

Climate change impacts on forest growth and tree mortality: a data-driven modeling study in the mixed-conifer forest of the Sierra Nevada, California

John J. Battles · Timothy Robards · Adrian Das ·
Kristen Waring · J. Keith Gilles · Gregory Biging ·
Frieder Schurr

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Abstract We evaluated the impacts of climate change on the productivity and health of a forest in the mixed-conifer region in California. We adapted an industry-standard planning tool to forecast 30-years of growth for forest stands under a changing climate. Four projections of future climate (two global climate models and two emission forecasts) were examined for forests under three management regimes. Forest structural and tree demographic data from the Blodgett Forest Research Station in El Dorado County were used to fit our projections to realistic management regimes. Conifer tree growth declined under all climate scenarios and management regimes. The most extreme changes in climate decreased productivity, as measured by stem volume increment, in mature stands by 19% by 2100. More severe reductions in yield (25%) were observed for pine plantations. The reductions in growth under each scenario also resulted in moderate increases in susceptibility to non-catastrophic (i.e., non fire) causes of mortality in white fir (*Abies concolor*). For the worst case, median survival probability decreased from the baseline rate of 0.997 year⁻¹ in 2002 to 0.982 year⁻¹ by the end of the century.

1 Introduction

Predictions indicate that climate change will have profound effects on the distribution, function, and productivity of California's forests (Lenihan et al. 2003; Hayhoe et al. 2004). Dynamic vegetation models using several different scenarios of potential future climates

J. J. Battles · T. Robards · A. Das · J. K. Gilles · G. Biging
Department of Environmental Science, Policy, and Management, UC Berkeley, Berkeley, CA, USA

J. J. Battles · K. Waring · F. Schurr
Center for Forestry, UC Berkeley, Berkeley, CA, USA

T. Robards
California Department of Forestry and Fire Protection, Sacramento, CA, USA

J. J. Battles (✉)
UC Berkeley, 137 Mulford Hall #3114, Berkeley, CA 94720-3114, USA
e-mail: jbbattles@nature.berkeley.edu

have consistently predicted a shift in dominance from needle-leaved to broad-leaved lifeforms and an increase in vegetation productivity (Lenihan et al. 2003, 2006). Despite the increasing spatial resolution of climate predictions and the improving realism of ecosystem models, the potential impact of climate change on managed forests in California has not been evaluated. Yet clearly forest management strategies can influence responses to a changing climate (Linder 2000; Lasch et al. 2002; Briceño-Elizondo et al. 2006). Moreover the analyses need to be conducted at a spatial scale that provides relevant planning information to the land manager (*sensu* Johnsen et al. 2001). Thus in this paper we evaluated the potential impact of climate change on a managed forest in California with an explicit focus on generating information relevant and credible to forest managers. To do so, we developed a case study for a mixed-conifer forest in the northern Sierra Nevada. This specificity allowed us to use data-driven modeling tools to project the effect of a changing climate on forest growth and tree mortality.

1.1 Background and approach

Forestlands are a dominant vegetation type within California, covering 45% of the state. Commercial forests (defined as forests growing at least 1.4 m³ of stem volume per hectare per year) represent 16% of the state (Standiford 2003). Ownership of commercial forest is nearly evenly split between public and private ownership (FRAP 2003).

Over 80% of the timberland in the state is found in three northern California resource areas. The North Interior (Klamath Mountains, northern Sierra Nevada Mountains, and Modoc Plateau) contains the largest holdings of growing stock with over 490 million m³ of wood (31% of the State total); the Sacramento resource area (Sierra Nevada Mountain counties from El Dorado to Plumas and other western Sacramento Valley counties) contains 391 million m³ (25% of the State total); and the North Coast resource area (northern California coast counties from Sonoma to Del Norte) contains 385 million m³ (25% of the State total). Results from FRAP (2003).

Most of the timber harvesting in the Sacramento resource area is for five conifer species (FRAP 2003). In El Dorado County, the 2004 conifer timber harvested was valued at \$23.3 million. This amounted to 5.9% of the state's total conifer harvests and nearly 12% of the state's conifer harvests from public forests.

For this paper, we took a case study approach. We performed an in-depth investigation of the impact of projected climate change for a specific forest at a specific location. We chose the productive mixed-conifer timberlands at Blodgett Forest Research Station in El Dorado County. At Blodgett we have access to long-term inventory data that is necessary to implement and check our modeling extrapolations. We also have examples of different forest management regimes that represent common practices used by commercial timber operations, small non-industrial landowners, and the US Forest Service (e.g., plantations, single tree selection, and minimal intervention since turn of the century harvesting). In addition, the soils are known to be productive, thus meeting an assumption in simulation models that plant growth is not limited by nutrient availability (e.g., Lenihan et al. 2003).

While we acknowledge the limited inferential power of a case study, this approach complements the state-wide projections of changes in forest resources (Lenihan et al. 2006). We have explicitly chosen a site that: (1) is in one of the two major timber producing regions of the State; (2) is a location with mixed ownership and mixed use; (3) is in the center of the mixed-conifer vegetation range and thus unlikely to be directly affected by species shifts in the next century; (4) is in a region where basic research has been conducted to quantify the impact of climate on forested ecosystems. By focusing on a site, we were

able to address two crucial aspects of a changing climate: effects on forest growth and impacts on non-catastrophic tree mortality.

