native range of the species in the southeastern United States. The distribution of loblolly pine in the region spans about an 8°C range in mean annual temperature and about a 600 mm range in mean annual rainfall (Figure 1; derived from the WorldClim database, <http://www.cec.org/tools-and-resources/north-american-environmental-atlas/map-files>).

In order to predict growth and evapotranspiration, the model was run separately for each site using 1975–2099 output from 20 downscaled GCMs (Table S2) that are part of the Multivariate Adaptive Constructed Analogs (MACA) dataset (MACAv2-LIVNEH, Abatzoglou & Brown, 2012). While four total Representative Concentration Pathways (RCPs) were defined by the Intergovernmental Panel on Climate Change (IPCC, van Vuuren et al., 2011), only RCP 4.5 (total radiative forcing has stabilized before 2100) and RCP 8.5 (high greenhouse gas concentrations by 2100) were used for the MACA downscaling (Figure 2). Therefore, only these two RCPs were utilized for this study. MACA is a gridded product with a spatial resolution of ~6 km and a daily temporal resolution. The 36 sites were extracted from MACA by

obtaining data from the grid cell that contained each of the 36 simulation locations (Table S1).

In order to calculate relative change in the future, a baseline period was established at the 36 locations used in this study using MACA data for the period from 1975–2005—a past period simulated by the 20 downscaled GCMs. We separated the future projections of temperature and precipitation for RCP 4.5 and 8.5 scenarios for two periods of 25 years during 21st century: mid-century (between years 2025 and 2049) and late-century (between years 2075 and 2099). Mean [CO<sub>2</sub>] for baseline, mid-century RCP 4.5 and 8.5, and late-century RCP 4.5 and 8.5 were 350, 454, 481, 533, and 815 μmol/mol, respectively.

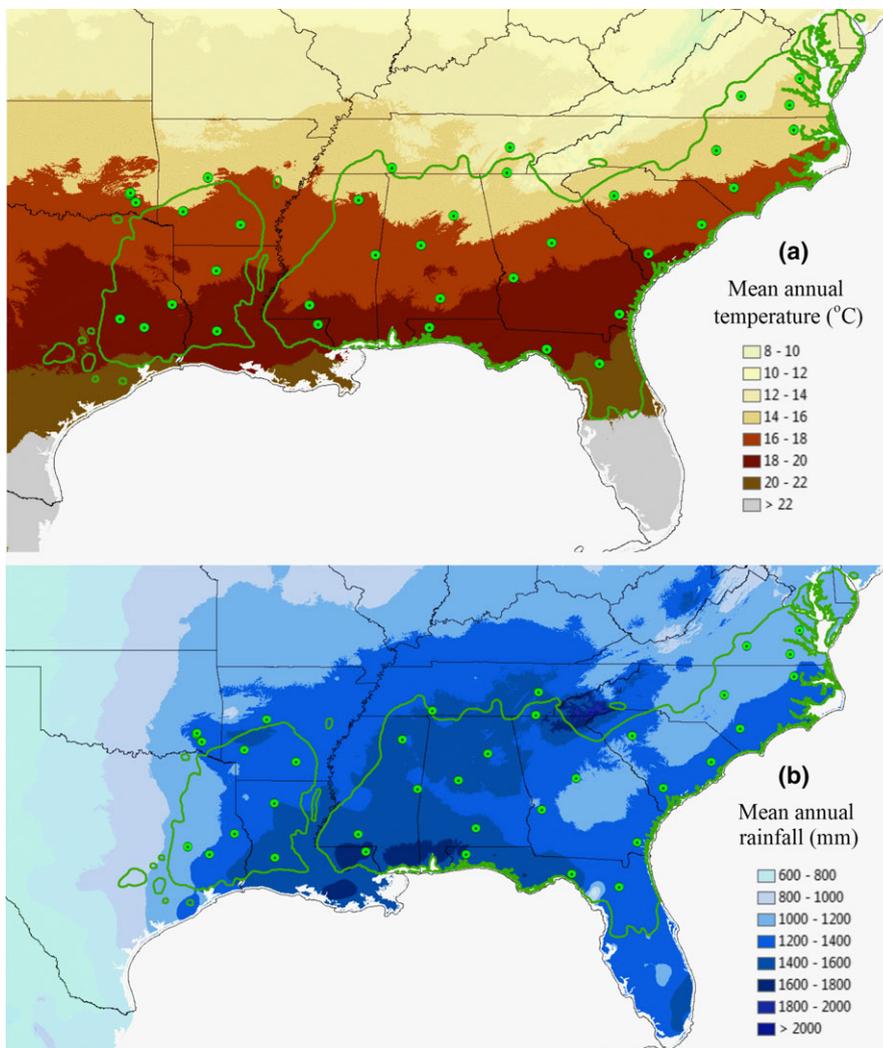
The 3-PG runs were made at each site assuming six different site qualities from very high to very low, which represent the potential range in growth that has been observed in the loblolly pine range (Zhao et al., 2016). Site quality was varied by changing the site index (SI, mean height of dominant trees at age 25 years) at 3 m steps, ranging from 15 to 30 m. Site index describes the potential of trees to grow at a particular location. This approach was taken, rather than limiting the analysis to the specified SI of each site at the current time, because SI can be changed by management intensity, for example, by the level of competing vegetation control or quantity and frequency of fertilizer applications. Using a range of SI for each site captures the potential growth capacity of planted and managed stands envisioning that management intensities from low to high can be applied under current and future climate conditions. Although SI is not a parameter in the 3-PG model, it was used to estimate the value of the Fertility Rating parameter, which is a site-specific parameter (Gonzalez-Benecke et al., 2016).

For each site and SI scenario, we ran the model for 25 years, from 1-year-old seedlings until age 25, assuming a constant initial stand density of 1,500 seedlings per ha. This represents the typical length of the growth period of a planted stand of loblolly pine until it is harvested and is often referred to as a rotation. We determined initial biomass using the height-biomass functions reported in Gonzalez-Benecke et al. (2016) and a relationship between SI and mean height of the stand at the end of first growing season (C.A. Gonzalez-Benecke, T.A. Martin, E.J. Jokela, unpublished data, see Supplemental Material). For example, that relationship predicted a mean height at the end of the first growing season of 0.33, 0.59, and 0.99 m for stands with SI = 15, 23 and 30 m, respectively.

Additionally, for the 36 sites, the effects of elevated CO<sub>2</sub> and climate on growth were separated by running the 3-PG model for the mean of the 20 downscaled climate models under RCP 4.5 and 8.5 projections at its specified elevated [CO<sub>2</sub>], or with it reduced to 350 μmol/mol, for the mid-century and late-century periods. Initial stand density and site index were assumed as 1,500 seedlings per ha and 22 m, respectively.

## 3 | RESULTS

The MACA climate model baseline (1975–2005) mean annual temperature of the 36 sites used in this study, which are located across

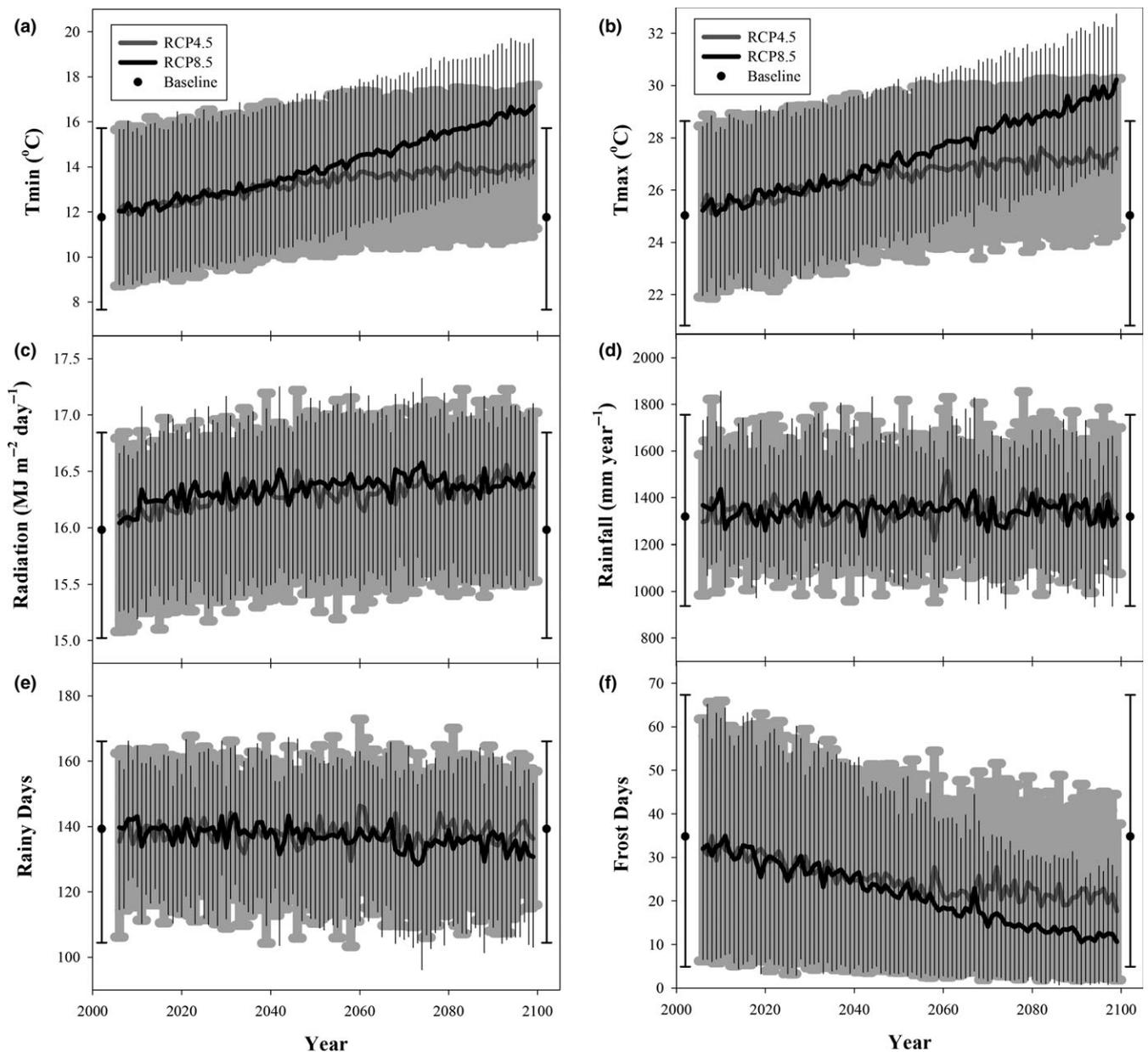


**FIGURE 1** Historical (1950–2000) mean annual temperature (a) and mean annual rainfall (b) for S.E. United States, which have been derived from the WorldClim database, courtesy of the Museum of Vertebrate Zoology, University of California, Berkeley, USA (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). The species natural distribution range is delimited by the green lines. The location of the 36 sites used for this analysis is marked by green circles

12 states in the southeastern United States, ranged from  $14.9^{\circ}\text{C}$  to  $21.6^{\circ}\text{C}$  (Figure 3). The mean annual precipitation of the sites ranged from 1,120 to 1,680 mm/year. The mean of the 20 downscaled GCM projections for the RCP 4.5 scenario indicated that under that scenario the region would have about a  $2^{\circ}\text{C}$  increase in mean air temperature in the 2025–2049 time period relative to the baseline, and about a  $2.5^{\circ}\text{C}$  increase in the 2075–2099 period. For the RCP 8.5 scenario, the multimodel mean projected temperatures increase to about  $2.5^{\circ}\text{C}$  and  $5^{\circ}\text{C}$  relative to the baseline for the same time periods, respectively. For both RCP scenarios, there was a somewhat larger increase in air temperature at cooler sites than warmer sites. Model projections for both RCP scenarios indicated a relatively small increase or decrease in rainfall, usually  $<100$  mm/year, compared to the mean annual precipitation which was  $>1,120$  mm/year at all of the sites. The largest projected changes in precipitation were in the RCP 8.5 scenario for the 2075–2099 time period.