2 Methods

2.1 Study site

Blodgett Forest Research Station is located on the western slope of the Sierra Nevada mountain range in California (38°52'N; 120°40'W). Olson and Helms (1996) provide a detailed description of Blodgett Forest, its management, and trends in forest growth and yield. Briefly, the central property of the research station consists of 1,214 ha of mixed-conifer forest divided into 109 management compartments (size range, 3–500 ha). The mixed-conifer forest type is composed of variable proportions of five coniferous and two hardwood tree species. Constituent canopy tree species include *Abies concolor* (white fir), *Pseudotsuga menziesii* var. *menziesii* (Douglas-fir), *Pinus lambertiana* (sugar pine), *Pinus ponderosa* (Pacific ponderosa pine), *Calocedrus decurrens* (incense-cedar), *Quercus kelloggii* (California black oak), and *Lithocarpus densiflorus* (tanoak). All seven tree species are common at the study site. The terrain in Blodgett is flat or gently sloping and elevation varies between 1,220 and 1,310 m. The climate is characterized by cool, wet winters and warm, dry summers. Mean annual precipitation is 160 cm; 78% falls between November and March. Typically, 25% of the precipitation falls as snow. The mineral soil is a well-drained, sandy loam that supports a productive site in terms of stem volume growth. Between 1900 and 1913, most of Blodgett Forest was logged and then burned to reduce logging slash. The University of California, Berkeley has operated Blodgett Forest as research and teaching facility since 1933.

2.2 Downscaled climate change scenarios

Consistent climate realizations were used by all researchers contributing to this series of papers. For selection criteria see Cayan et al. (2006). The global climate models used here were the GFDL model (version CM2.1, NOAA Geophysical Dynamics Laboratory, Princeton, NJ, USA; Anderson et al. 2004) and the PCM model. (Meehl and Washington group at NCAR in Boulder, CO, USA; Meehl et al. 2004). Impacts were analyzed for two greenhouse gas emissions scenarios: A2 (relatively high emissions) and B1 (low emissions). For the A2 scenario, CO₂ emissions continue to climb throughout the century, reaching almost 30 Gt year⁻¹ (gigatonnes per year). By the end of the century, the CO₂ concentration more than triples its pre-industrial level. For the B1 scenario, CO₂ emissions peak just below 10 Gt year⁻¹ in mid-century before dropping below current-day levels by 2100. This change corresponds to a doubling of CO₂ concentration relative to its pre-industrial level by the end of the century (Cayan et al. 2006). Results from these models were applied to one-eighth degree grid cells in California using a bias-corrected, statistically robust approach to downscaling (Cayan et al. 2006).

2.3 Growth modeling

We used CACTOS Version 5.8 (the California Conifer Timber Output Simulator, Wensel et al. 1986) as the base model for projecting future growth. Initially CACTOS was built without reference to climate. It was designed to provide short-term projections of tree

growth using tree and site characteristics. The fundamental assumption underlying CACTOS is that variability in tree growth can be adequately described by capturing a tree's biological mechanism and stand dynamics.

CACTOS has become the industry-standard for interior California. For example, it is used to project growth and yield in state timber harvesting permits (i.e., sustained yield plans and non-industrial timber management plans) submitted by licensed foresters and approved by state regulators. It is available online at <http://www.cnr.berkeley.edu/~wensel/cactos/cactoss.htm>.

Wensel and Turnblom (1998) noted that observed growth of stands used to develop CACTOS in 1978–1983 was consistently less than the growth predicted by CACTOS for the period between 1988–1991. Differences in climate between the period of model building (1978–1983) and model validation (1988–1991) was the suspected cause. This observation spurred a basic research effort focused on incorporating relevant climate parameters into growth and yield models (Wensel and Turnblom 1998; Yeh 1997; Yeh et al. 2000; Yeh and Wensel 2000).

Yeh and Wensel (2000) found that for the mixed-conifer forest of northern California (a region that includes Blodgett Forest) conifer tree growth declines with decreases in winter precipitation (October to February) and increases in summer temperature (June through September). Their model, which considers the effects of both current and previous year winter rain and summer temperature on tree growth, explained 67% of the observed growth variation for the two pine species (sugar pine and ponderosa pine) and 74% of the variation for the other three conifer species (white fir, Douglas-fir, and incense-cedar). Of the four climate parameters included in the model, tree growth for both species groups was most sensitive to the current summer temperature. While Yeh and Wensel (2000) provide the necessary parameters and equations, the climate module was never incorporated into CACTOS.

For this analysis, we ran CACTOS with the climate adjustments (CACTOS_{clim}) to better project growth under a changed climate. Note that while both pieces of this modeling tool have been peer-reviewed, the combined model has not. Therefore we spent considerable effort checking model output for systematic failures and ecologically unrealistic responses. For example, residual analyses of predicted versus observed growth in the reserve stands (see Section 2.4) under the most extreme climate were unbiased with respect to tree size. Error distributions were normal and the shifts in growth were scalar across the range of observed tree sizes. We also were careful not to apply the model to conditions far beyond the range of values used in model development. For example, the downscaled climate projections of winter precipitation and summer temperature were within the range of values included in Yeh and Wensel's (2000) analysis. They built the growth-climate relationships from climate data from more than 30 stations in northern California. The latitudinal and elevational variation of these stations was such that their fitting dataset contained the most extreme downscaled projections of climate for a site in El Dorado County at 1,219 m elevation (Yeh 1997). Thus for the results included in this report, we are confident in the direction of the trends and the relative magnitude of the changes. However as we note below, absolute results are very dependent on the details of the implementation and the specificity of the model.