The 3-PG model was initially run using the mean of MACA climate data simulated by the 20 downscaled GCMs over a historical period from 1975 to 2005 to create a baseline with which to compare growth and water use simulations using the RCP 4.5 and 8.5 scenarios later in the century (Figure 4). For a specific SI, baseline

growth was always greater at warmer sites than cooler sites. Above-ground biomass (AGB, Mg/ha) and net primary productivity (NPP,  $\text{Mg ha}^{-1} \text{ year}^{-1}$ ) were highest at sites with higher mean annual temperature ( $T_{\text{mean}}$ ) and a high SI (Figure 4a,b). The mean AGB between years 1 and 25 was low at cool sites ( $T_{\text{mean}} < 18^{\circ}\text{C}$ ) with low SI, ranging from 20 to 80 Mg/ha, but even cool sites could produce high AGB if the site had a high SI. At warmer sites ( $T_{\text{mean}} > 18^{\circ}\text{C}$ ), growth was higher across the range of SI compared to cooler sites. Mean annual NPP and projected leaf area index (LAI,  $\text{m}^2/\text{m}^2$ ) between years 1 and 25 exhibited the same general pattern of response to site temperature and SI as AGB (Figure 4b,c). The highest NPP and LAI occurred at sites with the combination of high  $T_{\text{mean}}$  and high SI. The lowest NPP and LAI occurred at cool sites with low SI. This pattern can also be seen in stand light use efficiency (LUE, g/MJ), indicating that warmer sites with higher SI had higher mean LUE over the 25-year growth period in addition to a higher mean LAI (Figure 4d). Stand evapotranspiration (ET, mm/year) also varied in a similar manner as growth and LAI across the temperature and SI gradients (Figure 4e). Stand mean annual ET over the 25-year period varied from  $\sim 200$  mm/year in cool, low SI sites to  $\sim 1,000$  mm/year in warm, high SI sites. This was reflected in water yield (WY,



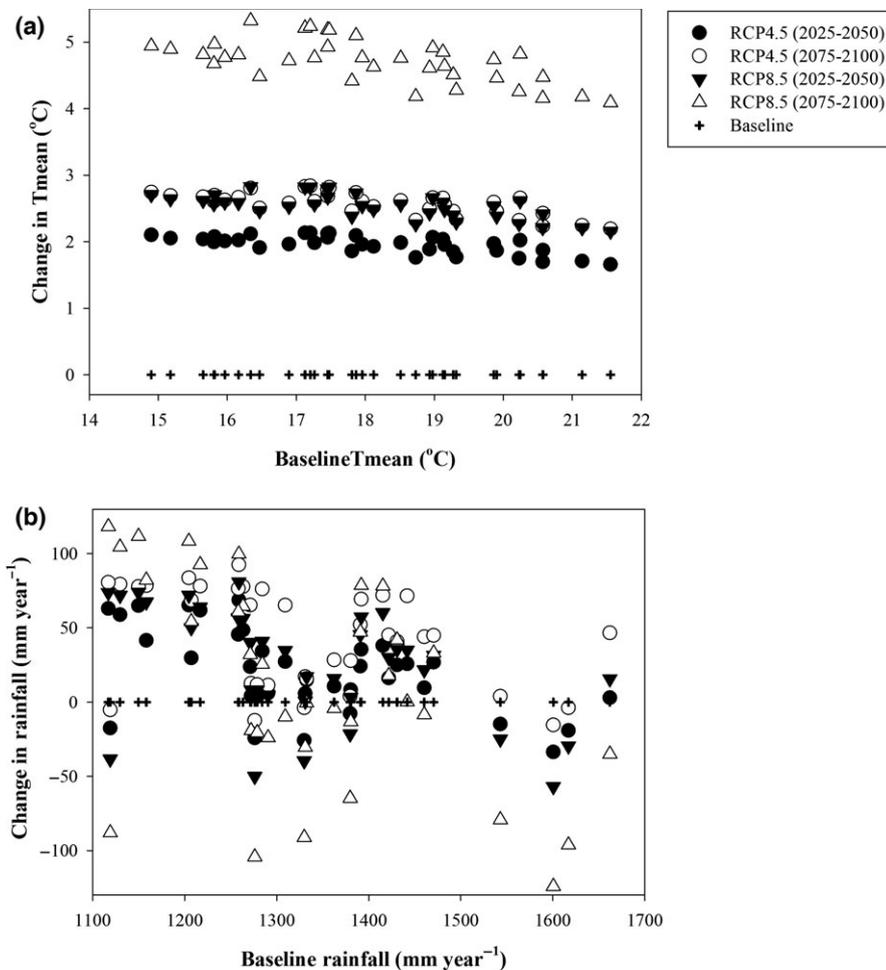
**FIGURE 2** Climate projections of 20 downscaled GCMs from the Multivariate Adaptive Constructed Analogs (MACA) dataset from 2005–2099 including mean annual (a) mean minimum monthly temperature ( $T_{min}$ ), (b) mean maximum monthly temperature ( $T_{max}$ ), (c) mean daily radiation, (d) total rainfall, (e) number of rainy days and (f) number of frost days, for 36 sites in S.E. United States for two Representative Concentration Pathways (RCP) 4.5 (gray) and 8.5 (black). Solid line represents the mean value and the vertical lines represent the range of variation across all sites and climate models. MACA climate model baseline values (1975–2005) are represented by filled circles (mean) and whiskers (range for 36 sites) at the beginning and end of the century

mm year), which showed the opposite pattern. Sites with the lowest SI had WY values of  $\sim 1,000$  mm/year, while sites with  $SI > 25$  had  $WY < 600$  mm/year. The effect of site temperature on mean annual WY between years 1 and 25 was evident, but it was less pronounced compared with NPP, LAI and AGB.

### 3.1 | Predicted responses to future climates

The predicted effects of RCP 4.5 and 8.5 on AGB, NPP, LAI, LUE, ET, and WY averaged across the 20 downscaled GCMs for the time

periods from 2025 to 2049 and from 2075 to 2099 are shown in Figures 5–10 as the relative difference from the MACA climate model baseline values shown in Figure 4. It is important to note that the mean annual temperature ( $T_{mean}$ ) on the x-axes of these graphs represents the MACA baseline mean annual temperature from the x-axis of Figure 3, not the average annual temperature from the RCP 4.5 or 8.5 scenarios. To see the change in temperature projected under these scenarios, refer to the y-axis of Figure 3. For the 2025–2049 time period, at sites with a baseline  $T_{mean} < 18^{\circ}\text{C}$ , AGB growth was predicted to increase about 10%–30% above baseline AGB



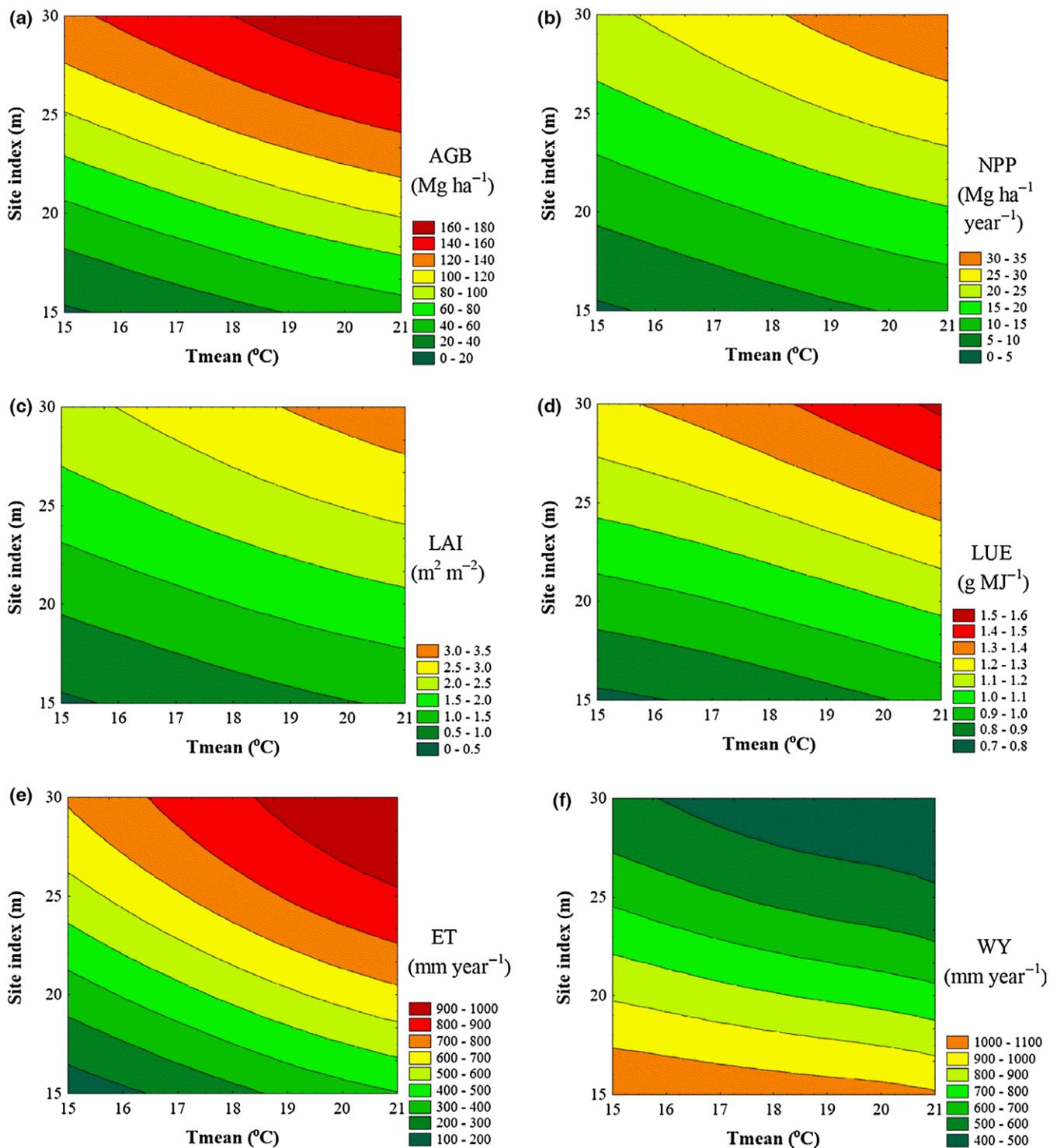
**FIGURE 3** Mean change in (a) mean annual temperature ( $T_{\text{mean}}$ ) and (b) rainfall for 36 sites in S.E. United States for two Representative Concentration Pathways (RCP) 4.5 (circle) and 8.5 (triangle) during mid-century (black filled) and late-century (open filled) periods. For reference, MACA climate model baseline (1975–2005) difference (zero value) is represented as a cross for each site. The x-axes represent an average of the 20 downscaled global climate models (GCMs) for the MACA climate model baseline period (1975–2005), which is a past period simulated by the 20 downscaled GCMs, at the 36 locations used in this study. The y-axes represent mean changes (across 20 downscaled GCMs) in temperature or rainfall as compared to the mean MACA climate model baseline period