We explored three management strategies that span the range of forest conditions and silvicultural regimes employed in the timberlands of the region. We projected 30 years of growth under a changed climate for mature, second growth, mixed-conifer stands that have not been managed since they were initially logged (usually clear-cut) at the turn of the century. The only current management in these stands is suppression of wildfire. This forest

structure (referred to at Blodgett as ‘reserve stands’) has elements of late seral/old growth forests and represents approximately 13% of the mixed-conifer forest in public lands in the northern Sierra Nevada (Franklin and Fites-Kaufman 1996). We also modeled 30 years of growth for 20-year old ponderosa pine plantations. Small plantations (~8 ha) of ponderosa pine on an approximate 50-year rotation are a common management regime for large industrial operations in El Dorado County. Finally, we simulated growth for single tree selection treatments. Single tree selection is a low-intensity alternative where individual trees are removed relatively uniformly throughout the stand on a periodic cycle.

For these results, we considered four climate change scenarios (described above). We used the downscaled climate scenarios for the closest gridpoint to Blodgett Forest (gridpoint location: 38°49'N; 120°41'W). The downscaled climate projections for the Blodgett area share a similar baseline climate (1971–2000) with respect to the climate-related growth parameters. However, the modeled climates are slightly drier and warmer than observed at Blodgett Forest (Table 1).

2.4 Growth projections in the reserve compartments

We tied our growth projections in the reserve compartments to our data as closely as possible. Note that all of our 30-year projections for the reserve stands are anchored to the volume of surviving trees measured in our 1971–2000 inventory. This ‘anchor’ to the inventory serves to isolate climate effects from variations in the growth projections.

CACTOS’ primary function is to predict growth in managed stands. It includes functions to simulate mortality and ingrowth (i.e., recruitment). However these aspects of population dynamics are much more difficult to model, particularly under novel conditions. Also, the work of Wensel’s research team did not address how climate may influence mortality and recruitment independent of growth. Therefore we used CACTOS_{clim} to isolate the changes in tree diameter increment only. The sub-routines that estimate mortality and ingrowth in CACTOS were disabled. Instead, we used the same empirically-based mortality and recruitment rates (measured from periodic inventories) for all climate scenarios. We considered climate effects on non-catastrophic mortality separately (see Section 2.7).

We setup CACTOS_{clim} to run in annual time steps so we could adjust growth projections for the specific climate influences in each year. Every 10 years, we reset the forest

Table 1 Comparison of downscaled climate scenarios to the historical baseline period: 1971–2000

Climate models (1971–2000)	^a Total winter precipitation (cm)		^b Mean summer temperature (°C)	
	Mean	Std	Mean	Std
^c Blodgett (obs)	111.8	47.1	19.66	0.98
^d GFDL A2	81.4	30.3	21.77	0.73
GFDL B1	81.3	30.3	21.74	0.74
PCM A2	83.1	32.7	21.71	0.52
PCM B1	83.0	32.7	21.68	0.54

^a Winter includes October, November, December, January, and February.

^b Summer includes June, July, August, and September.

^c Values for Blodgett are the observed values from the long-term weather station at the research forest.

^d GFDL refers to the projections from the NOAA’s Geophysical Dynamics Laboratory; PCM refers to the National Center for Atmospheric Research/Department of Energy Parallel Climate model. A2 (higher) and B1 (lower) are emission scenarios.

composition and structure using the data inventory. For example, we used the 1970's inventory of the reserve stands to initiate the model (approximately 70 year old second growth stands). We then ran CACTOS_{clim} for 10 years and captured the annual results. For the next 10-year run, we re-initiated the model using the 1980's inventory thereby accounting for mortality and recruitment. We repeated this process for three cycles to get 30-year projections. Thus the only changes in each 30-year projection were the climate parameters. Note that strictly speaking, this modeling framework does not forecast forest growth for the different time periods. Instead, it predicts growth of the current forest under alternative future climates.

This data-structured method limits the propagation of growth effects due to climate change and thus provides a conservative estimate of impacts. In short, our projections may underestimate the severity of growth impacts. On the other hand, we did not include any CO₂ fertilization effect in our models. The magnitude and persistence of forest productivity increases due to CO₂ enrichment is an area of active research (Korner et al. 2005). Thus our exclusion of CO₂ enrichment may bias our projections toward lower growth if fertilization effects exists. The primary measure of growth was stem wood volume increment. This measure includes the main bole of the tree but excludes the stump and branches.

There were four reserve compartments located throughout Blodgett Forest available for analysis and growth projections. These are aggrading stands that have nearly doubled their basal area in the last 30 years. At the beginning of the 30-year model runs, the reserve stands had an average density of 460 stems per hectare, an average basal area of 45.3 m² ha⁻¹, and an average total stem volume of 406 m³ ha⁻¹. These stands were well-mixed with respect to the abundance of conifer species.

2.5 Growth projections under single tree selection

There were two compartments at Blodgett under long-term single tree selection. The goal of this management regime is to create stable, uneven-aged stands that can be periodically harvested on a sustainable basis. We used the Blodgett inventory data to parameterize the starting conditions in each stand. At the beginning of the period, the average density was 510 trees per hectare, the average basal area was 38.5 m² ha⁻¹, and the average total stem volume was 296 m³ ha⁻¹. In year 10, these stands were harvested under a single tree prescription that removed on average 13% of the trees and 19% of the basal area. Thus like the simulations of the reserve stand, we ran CACTOS_{clim} in annual time steps with the subroutines for ingrowth and mortality disabled for 10 years and then reset our simulations for the next decade using the inventory data from Blodgett Forest.