growth in both the RCP 4.5 and 8.5 scenarios (Figure 5). However, at warmer sites either no change in AGB or a small decrease (10% or less) was predicted. For the 2075–2099 time period, the greatest relative increases in AGB were also at cooler sites, compared to warmer sites, across the entire range of SI. There were also much larger differences between the RCP 4.5 and RCP 8.5 scenarios at the end of the century compared to the response at mid-century. At the end of the century, the model predicted that the relative increase in AGB at cool sites (baseline  $T_{\text{mean}} < 18^{\circ}\text{C}$ ) with low SI would be 20%–60% greater than the baseline under RCP 4.5 and 40%–100% greater under RCP 8.5. In warmer areas with high SI, a smaller number of sites were predicted to have a negative response ( $\leq 10\%$ ) compared to baseline AGB growth.

The same pattern shown in the relative change in AGB could be seen in NPP and LAI (Compare Figure 5 with Figures 6 and 7). Both NPP and LAI were predicted to increase at cool sites, and there was little, or a small negative, change in relative growth at warm sites, especially those with higher SI. The effect of RCP 4.5 and 8.5 on NPP and LAI was small for the mid-century time period, but increased substantially at the end of the century at the coolest sites with low SI. At high SI sites, NPP and LAI exhibited a small decrease at the warmest sites and either no change or a slight increase at intermediate sites (baseline  $T_{\text{mean}}$  between 17 and  $20^{\circ}\text{C}$ ). Little or no

relative change in LUE was predicted for any of the sites under either RCP scenario (Figure 8).

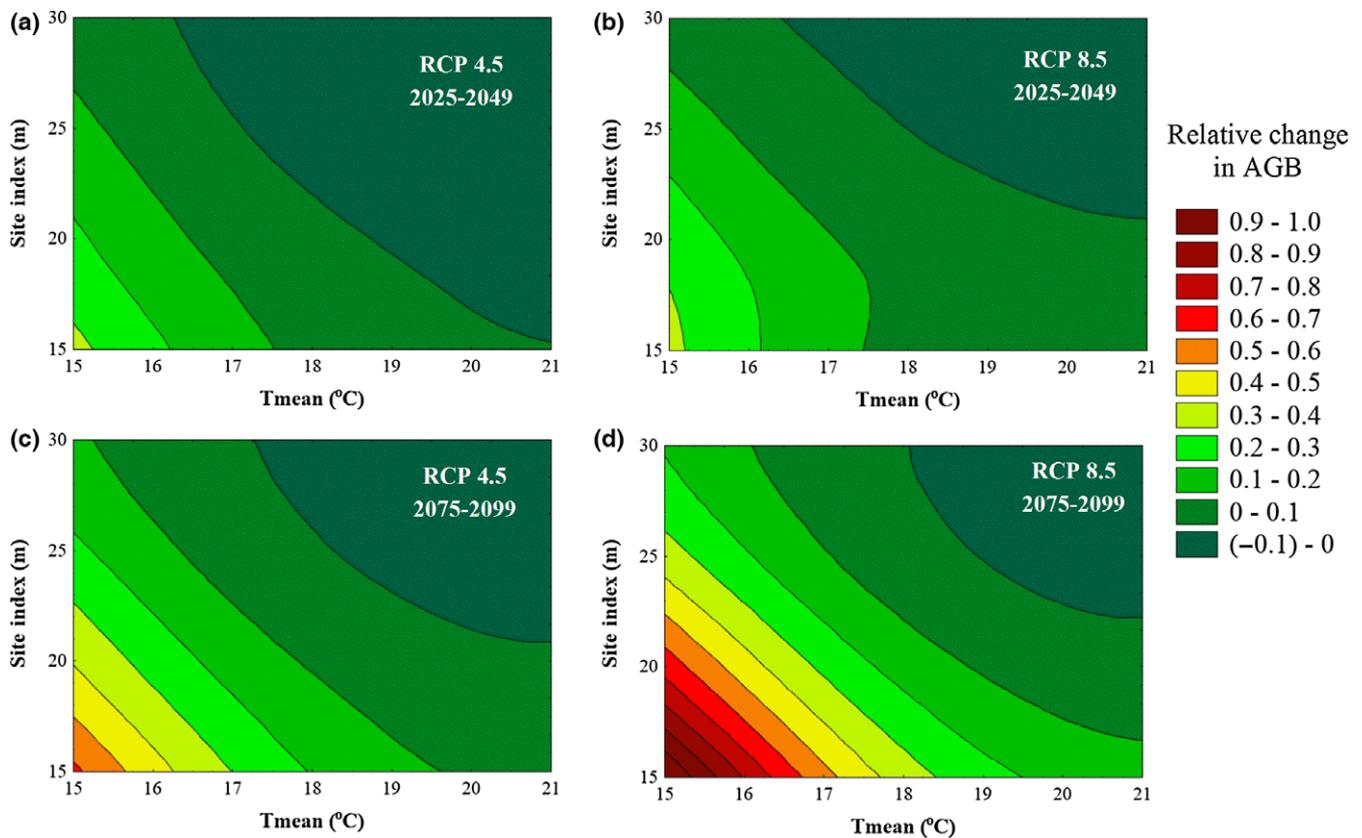
Under both RCP 4.5 and 8.5 scenarios, ET had very similar patterns to those of NPP and LAI (Figure 9). There was a larger relative increase in ET at cooler sites with low SI, compared to warmer sites with high SI. Modest increases in ET were predicted for mid-century rotations under both RCP 4.5 and 8.5 scenarios. For the 2075–2099 period under RCP 8.5, the relative increase in ET was from 40% to 90% at cool sites (baseline  $T_{\text{mean}} < 18^{\circ}\text{C}$ ) and 15 to 25 m SI. Under RCP 4.5 at the end of the century, the relative increase in ET was between 20% and 60% for the same sites. The relative change in WY across both RCPs and for both time periods ranged from  $-20\%$  to  $+20\%$  across the range of sites (Figure 10). For rotations growing at mid-century, many of the sites were predicted to have a relative decrease in WY of 10%–20%, with only high SI sites in the warmest areas having either no change in WY or a slight increase. Comparing mid-century and end-of-century rotations under the RCP 4.5 scenario, WY was generally higher in late-century than in mid-century. For RCP 8.5, there was less difference between the two time periods, but the greatest relative decrease ( $-10\%$  to  $-20\%$ ) was predicted to extend into warmer sites compared with predictions for mid-century rotations.



**FIGURE 4** Baseline values between years 1 and 25 for aboveground biomass (AGB) (a), net primary productivity (NPP) (b), leaf area index (LAI) (c), light use efficiency (LUE) (d), stand evapotranspiration (ET) (e), and stand water yield (WY) (f) for loblolly pine stands growing in sites with different site index and baseline mean annual temperature ( $T_{\text{mean}}$ ).  $T_{\text{mean}}$  is the MACA baseline mean annual temperature, which is shown on the x-axis of Figure 3. Baseline values for variables (a–f) were generated using MACA climate model baseline values (simulated from 1975–2005) averaged across 20 downscaled global climate models (GCMs)

The predicted changes in the absolute values of AGB, NPP, LAI, LUE, ET, and WY averaged across the 20 downscaled GCMs under RCP 4.5 and 8.5 for rotations in years 2025–2049 and 2075–2099 are shown in Figs S1–S6. As with the relative changes described in

the previous section, in general, the greatest absolute changes in AGB, NPP, LAI, LUE, and ET occurred at cooler sites, compared to warmer ones. One difference between the graphs of relative and absolute change was that the absolute change in growth and water



**FIGURE 5** Climate change effects on mean aboveground biomass (AGB) between years 1 and 25 for loblolly pine stands growing in sites with different site index and baseline mean annual temperature ( $T_{\text{mean}}$ ). Panel (a), (b), (c), and (d) show relative change against baseline (1975–2005) for different RCPs (4.5 and 8.5) and periods during the century (2025–2049 and 2075–2099)

use was more affected by site temperature than site SI whereas the relative change was sensitive to both. The greatest absolute change in growth and water use was in the RCP 8.5 end-century scenario. In that scenario, the change in AGB ranged from 20 to 40 Mg/ha at cooler sites to 0 to  $-10$  Mg/ha at warmer sites. Similarly, LAI increased by 0.6 to  $-0.4$   $\text{m}^2/\text{m}^2$ , LUE ranged from 0.2 to  $-0.1$  g/MJ, and ET ranged from  $+250$  to  $-50$  mm/year at the cooler and warmer portions of the range, respectively. The absolute change in WY was more sensitive to SI than to site temperature, and for the RCP 8.5 late-century scenario, it ranged from  $-150$  mm/year at low SI sites to 0 mm/year at high SI sites.

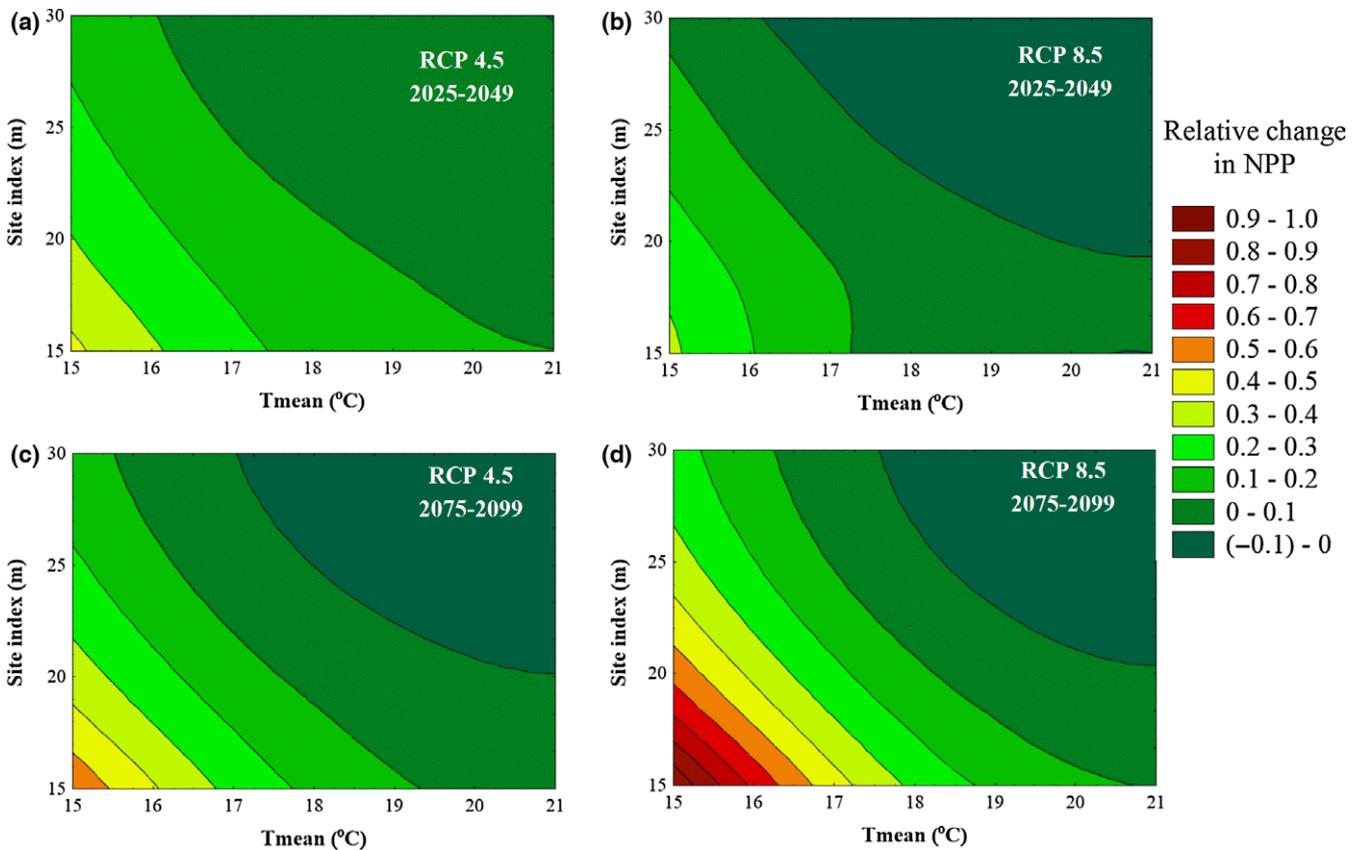
### 3.2 | Effect of $\text{CO}_2$ and climate on RCP 4.5 and 8.5 growth estimates

For both mid- and late-century simulations, there was a difference in response at cooler sites compared with warmer sites (Figure 11). For mid-century simulations, at sites with a baseline  $T_{\text{mean}} > 18^\circ\text{C}$ , the increase in aboveground biomass can be attributed solely to elevated  $[\text{CO}_2]$ . However, at sites  $< 18^\circ\text{C}$ , the increase in growth was due to a combination of changes in climate factors and the effect of increased atmospheric  $[\text{CO}_2]$ . The effect of climate was relatively greater than the effect of  $\text{CO}_2$  on growth at sites with a baseline

$T_{\text{mean}} < 16^\circ\text{C}$ . For the late-century simulations using RCP 4.5 projections, the effect of climate and  $\text{CO}_2$  on growth was very similar to the patterns seen from the mid-century simulations. However, using the late-century RCP 8.5 projections the model predicts that changes in climate factors alone (in the absence of elevated  $\text{CO}_2$ ) would reduce growth slightly (3%–5%) but when combined with elevated  $\text{CO}_2$ , growth will be higher than the current baseline at all sites. For RCP 8.5 projections, only for sites with a baseline  $T_{\text{mean}} < 16^\circ\text{C}$  are climate factors predicted to have a positive effect on growth. For those sites changes in climate alone are predicted to increase growth by 11% and when coupled with elevated  $\text{CO}_2$ , the mean growth response increases by 33%.

### 3.3 | Yearly growth and leaf area development on specific sites

In order to illustrate the effects of climate change scenarios on the dynamics of AGB and LAI, we selected two sites that represent cool (mean annual temperature of  $15.2^\circ\text{C}$ , Rhea County, TN) and warm (mean annual temperature of  $20.6^\circ\text{C}$ , Allen County, LA) conditions (Table S1) growing under contrasting site productivity conditions, represented as high (27 m) or low (18 m) SI. The baseline (1975–2005) and RCP 4.5 and 8.5 multimodel mean values were shown



**FIGURE 6** Climate change effects on mean net primary productivity (NPP) between years 1 and 25 for loblolly pine stands growing in sites with different site index and baseline mean annual temperature ( $T_{\text{mean}}$ ). Panel (a), (b), (c), and (d) show relative change against baseline (1975–2005) for different RCPs (4.5 and 8.5) and periods during the century (2025–2049 and 2075–2099)

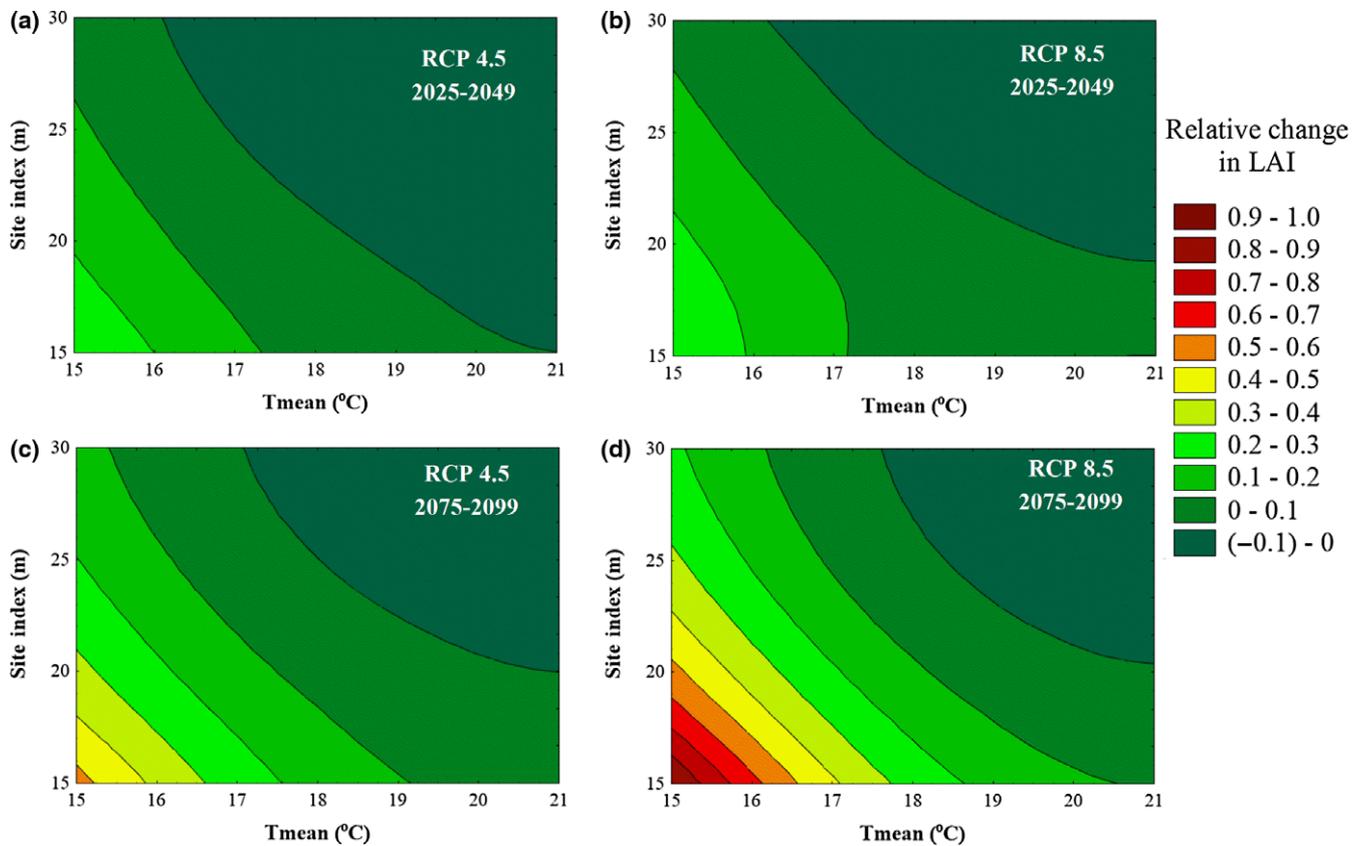
annually to illustrate how stand development was predicted to change (Figures 12–14). At the warmer site, for either SI, there was little effect of the RCP scenarios on AGB (Figure 12). The largest effects on growth were seen in the simulations for the cooler-low SI site, with a noticeable increase in AGB after about age 8. In addition, compared with the baseline AGB, there were higher growth trajectories for RCP 8.5 and 4.5 scenarios from ages 8 to 25 for this same site. For the cool site with a high SI, a similar separation was observed beginning in mid-rotation years (starting about age 10–18) but by the end of the rotation, there was little effect on AGB from either RCP scenario compared with the baseline.

Net primary productivity and LAI had similar patterns of development over time and peaked earlier at the high SI site compared to the low SI site (Figures 13 and 14). At high SI, after maximum LAI was achieved, LAI and NPP tended to be slightly lower than baseline at the 20.6°C site, and slightly higher than baseline at the 15.2°C site. As with AGB, the most noticeable differences in LAI and NPP were seen at the cool site with a low SI. In that situation, LAI and NPP both increased more rapidly in the RCP 8.5 scenario than the baseline, reaching a maximum at age 11 in the RCP 8.5, 2075–2099 scenario compared to age 15 for the baseline. That difference remained until the end of the rotation (age 25). The other RCP simulations were intermediate between baseline and the RCP 8.5,

2075–2099 scenario, and there was little difference detected among those scenarios and time periods.