2.6 Growth projections in simulated pine plantations

We generated 20-year old ponderosa pine plantations with tree sizes and spacing typical for pine plantations in El Dorado County at 1,219 m elevation. Specifically, we used the Forest Stand Generator (a utility for the CACTOS model, Biging et al. 1991) to produce four, 20-year old simulated plantations. These four stands varied in site productivity (site index=80 and 120) and initial density (4.9×4.9 m spacing and 6.1×6.1 m spacing). At age 20, the average density was 345 trees per hectare, the average basal area was 20.9 m² ha⁻¹, and the average total stem volume was 127 m³ ha⁻¹. We ran CACTOS_{clim} simulations (with the ingrowth and mortality subroutines disabled) for 30 years under the different climate scenarios to estimate annual tree growth through age 50.

2.7 Assessing uncertainty in the growth projections

When modeling growth in the reserve and single-tree selection stands, we calculated confidence intervals that account for the spatial variability among stands and the differences in harvest implementation (single-tree selection only). For the pine plantations, these intervals represent the variation due to differences in site fertility and initial density. The confidence intervals do not, however, incorporate the uncertainty and stochasticity inherent in the downscaled climate predictions. By design, consistent climate realizations with no stochastic modeling were used by all researchers contributing to this series of papers. CACTOS growth projections may be made in either a deterministic or a stochastic mode (Wensel et al. 1986). Since the climatic inputs to the CACTOS model were deterministic, we therefore used the deterministic mode of projection in all CACTOS_{clim} runs.

2.8 Modeling non-catastrophic tree mortality

Radial stem growth in trees has proven to be a reliable indicator of mortality risk (e.g., Pacala et al. 1996). Typically, growth-mortality functions are based on the most recent five years of growth (Kobe et al. 1995; Wyckoff and Clark 2000). However recent work has documented a relationship between longer-term growth characteristics and tree decline, including lifetime growth rates, long-term growth trends and abrupt changes in growth (Pedersen 1998; Cherubini et al. 2002; Suarez et al. 2004). But relatively few attempts have been made to incorporate these characteristics in modeling the probability of mortality (Bigler and Bugmann 2004; Das et al. 2007).

In 2005, we sampled growth chronologies for 69 white fir trees at Blodgett Forest in the reserve stand. White fir is a core species in the mixed-conifer forest type (relative dominance in reserve stand=18%). It is a fire-sensitive, shade-tolerant species.

We had previously built two logistic regression equations for white fir that predict the likelihood of survival. One equation used the most recent five years of growth as the predictor variable (standard method, *sensu* Wyckoff and Clark 2000). The other used two different aspects of the growth chronology as predictor variables – long-term growth (last 25 years) and the number of abrupt changes in growth in the last 25 years (two parameter model, Das et al. 2007). These equations were fit for trees sampled in old-growth forests of the southern Sierra Nevada. External validation of these models showed that the standard method correctly classified the status (dead/alive) of white fir trees ($n=279$) in 68.8% of the cases; the two parameter model correct classification rate was 73.5%. (Table A1 in Das et al. 2007). Both of these logistic regression equations provide likelihoods of survival that were then extrapolated to annual survival probabilities using Monte Carlo simulations (Wyckoff and Clark 2000). The results are summarized in ‘vulnerability profiles’ that show the distribution of individual survival probabilities.

To explore the impact of climate change, we calculated the climate-related growth residuals for white fir at Blodgett Forest from 1978–2002 using measured climate data from Blodgett Forest and the predicted growth residuals from Yeh and Wensel (2000). We then subtracted the climate residuals from the measured chronology. The remaining time series of tree growth presumably contains influences on growth rates unrelated to climate (i.e., growth due to competition, canopy status, and microsite). We then calculated the climate-related growth adjustments from the climate change scenarios for three future 25-year periods 2006 to 2030 (2030), 2041 to 2065 (2065), and 2076–2100 (2100). We added these climate adjustments to the non-climatic growth chronology to estimate individual growth

chronologies under a changing climate. We then constructed vulnerability profiles for 69 white fir trees for four years: 2002 (baseline) and three projections – 2030, 2065, and 2100. We compared results using two different growth-mortality relationships: one based only on the most recent five year of growth (i.e., standard method) and the other based on the last 25 years of growth (i.e., two parameter model, Das et al. 2007).

3 Results

3.1 Climate change impact on forest growth

All four downscaled climate realizations for our case study site in El Dorado County predicted climatic conditions that lead to reduced conifer growth during the next century. For this site, there was no trend in winter precipitation in any of the climate scenarios (Figs. 1a and 2a). Thus increased summer temperature (Figs. 1b and 2b) was the primary driver of these changes. The relative impact of climate change was greater for white fir, incense-cedar, and Douglas-fir compared to ponderosa pine and sugar pine (Figs. 3 and 4). For all climate realizations, growth reductions increased with time (Figs. 3 and 4).

The most severe reductions in tree diameter growth were realized under the GFDL A2 scenario. In particular, summer temperatures increased most dramatically in the end of the

Fig. 1 Summary of downscaled climate projections from GFDL model. Projections for gridpoint (38°49'N; 120°41'W) closest to Blodgett Forest in El Dorado county. **a** Total winter precipitation is defined as precipitation during October, November, December, January, and February. **b** Mean monthly summer temperature includes June, July, August, and September. Season definitions follow Yeh and Wensel (2000)

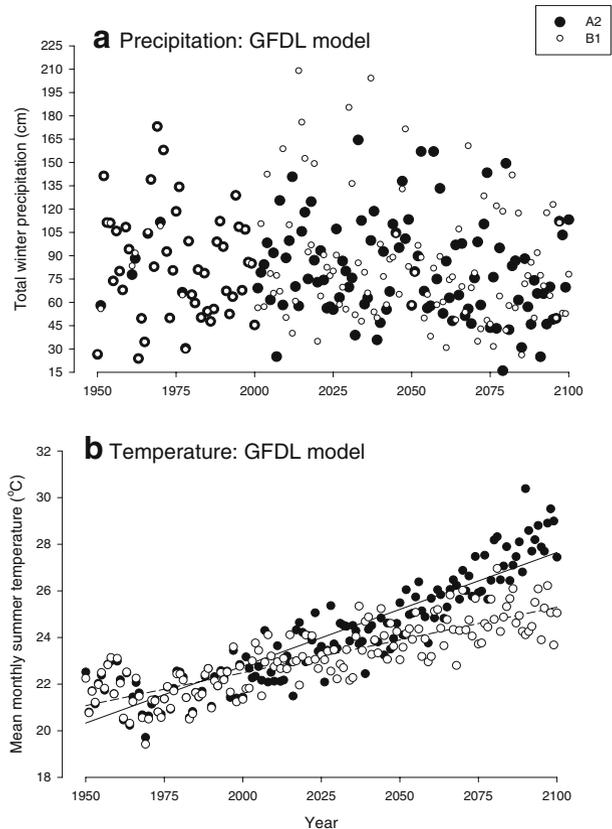
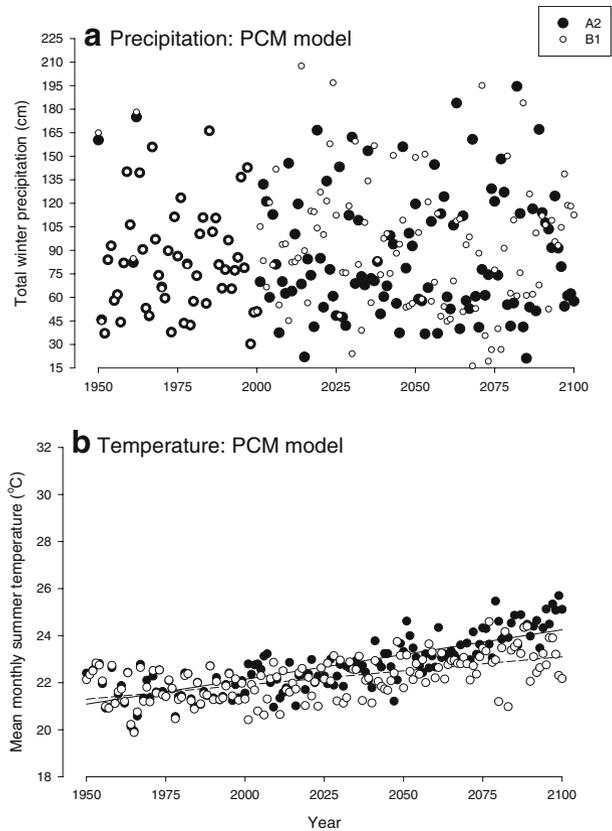


Fig. 2 Summary of downscaled climate projections from PCM model. Projections for gridpoint (38°49'N; 120°41'W) closest to Blodgett Forest in El Dorado county. **a** Total winter precipitation is defined as precipitation during October, November, December, January, and February. **b** Mean monthly summer temperature includes June, July, August, and September. Season definitions follow Yeh and Wensel (2000)

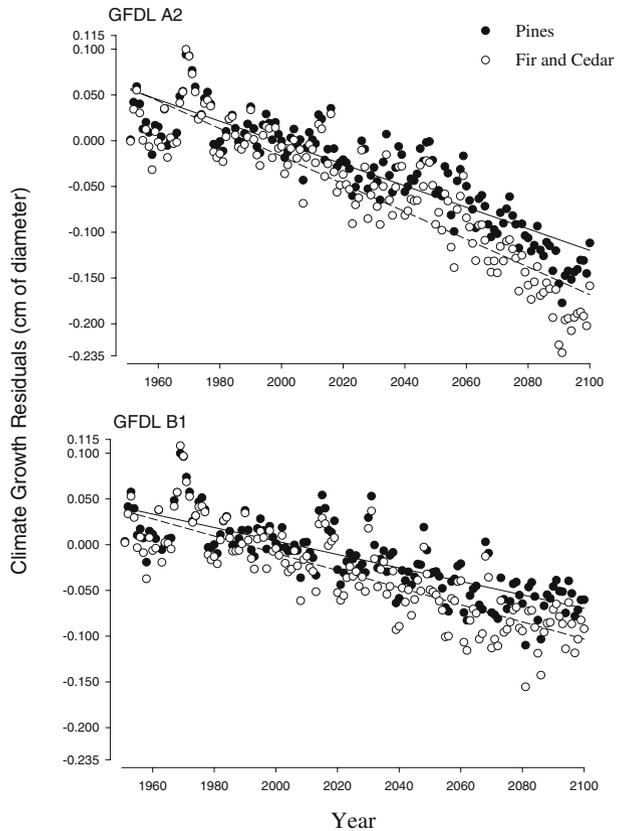


century projection (Fig. 1, 2071–2100). This temperature increase led to reductions in tree growth during the last 30 years that were greater than the 100-year linear trend in the GFDL A2 scenario (Fig. 3).

Based on the $CACTOS_{clim}$ modeling, stem volume growth declined under all four climate projections. Declines were typically most severe for the pine plantations and least severe under single tree selection (Tables 2, 3, and 4). Tree growth was consistently lower under the GFDL projections, and the A2 emission scenario always reduced growth more than the B1 scenario (Tables 2, 3, and 4). By the end of the century (i.e., 2071–2100), the severity of the declines, as measured by stem volume increment, ranged from a minimum of 5% relative to baseline (single tree selection, PCM B1) to a maximum of 25% (pine plantation, GFDL A2).