## 4 | DISCUSSION

For the MACA baseline period, the model simulations show the highest stand productivity in the warm part of the species' range. This matches observations of stand growth across the region (Gonzalez-Benecke et al., 2016; Sabatia & Burkhardt, 2014). The model also predicts that the highest absolute productivity under the RCP 4.5 and 8.5 scenarios will still occur in the warm part of the range in both mid- and late-century time periods, but AGB and NPP on those sites will either remain constant or decrease by as much as 10% compared to the baseline period. Although on an absolute basis, growth was predicted to be substantially less at the cool sites compared to the warm ones, on a relative basis, the largest increase in growth was at the cool sites. This was evident in the RCP 4.5 and 8.5 simulations made in the 2025–2049 time period, but it was much more pronounced in the simulations for 2075–2099 time period. Across the range of sites and climate scenarios there was a greater relative growth increase when SI was low compared to when it was high. The large difference in growth between the cool and



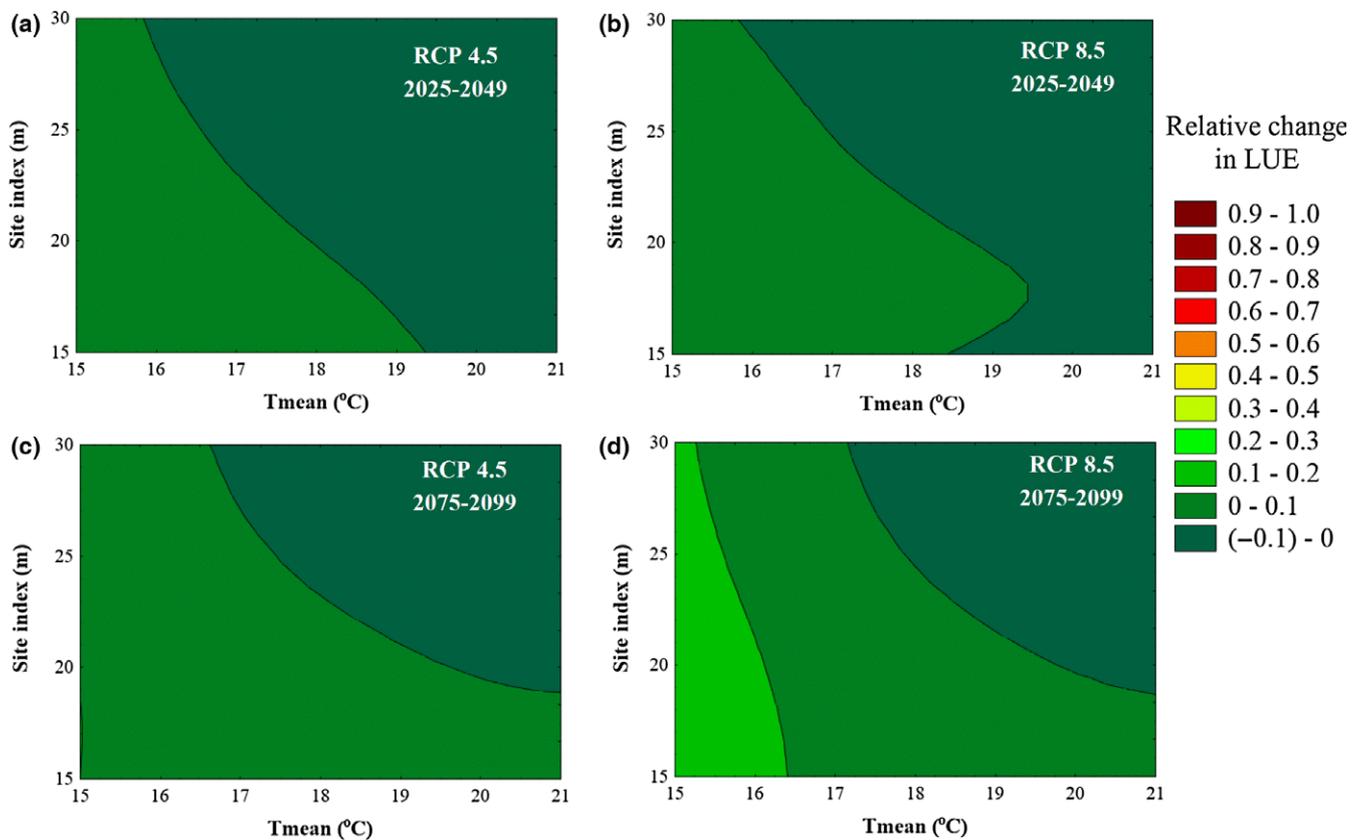
**FIGURE 7** Climate change effects on mean leaf area index (LAI) between years 1 and 25 for loblolly pine stands growing in sites with different site index and baseline mean annual temperature ( $T_{\text{mean}}$ ). Panel (a), (b), (c), and (d) show relative change against baseline (1975–2005) for different RCPs (4.5 and 8.5) and periods during the century (2025–2049 and 2075–2099)

warm sites, and low and high SI, in response to the projected changes in  $[\text{CO}_2]$ , temperature, and precipitation was consistent with our first and second hypotheses. At cool sites, across all levels of SI, relative AGB growth, NPP, and LAI increased. However, at warm sites, relative AGB growth, NPP, and LAI only increased if SI was low and stayed the same or decreased slightly if SI was high, which only partly supported our third hypothesis.

Cool sites (mean annual air temperatures  $<18^\circ\text{C}$ ) are located in a large geographic area covering more than one-half of the loblolly pine range (see Figure 1). These sites are in the northern part of the range, corresponding to the upper Coastal Plain and Piedmont physiographic regions. Approximately 61% of the total hectares of planted loblolly pine stands are in this portion of the species' range; 47% in the  $16\text{--}18^\circ\text{C}$  isotherm, 12% in the  $14\text{--}16^\circ\text{C}$  and 2% in the  $12\text{--}14^\circ\text{C}$ . Warm sites (mean annual air temperatures  $>18^\circ\text{C}$ ) correspond geographically to the lower Coastal Plain and represent approximately 39% of all hectares planted in loblolly pine in the region, with 33% in the  $18\text{--}20^\circ\text{C}$  isotherm and 6% in the  $14\text{--}16^\circ\text{C}$  isotherm (based on data from USDA Forest Service, Forest Inventory and Analysis Program, [www.fia.fs.us](http://www.fia.fs.us)).

All climate conditions were run at each site with five different SI to simulate different forest management intensity and site growth potential. This revealed that the stands that were growing slowly

had the greatest relative increases in growth from projected changes in climate and  $[\text{CO}_2]$ . This modeled response was consistent with a recent analysis of the measured growth response of 850 loblolly pine stands to a wide range of different silvicultural manipulations (Zhao et al., 2016). They found that low SI sites responded much more to management manipulations (such as a fertilizer application) than high SI sites. Their analysis indicated that a stand with a SI = 15 m had the potential to double its productivity under the most intensive management regime currently possible. However, that capacity to respond to management activities decreased linearly as the inherent SI increased; to the point that stands with an SI = 30 had only a very small positive, or negative, response to any added management activity. The close correspondence between the measured response of loblolly pine stands to changes in growing conditions due to silvicultural manipulations and the predictions of the 3-PG model to changes in growing conditions due to climate and  $[\text{CO}_2]$  strongly suggest that the model has revealed that an important aspect of how managed forests will respond to climate change, that is, that there will be regional and local variation in the response to climate change due to the growth potential of different sites. This suggests that there will be a predictable continuum of growth responses to climate change among forest stands with different growth potentials.

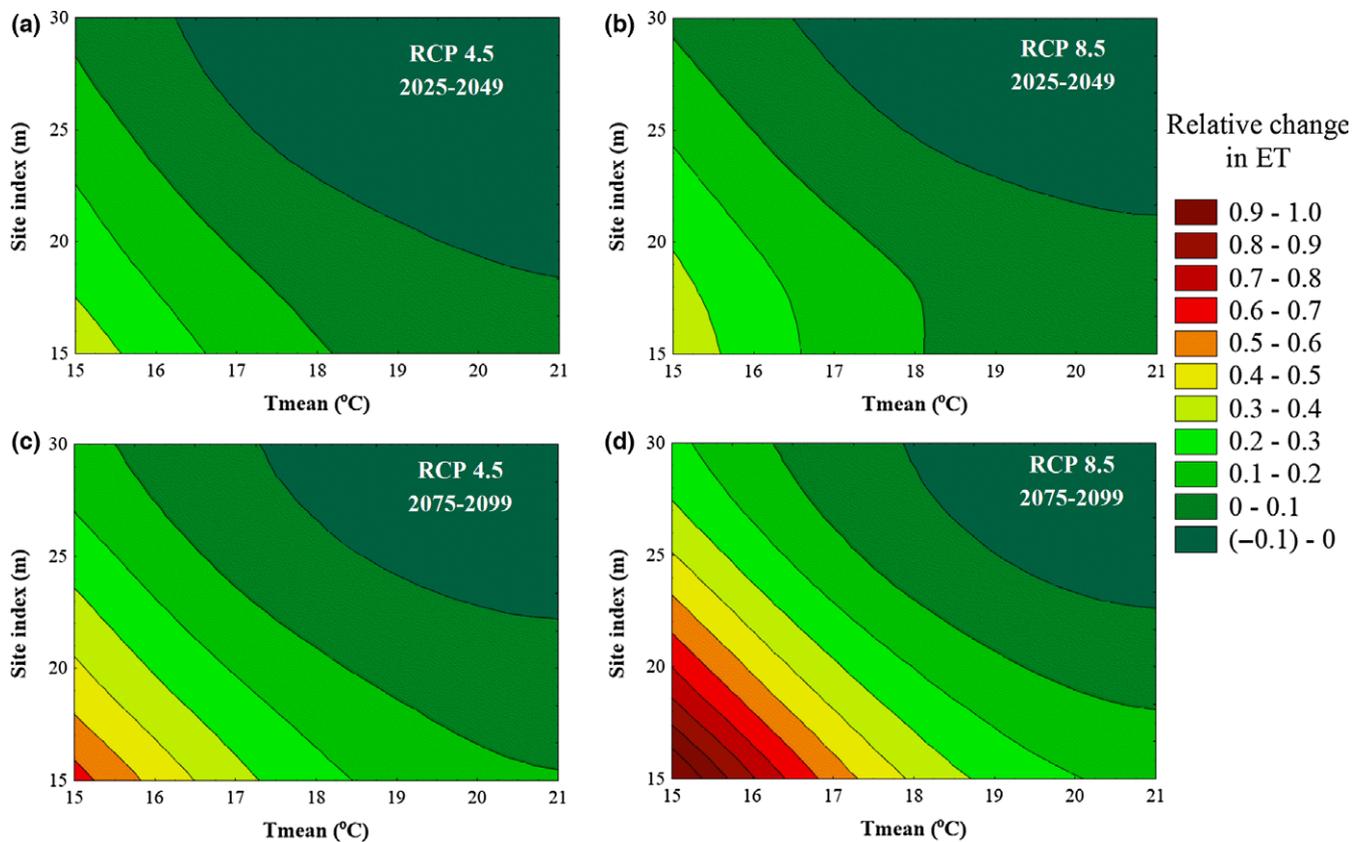


**FIGURE 8** Climate change effects on mean light use efficiency (LUE) between years 1 and 25 for loblolly pine stands growing in sites with different site index and baseline mean annual temperature ( $T_{\text{mean}}$ ). Panel (a), (b), (c), and (d) show relative change against baseline (1975–2005) for different RCPs (4.5 and 8.5) and periods during the century (2025–2049 and 2075–2099)

Changes in precipitation,  $[\text{CO}_2]$ , and air temperature projected for RCP 4.5 and 8.5 from the 20 downscaled climate models used in this study all contributed to the predicted growth response. The RCP 4.5 scenario represents a gradual reduction in greenhouse gas emissions beginning in the early part of the 21st century which would result in stabilization of radiative forcing and an atmospheric  $[\text{CO}_2]$  at about  $543 \mu\text{mol/mol}$  by the end of the century (Meinshausen et al., 2011). The RCP 8.5 scenario assumes that emissions will increase throughout the century resulting in atmospheric  $[\text{CO}_2]$  of over  $900 \mu\text{mol/mol}$  by the end of the century. The means of the projections of the downscaled climate models indicated that there would be an increase in air temperature of  $1\text{--}3^\circ\text{C}$ , depending on the site, in the RCP 4.5 and 8.5 scenarios for the 2025–2049 time period as well as in the RCP 4.5 scenario for the 2075–2099 time period. A mean  $4\text{--}5^\circ\text{C}$  increase in mean air temperature was projected for the RCP 8.5 scenario for the 2075–2099 time period. In contrast, the means of the projections of downscaled climate models produced only small changes in precipitation over the 21st century compared to the baseline period.

Both  $\text{CO}_2$  and climate caused an increase in growth at cool sites. In contrast, only elevated  $\text{CO}_2$  was responsible for increased growth at warm sites. For the 2025–2049 time period, there was almost no difference in growth under the RCP 4.5 and 8.5 scenarios because

air temperatures and  $[\text{CO}_2]$  were quite similar in the two scenarios during that time period. However, in the 2075–2099 time period, positive effects on growth were evident in the relative and absolute growth responses to RCP 4.5 and 8.5. The relatively larger increases in growth at cool sites in the RCP 8.5 scenario in the 2075–2099 time period were produced by a combination of a large increase in air temperature ( $4\text{--}5^\circ\text{C}$ ) and a large increase in  $[\text{CO}_2]$ . Those high temperatures were detrimental to growth at warmer sites, but partially counteracted by the increase in  $[\text{CO}_2]$ . The positive growth response of AGB, NPP, and LAI to such a large change in air temperature was consistent with empirical measurements of growth at sites with equal or lower mean annual temperatures (Gonzalez-Benecke et al., 2016). A similar pattern of response was observed in a study of loblolly pine seedlings grown in cool and warm locations under ambient and elevated  $\text{CO}_2$  and ambient and elevated air temperature (Wertin, McGuire, van Iersel, Ruter, & Teskey, 2012). In that study, the cool site had larger relative growth increases under elevated  $[\text{CO}_2]$  and temperature than the warm site. At the cool site, elevated air temperature increased the length of the growing season by a few weeks and created more favorable conditions for photosynthesis. The increase in atmospheric  $[\text{CO}_2]$  increased leaf-level carbon gain at both the cool and warm sites. The effect of  $[\text{CO}_2]$  compensated for the detrimental effect of higher air temperatures on net



**FIGURE 9** Climate change effects on mean stand evapotranspiration (ET) between years 1 and 25 for loblolly pine stands growing in sites with different site index and baseline mean annual temperature ( $T_{\text{mean}}$ ). Panel (a), (b), (c), and (d) show relative change against baseline (1975–2005) for different RCPs (4.5 and 8.5) and periods during the century (2025–2049 and 2075–2099)

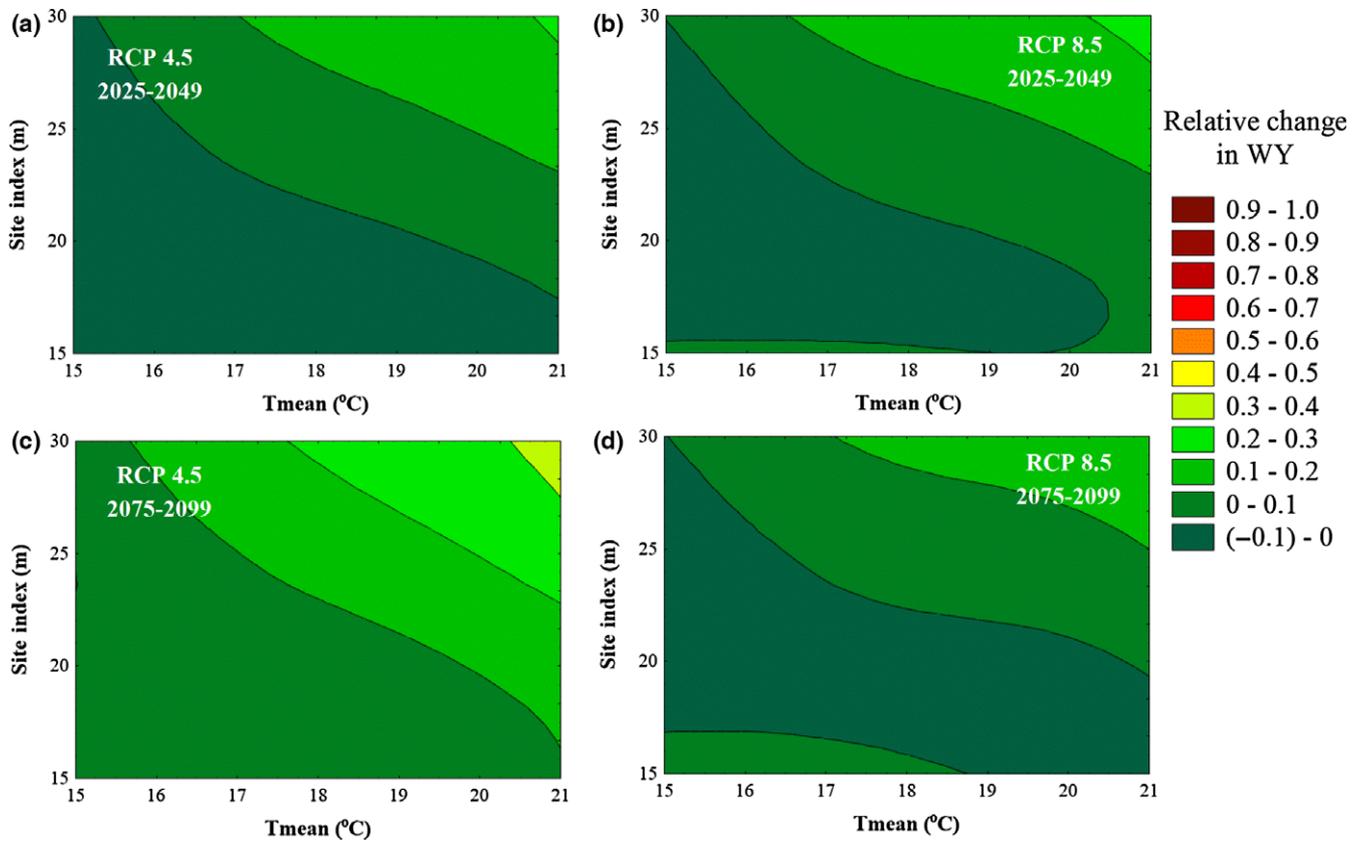
photosynthesis at the warm site. While there are many differences between a one-year study of seedlings and the simulation of the growth of stands over a 25-year period, the growth patterns observed in the Wertin et al. (2012) study and those predicted using the 3-PG model were consistent, suggesting that the leaf-level physiological responses of loblolly pine to climate change are similar in trees and seedlings.

The response to elevated  $[\text{CO}_2]$  used in the model was based on the results from the free air  $\text{CO}_2$  enrichment (FACE) study conducted in a loblolly pine plantation in North Carolina (Oren et al., 2001). The  $\text{CO}_2$  function (Almeida et al., 2009), which we parameterized for loblolly pine, was able to adequately replicate the growth response to elevated  $[\text{CO}_2]$  observed in the FACE study. However, the FACE study had a target  $[\text{CO}_2]$  of  $550 \mu\text{mol/mol}$ , so our predictions of the effect of  $[\text{CO}_2]$  on growth at  $[\text{CO}_2] > 550 \mu\text{mol/mol}$  have a high degree of uncertainty. This pertains particularly to the RCP 8.5 scenario in the 2075–2099 time period, which used a mean  $[\text{CO}_2]$  of  $815 \mu\text{mol/mol}$ . The RCP 4.5 scenarios used  $[\text{CO}_2]$  of 454 and  $481 \mu\text{mol/mol}$  for the mid- and late-century simulations and the mid-century RCP 8.5 scenario used  $533 \mu\text{mol/mol}$ ; all of which were within the estimation range provided by the loblolly pine FACE study.

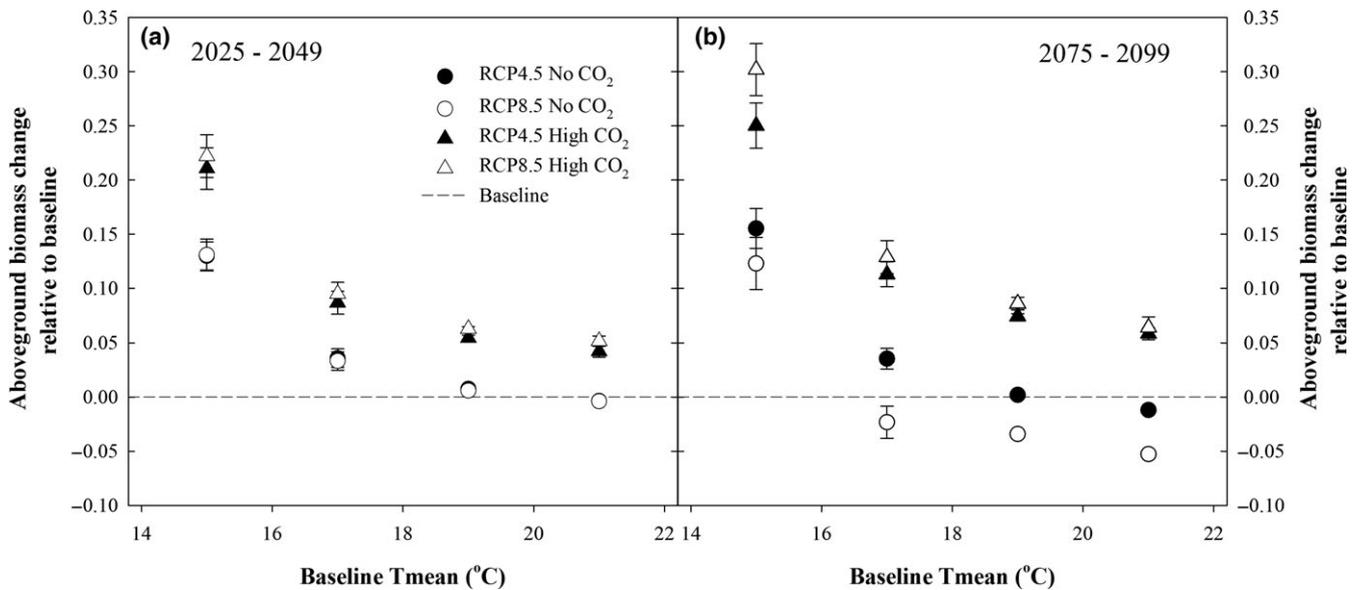
Evapotranspiration followed the same patterns as seen in growth and LAI in the two time periods and for the two RCP scenarios.