These growth declines translated into substantial absolute losses of potential timber yield in all management regimes. As noted above, the losses were most severe under the GFDL A2 scenario during the interval between 2071 and 2100. For example, the growth obtained in reserve stands during the baseline interval (1971–2000) was reduced by 19% in 2071–2100 (Fig. 5). This reduction represents a net (average) loss of $3.86 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ of production during the interval. A similar result was observed for single tree selection (Fig. 6). While the proportional reductions (25%) were greatest for the pine plantations (Fig. 7), a smaller net loss of wood production was realized $-2.98 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$. To convert these stem volume increments to timber yield, we used Spelter's (2002) log scaling

Fig. 3 Summary of climate-related growth residuals. Climate projections from GFDL model. Downscaled for site in El Dorado county. Projections based on Yeh and Wensel (2000). Projections assume no CO₂ fertilization effect

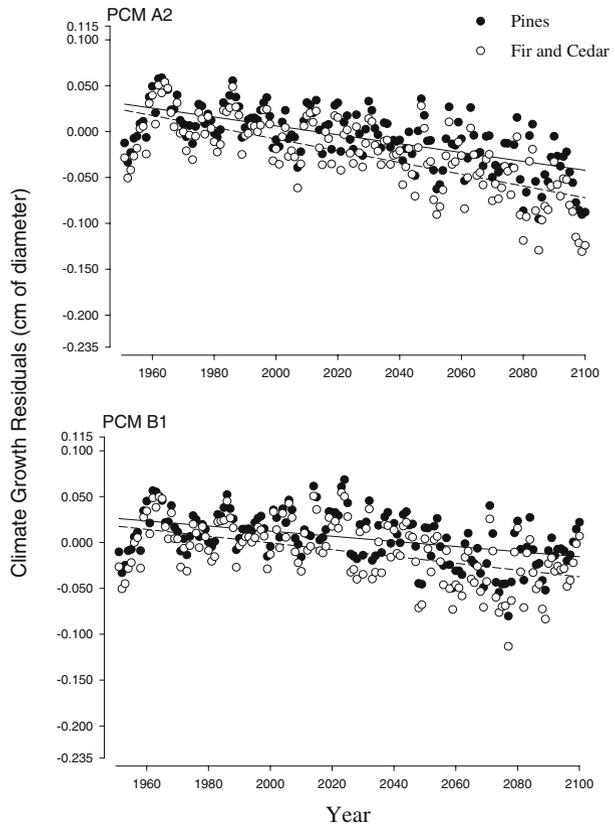


conversion for the diameter range of trees in our stands ($5.93 \text{ m}^3 = 1 \text{ MBF}$). We report these values in thousands of board feet per acre (MBF ac^{-1}) – the timber yield measurement used by the US lumber trade. Thus by the end of the century, the GFDL A2 scenario resulted in an average net loss of $0.26 \text{ MBF ac}^{-1} \text{ year}^{-1}$ in the reserve stands, $0.23 \text{ MBF ac}^{-1} \text{ year}^{-1}$ under single tree selection, and $0.20 \text{ MBF ac}^{-1} \text{ year}^{-1}$ in pine plantations.

3.2 Climate change impacts on non-catastrophic mortality for a major tree species

For 2002, there was no difference in survival probability estimates for growth chronologies reconstructed from the climate scenarios and for the observed growth chronology. In all instances the median annual survival probability for sampled white fir trees was $\geq 0.997 \text{ year}^{-1}$ based on the standard growth-mortality function (Table 5). The consistency of these results provides some assurance that our approach to reconstructing individual growth chronologies under different climate scenarios captures the climate-related variability in growth. Note that only larger trees (diameter at breast height $\geq 23 \text{ cm}$) were included in the sample. The lower size limit was set to match the size limit of trees considered merchantable. Of the 69 trees, 47 were in the upper stratum of the forest (i.e., not shaded from above). The remaining 22 were in the intermediate stratum (i.e., not in the understory but not in the canopy). For trees of this stature, the estimated survival rate for 2002 (i.e., trees were at very low risk of dying in any given year) fits the empirical

Fig. 4 Summary of climate-related growth residuals. Climate projections from PCM model. Downscaled for site in El Dorado county. Projections based on Yeh and Wensel (2000). Projections assume no CO₂ fertilization effect



demographic data. Currently, these trees are experiencing low annual mortality rates (typically <0.1% year⁻¹).

In general, only moderate decreases in survival were projected for the next 100 years (Table 5). The most severe decrease in survival probability occurred under the GFDL A2 scenario. By the end of the century, median survival probability was reduced by 1.5

Table 2 Cactus_{clim} stem volume growth projections for a reserve stand (mature, unmanaged) mixed-conifer forest in El Dorado County

Time period	^a GFDL		PCM	
	A2	B1	A2	B1
1971–2000	20.02 (1.54)	19.76 (1.64)	19.65 (1.73)	19.63 (2.20)
2001–2030	19.03 (1.46)	18.56 (1.51)	18.72 (1.58)	19.21 (1.58)
2036–2065	18.20 (1.39)	17.68 (1.38)	18.30 (2.29)	18.56 (1.49)
2071–2100	16.16 (1.22)	17.06 (1.43)	17.43 (1.34)	18.26 (1.93)

^a Climate simulations are based on downscaled results from two global climate models (GFDL and PCM) under two emission scenarios: A2 (higher CO₂ emissions) and B1 (more moderate emission increases). Ingrowth and mortality are tied to empirical results. Means with standard errors in parentheses are based on average growth in each 30-year climate projection for four compartments (i.e., *n*=4). Units: m³ ha⁻¹ year⁻¹. Mean volume growth is reported (m³ ha⁻¹ year⁻¹) followed by the standard error in parentheses.