While mean annual ET at warm sites was not affected very much by the changes in air temperature or atmospheric  $[\text{CO}_2]$ , the relative changes in ET were greater at cool sites, and substantially greater in the late-century simulations, especially for RCP 8.5, in which 60%–100% increases in ET were predicted for some sites. That corresponded to an absolute increase in ET between 200 and 250 mm/year at the coolest sites and resulted in a decrease in WY of up to 20% (corresponding to a reduction of 100–150 mm/year in absolute mean WY) in both mid-century and late-century time periods. While the increase in ET was not enough to produce significant water stress at cool or warm sites because of the quantity of rainfall these sites were predicted to receive was sufficient to meet ET demand, it indicates that there could be less ground water storage and runoff for streams in the future.

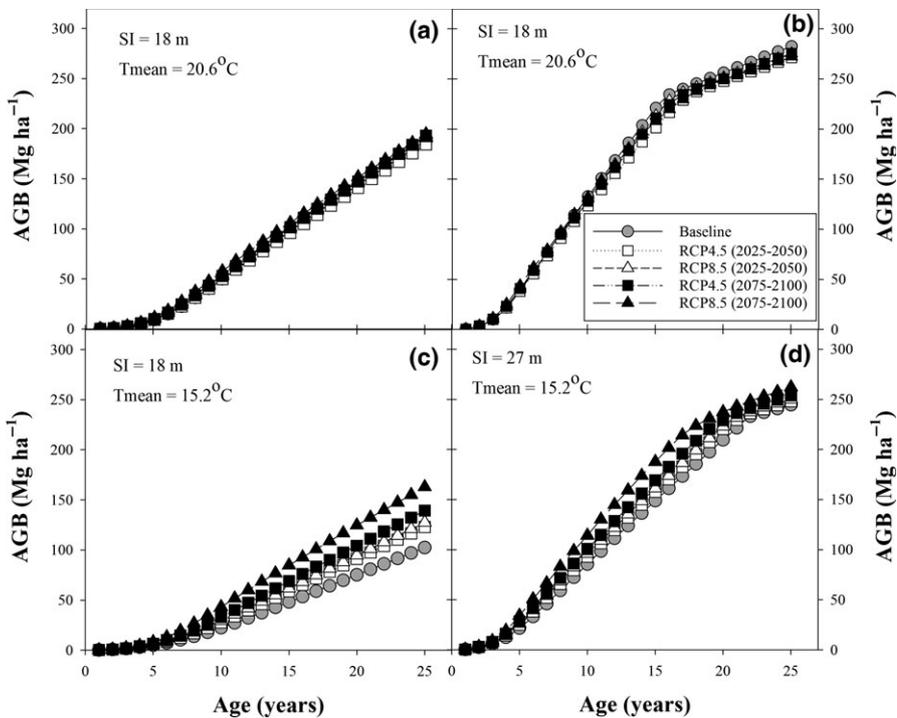
The increase in growth predicted by the model under future climate scenarios was consistent with many studies on the effect of elevated temperature on trees. Way and Oren (2010) found that almost all studies of elevated temperature reported a positive effect of higher temperature on growth for both deciduous and coniferous tree species. While the magnitude of the response differed among species and functional groups, there was almost always an increase in growth in elevated air temperature treatments, as long as adequate water was available for growth.



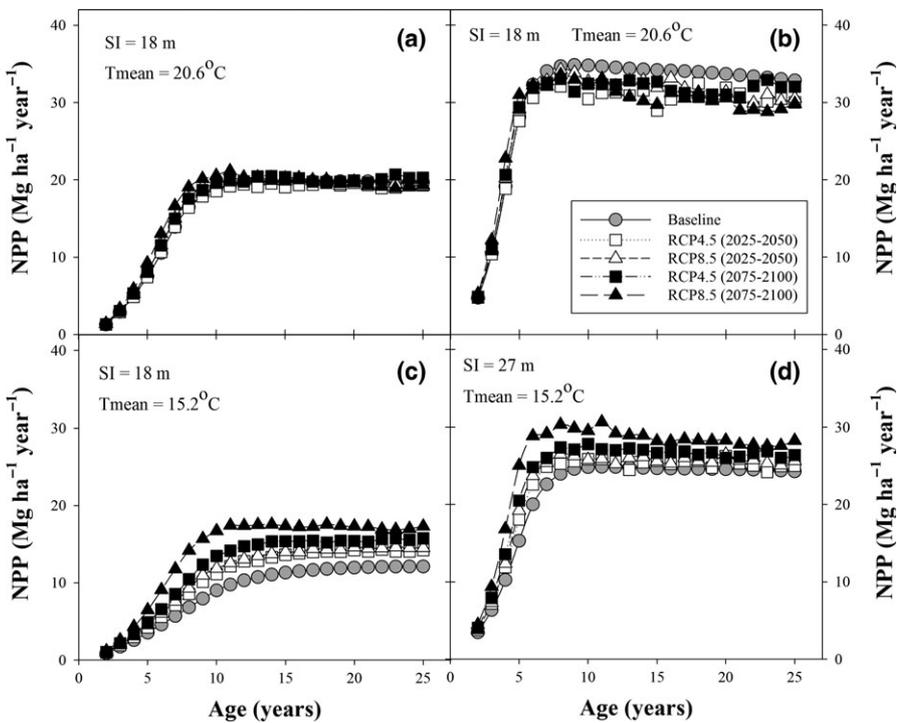
**FIGURE 10** Climate change effects on mean stand water yield (WY) between years 1 and 25 for loblolly pine stands growing in sites with different site index and baseline mean annual temperature ( $T_{mean}$ ). Panel (a), (b), (c) and (d) show relative change against baseline (1975–2005) for different RCPs (4.5 and 8.5) and periods during the century (2025–2049 and 2075–2099)



**FIGURE 11** Separate effects of elevated  $[CO_2]$  and climate on aboveground biomass at age 25 years for loblolly pine stands. Panel (a) and (b) show the relative change against baseline (1975–2005) for different RCPs (4.5 and 8.5) under elevated  $[CO_2]$  (triangles) and baseline  $[CO_2]$  (circles) for different periods during the century (2025–2049, a; 2075–2099, b)



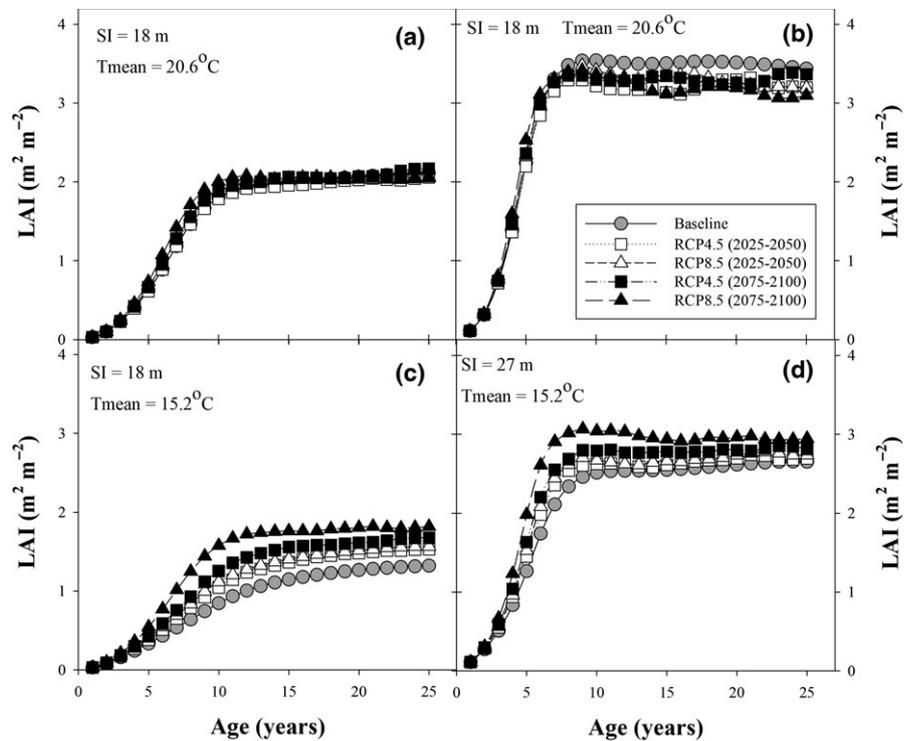
**FIGURE 12** Case study. Time series of aboveground biomass (AGB,  $\text{Mg ha}^{-1}$ ) of two selected sites growing under different climate scenarios (RCP4.5 and RCP8.5) in two future periods during the century (2025–2049 and 2075–2099). Baseline represents years between 1975 and 2005. The two sites selected represent cold (Baseline  $T_{\text{mean}} = 15.2^\circ\text{C}$ , Rhea County, TN) and warm (Baseline  $T_{\text{mean}} = 20.6^\circ\text{C}$ , Allen County, LA) locations



**FIGURE 13** Case study. Time series of net primary productivity (NPP,  $\text{Mg ha}^{-1} \text{ year}^{-1}$ ) of two selected sites growing under different climate scenarios (RCP4.5 and RCP8.5) in two future periods during the century (2025–2049 and 2075–2099). Baseline represents years between 1975 and 2005. The two sites selected represent cold (Baseline  $T_{\text{mean}} = 15.2^\circ\text{C}$ , Rhea County, TN) and warm (Baseline  $T_{\text{mean}} = 20.6^\circ\text{C}$ , Allen County, LA) locations

The 3-PG model uses mean monthly air temperature as an input, so it does not account for the possible effects of heat waves on physiological processes and growth. However, a study of the combined effects of repeated heat waves under ambient and elevated  $[\text{CO}_2]$  and high and low water availability has been conducted using loblolly pine and northern red oak (*Quercus rubra*) seedlings (Amey et al., 2012; Bauweraerts et al., 2013). The heat wave treatments of

+6°C and +12°C were repeated every 2 or 4 weeks, respectively, to provide the same monthly mean temperature and heating degree days as a constant +3°C treatment that was also included in the experiment. The results demonstrated that both species had a high resistance to thermal stress. Growth and leaf net photosynthesis in the biweekly +6°C heat wave treatment did not differ significantly from that of the constant +3°C treatment. The +12°C treatment did



**FIGURE 14** Case study. Time series of mean annual projected leaf area index (LAI, per  $\text{m}^2/\text{m}^2$ ) of two selected sites growing under different climate scenarios (RCP4.5 and RCP8.5) in two future periods during the century (2025–2049 and 2075–2099). Baseline represents years between 1975 and 2005. The two sites selected represent cold (Baseline  $T_{\text{mean}} = 15.2^\circ\text{C}$ , Rhea County, TN) and warm (Baseline  $T_{\text{mean}} = 20.6^\circ\text{C}$ , Allen County, LA) locations

reduce net photosynthesis under ambient  $[\text{CO}_2]$ , but that reduction was completely compensated for increased photosynthesis in elevated  $[\text{CO}_2]$ . The response of loblolly pine seedlings was consistent with a number of other tree species that also exhibited remarkable tolerance to high temperatures (Teskey et al., 2015). However, the timing of heat stress can affect its severity. For example, heat stress during leaf development had an effect on sugar maple (*Acer saccharum*) tree growth but not on other co-occurring tree species that had slightly different times of bud-burst (Filewood & Thomas, 2014), and heat stress has more effect during periods of water deficits (Bauwerdaerts et al., 2013), so it is possible that if extreme heat events ( $\geq +10^\circ\text{C}$  over the mean), which are rare now, become more common or have longer duration, then the effects of heat waves may be important to incorporate into process modeling of tree growth. However, the long-term effects of heat waves on tree growth are currently unknown (Teskey et al., 2015).