Table 3 $Cactos_{clim}$ stem volume growth projections for single-tree selection management in a mixed-conifer forest in El Dorado County

Time Period	^a GFDL		PCM	
	A2	B1	A2	B1
1971–2000	17.08 (1.80)	17.07 (1.78)	17.01 (1.88)	16.98 (1.88)
2001–2030	15.91 (2.22)	16.52 (1.75)	16.65 (1.84)	17.08 (1.83)
2036–2065	15.49 (1.53)	15.69 (1.59)	16.25 (1.80)	16.49 (1.74)
2071–2100	13.69 (1.30)	15.12 (1.72)	15.45 (1.56)	16.19 (1.94)

^aClimate simulations are based on downscaled results from two global climate models (GFDL and PCM) under two emission scenarios: A2 (higher CO₂ emissions) and B1 (more moderate emission increases). Management interventions, ingrowth and mortality are tied to empirical results. Means with standard errors in parentheses are based on average growth in each 30-year climate projection for two compartments (i.e., $n=2$). Units: $m^3 ha^{-1} year^{-1}$. Mean volume growth is reported ($m^3 ha^{-1} year^{-1}$) followed by the standard error in parentheses.

percentage units to $0.983 year^{-1}$ (Table 5, Fig. 8). However the impact of a changing climate on non-catastrophic mortality was not uniformly distributed through the population. Slower-growing trees were disproportionately affected. Survival rates of the lower quartile of trees decreased more steeply than the median (Table 5). Through time, the weaker trees were projected to get weaker as evidenced by the progressive skew in the vulnerability profiles (e.g., Fig. 8).

The predicted reductions in survival probability under future climates were slightly more severe when survival was modeled using the two-parameter growth mortality function (Fig. 9). As noted above, growth reductions worsened with time. The two-parameter model considers more of the growth record (25 years as opposed to 5) as well as any sharp annual decreases that might occur in that period.

4 Discussion

4.1 Tree Growth

The four climate scenarios examined showed a distinct link between increasing summer temperatures and stem volume growth declines. Given the lack of any trend in the winter

Table 4 $Cactos_{clim}$ stem volume growth projections for pine planation simulations (initial conditions=20 yr-old plantations) in El Dorado County

Time Period	^a GFDL		PCM	
	A2	B1	A2	B1
1971–2000	11.95 (3.09)	11.95 (3.09)	11.84 (3.08)	11.82 (3.07)
2001–2030	11.19 (2.97)	11.43 (3.01)	11.58 (3.03)	11.96 (3.09)
2036–2065	10.54 (2.86)	10.69 (2.88)	11.20 (2.98)	11.48 (3.02)
2071–2100	8.97 (2.60)	10.15 (2.80)	10.54 (2.86)	11.18 (2.97)

^aClimate simulations are based on downscaled results from two global climate models (GFDL and PCM) under two emission scenarios: A2 (higher CO₂ emissions) and B1 (more moderate emission increases). Means with standard errors in parentheses are based on average growth in each 30-year climate projection for simulations with four different starting conditions (i.e., $n=4$). Units: $m^3 ha^{-1} year^{-1}$. Mean volume growth is reported ($m^3 ha^{-1} year^{-1}$) followed by the standard error in parentheses.

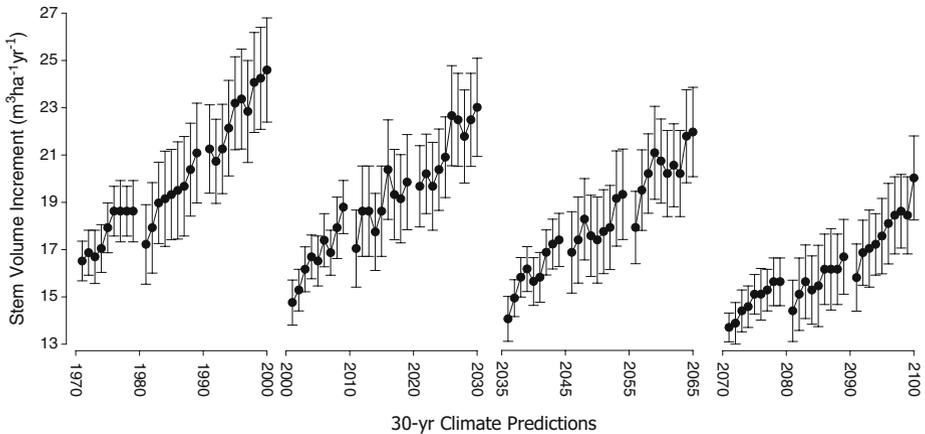


Fig. 5 *Cactus_{clim}* growth projections for reserve mixed-conifer stands in El Dorado county. Climate simulations based on the downscaled GFDL model under the A2 emission scenario. Ingrowth and mortality tied to empirical results. Means and standard errors based on annual growth projection for the four reserve stands (i.e., $n=4$)

precipitation patterns (Figs. 1 and 2), these summer temperatures were the drivers of change in the *CACTOS_{clim}* models. Summer drought is a typical aspect of the Mediterranean climate experienced by the Sierran mixed-conifer forest. The intensity and extent of the moisture deficit that develops during the summer are considered to be limiting factors in the growth and viability of Sierran conifers (Royce and Barbour 2001a). Higher summer temperatures in a Mediterranean climate (absent any changes in precipitation) could induce greater tree water stress through higher evapotranspiration rates and/or faster depletion of moisture in the soil profile. These changes would hasten the onset of drought stress that occurs in the late summer and early fall before the winter rains return. The result would be a shorter growing season due to lack of moisture, which is already recognized as a primary growth constraint on most commercial timber sites in Sierran forests (Royce and Barbour 2001b).