Measurements taken at the stand level on different tree species in other regions have already detected a positive effect of warming and elevated atmospheric  $[\text{CO}_2]$  on forest productivity (Bosela et al., 2016; Charru et al., 2014; Schaphoff et al., 2016), but in areas where droughts have increased, forest productivity has decreased, despite increased temperature and atmospheric  $[\text{CO}_2]$  (Bonal, Burban, Stahl, Wagner, & Hérault, 2016; Sun et al., 2015).

An assessment of climate change effects on growth for the loblolly pine region was conducted by Huang, Abt, Kindermann, and Ghosh (2011) using four Hadley III climate change scenarios from the IPCC's Fourth Assessment Report (IPCC 2007) and two stand-level biometric growth models that incorporated maximum and minimum temperature and precipitation. Huang et al. (2011) predicted

more growth in cooler parts of the region (upper Coastal Plain and Piedmont regions) and less in the warmer lower Coastal Plain, which was in good agreement with our results using many more climate projections and a different modeling approach. The two studies vary somewhat in the magnitude of the growth response but the trends and pattern of responses were very similar.

Our analysis indicated that 80% of the area of the planted loblolly stands is located in the thermal band between 16 and  $20^\circ\text{C}$  mean annual temperature, with 47% of the hectares of planted pine located between 16– $18^\circ\text{C}$  and 33% located between 18– $20^\circ\text{C}$ . Our simulations of future productivity indicated that increases in productivity should be expected for a large majority of those stands, with the exception of high SI conditions in the 18– $20^\circ\text{C}$  isotherm, which will see little change from the current high levels of productivity these stands already achieve. Stands in the 16– $18^\circ\text{C}$  isotherm are predicted to increase in growth by as much as 20% over current levels of productivity in mid-century and by substantially more at the end of the century. Across both isotherms, lower SI conditions were consistently predicted to have increased productivity over current levels under the projected future climates used in our simulations.

The 3-PG model predicted an increase in growth and water use in the cooler part of the loblolly pine region and either no change or a slight decrease in growth and water use in the warmer part of the range under both RCP 4.5 and 8.5 scenarios for stands growing at mid-century or at the end of the century. As 47% of the planted loblolly pine stands are located in a band of mean annual temperature between 16 and  $18^\circ\text{C}$ , this means that an increase in productivity can be expected for many planted loblolly pine stands during this century.

However, there are several caveats regarding that prediction that should be considered. We used the mean of the growth predictions made using climate projections from 20 downscaled GCMs, and assumed that the GCMs had equal accuracy. However, the 20 downscaled climate models produced a wide range of air temperature and precipitation projections. If GCMs that projected higher, or lower, values than the mean of the 20 downscaled models were actually more accurate than the mean, the growth predictions from the 3-PG model will be inaccurate. We did not investigate the differences in predicted growth caused by variation in the projected climate among the 20 models because we chose to focus on the variation in growth caused by inherent or manipulated site growth potential. However, modeled climate variation is also important to consider in future studies. Also, while the response to CO<sub>2</sub> was verified using a long-term FACE study, which is arguably the best information currently available on the response of loblolly pine to elevated CO<sub>2</sub>, that information does not extend to [CO<sub>2</sub>] beyond 550 μmol/mol. Therefore, model accuracy for the RCP 8.5 simulations for the 2075–2099 time period has a high degree of uncertainty. The FACE study did not include an elevated temperature treatment, so a possible interaction between temperature and CO<sub>2</sub> cannot be ruled out. Finally, the 3-PG model assumes that the stands received silvicultural management including controlled planting density, uniform spacing, and weed control and that growth was not affected by insects and diseases. While these are reasonable assumptions for lands actively managed for timber production, it also means that the results of the simulations reported here pertain only to managed stands of loblolly pine and should not be extended to unmanaged stands, or forests of deciduous species or a mixture of deciduous and evergreen species in this region or elsewhere.

## ACKNOWLEDGEMENTS

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## REFERENCES

- Abatzoglou, J. T., & Brown, T. J. (2012). A comparison of statistical downscaling methods suited for wildfire applications. *International Journal of Climatology*, *32*, 772–780.
- Almeida AC, Sands PJ, Bruce J, Siggins AW, Leriche A, Battaglia M, Batista TR (2009) Use of a spatial process-based model to quantify forest plantation productivity and water use efficiency under climate change scenarios. In: *Interfacing modelling and simulation with mathematical and computational sciences* (eds Anderssen R. S., Braddock R. D., Newham L. T. H.), Cairns, MODSIM Congress.
- Ameje, M., Wertin, T. M., Bauweraerts, I., McGuire, M. A., Teskey, R. O., & Steppe, K. (2012). The effect of induced heat waves on *Pinus taeda* and *Quercus rubra* seedlings in ambient and elevated CO<sub>2</sub> atmospheres. *New Phytologist*, *196*, 448–461.
- Bauweraerts, I., Wertin, T. M., Ameje, M., McGuire, M. A., Teskey, R. O., & Steppe, K. (2013). The effects of heat waves, elevated [CO<sub>2</sub>] and low soil water availability on northern red oak (*Quercus rubra* L.) seedlings. *Global Change Biology*, *19*, 517–528.
- Bonal, D., Burban, B., Stahl, C., Wagner, F., & Hérault, B. (2016). The response of tropical rainforests to drought-lessons from recent research and future prospects. *Annals of Forest Science*, *73*, 27–44.
- Bosela, M., Štefančík, I., Patrás, R., & Vacek, S. (2016). The effects of climate warming on the growth of European beech forests depend critically on thinning strategy and site productivity. *Agricultural and Forest Meteorology*, *222*, 21–31.
- Charru, M., Seynave, I., Hervé, J. C., & Bontemps, J. D. (2014). Spatial patterns of historical growth changes in Norway spruce across western European mountains and the key effect of climate warming. *Trees*, *28*, 205–221.
- Filewood, B., & Thomas, S. C. (2014). Impacts of a spring heat wave on canopy processes in a northern hardwood forest. *Global Change Biology*, *20*, 360–371.
- Gonzalez-Benecke C. A., Teskey R. O., Martin T. A., Jokela E. J., Fox T. R., Kane M. B., & Noormets A. (2016). Regional validation and improved parameterization of the 3-PG model for *Pinus taeda* stands. *Forest Ecology and Management*, *361*, 237–256.
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*, 1965–1978.
- Huang, J., Abt, B., Kindermann, G., & Ghosh, S. (2011). Empirical analysis of climate change impact on loblolly pine plantations in the Southern United States. *Natural Resource Modeling*, *24*, 445–476.
- IPCC (2007). *Climate change 2007: Synthesis report. Contribution of working groups I, II and III to the fourth assessment report of the intergovernmental panel on climate change*. Core Writing Team, RK Pachauri, A Reisinger (Eds.). (p. 104). Geneva Switzerland: IPCC.
- Landsberg, J., & Sands, P. (2011). *Physiological ecology of forest production: Principles, processes and models*. New York: Academic Press.
- Landsberg, J., & Waring, R. (1997). A generalized model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *Forest Ecology and Management*, *95*, 209–228.
- Lieth, H. (1973). Primary production – terrestrial ecosystems. *Human Ecology*, *1*, 303–332.
- Meinshausen, M., Smith, S. J., Calvin, K., Daniel, J. S., Kainuma, M. L. T., Lamarque, J-F., ... van Vuuren, D. P. P. (2011). The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. *Climatic Change*, *109*, 213–241.
- Mekonnen, Z., Grant, R. F., & Schwalm, C. (2016). Contrasting changes in gross primary productivity of different regions in North America as affected by warming in recent decades. *Agricultural and Forest Meteorology*, *218–219*, 50–64.
- Oren R., Ellsworth D. S., Johnsen K. H., Phillips N., Ewers B. E., Maier C., ... van Katul, G. G. (2001). Soil fertility limits carbon sequestration by forest ecosystems in a CO<sub>2</sub>-enriched atmosphere. *Nature*, *411*, 469–472.
- Peters, E. B., Wythers, K. R., Shang, S., Bradford, J. B., & Reich, P. B. (2013). Potential climate change impacts on temperate forest ecosystem processes. *Canadian Journal of Forest Research*, *43*, 939–950.
- Reyer, C., Lasch-Born, P., Suckow, F., Gutsch, M., Murawski, A., & Pilz, T. (2014). Projections of regional changes in forest net primary productivity for different tree species in Europe driven by climate change and carbon dioxide. *Annals of Forest Science*, *71*, 211–225.
- Robertson, G., Gaulke, P., McWilliams, R., LaPlante, S., & Guldin, R. (2011). *National Report on Sustainable Forests –2010*. United States Department of Agriculture Forest Service Report FS-979. US Government Printing Office, Washington DC. 214 pp.

- Sabatia, C. O., & Burkhart, H. E. (2014). Predicting site index of plantation loblolly pine from biophysical variables. *Forest Ecology and Management*, 326, 142–156.
- Schaphoff, S., Reyer, C. P. O., Schepaschenko, D., Gerten, D., & Shvidenko, A. (2016). Tamm Review: Observed and projected climate change impacts on Russia's forests and its carbon balance. *Forest Ecology and Management*, 361, 432–444.
- Sun, S., Sun, G., Caldwell, P., McNulty, S. G., Cohen, E., Xiao, J., & Zhang, Y. (2015). Drought impacts on ecosystem functions of the U.S. National Forests and grasslands: Part I evaluation of a water and carbon balance model. *Forest Ecology and Management*, 353, 260–268.
- Teskey, R. O., Wertin, T., Bauweraerts, I., Ameye, M., McGuire, M. A., & Steppe, K. (2015). Responses of tree species to heat waves and extreme events. *Plant, Cell and Environment*, 38, 699–1712.
- van Vuuren, D. P., Edmonds, J., Kainuma, M., et al. (2011). The representative concentration pathways: An overview. *Climate Change*, 109, 5–31.
- Way, D. A., & 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 Physiology*, 30, 669–688.
- Wertin, T. A., McGuire, M. A., van Iersel, M., Ruter, J., & Teskey, R. O. (2012). Effects of elevated temperature and [CO<sub>2</sub>] on photosynthesis, leaf respiration, and biomass accumulation of *Pinus taeda* seedlings at cool and warm sites within the species current range. *Canadian Journal of Forest Research*, 42, 943–957.
- Zhao, D., Kane, M., Teskey, R., Fox, T. R., Albaugh, T. J., Allen, H. L., & Rubilar, R. (2016). Maximum response of loblolly pine plantations to silvicultural management in the southern United States. *Forest Ecology and Management*, 375, 105–111.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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