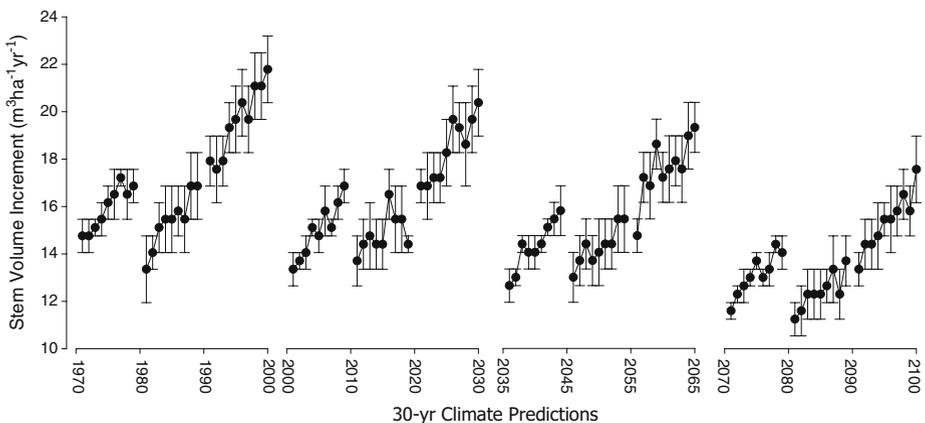


Fig. 6 *Cactus_{clim}* growth projections for single-tree selection management in mixed conifer stands in El Dorado county. Climate simulations based on the downscaled GFDL model under the A2 emission scenario. Means and standard errors based on annual growth projection for the two single-tree compartments (i.e., $n=2$)

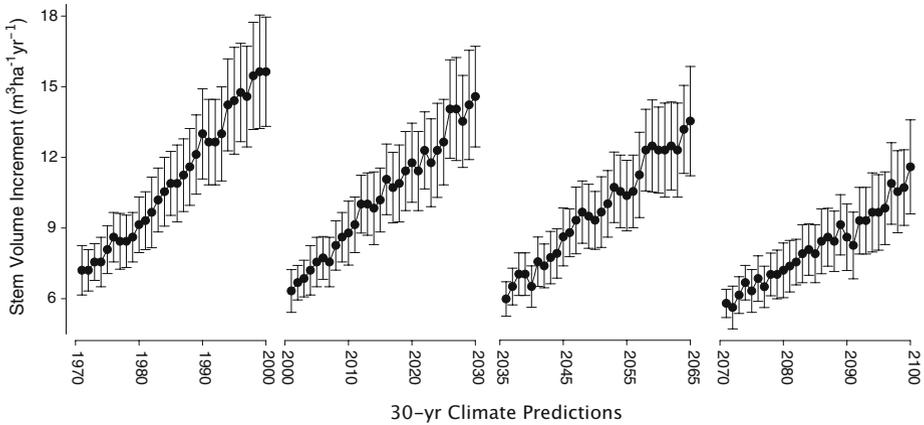


Fig. 7 $Cactus_{clim}$ growth projections for simulated ponderosa pine plantations typical of plantations in El Dorado county. Climate simulations based on the downscaled GFDL model under the A2 emission scenario. Means and standard errors based on annual growth projection for the four simulations (i.e., $n=4$)

Given the relationship between tree growth and summer temperature, it was not surprising that the most severe effects of projected climate change coincided with the most severe increases in temperature. The accelerated increase in summer temperature projected for 2071–2100 under the GFDL A2 scenario (Fig. 1) resulted in the most severe projected reductions in tree growth for all management regimes (Tables 2, 3, and 4). However management decisions clearly had an impact on the magnitude of the change.

Despite cultivating a species that is most tolerant of summer temperature (ponderosa pine, Figs. 2 and 4), plantations showed the biggest relative loss of stem volume increment and a comparable absolute loss of timber production. Silvicultural practices at least partially explain this result. In the Sierra Nevada, pine plantations are typically harvested on a 50-year rotation. At the start of our 30-year simulation, the trees in a 20-year pine plantation were on average smaller and younger than the trees in the reserve and single tree selection stands. The pine plantations started with a lower initial volume of wood, and the trees also spent a greater proportion of their life in the changed climate. In other words, there was less ‘biological inertia’ in the pine plantations and thus the effects of climate change were observed more keenly.

A wealth of studies have modeled the impact of climate change on forest growth. The results vary by forest region, climate scenario, and modeling approach (reviewed in Bugmann et al. 2001). While a definitive review is beyond the scope of this paper, recent research suggests that there may be a latitudinal trend in the response of upland conifer forests. In temperate latitudes, the growth of conifer forests more often declines under projected future climates while productivity of conifer forests in boreal latitudes more often increases (Linder 2000; Bugmann et al. 2001; Lasch et al. 2002; Briceño-Elizondo et al. 2006). Our results follow this trend. Growth declined in this temperate conifer forest under every management regime. Too few papers have addressed the interacting effects of management and climate change to draw any general conclusions other than to note that forest management does influence the response (Linder 2000).

The magnitude and persistence of any changes in forest productivity related to changes in CO_2 concentrations are crucial to projections of tree growth and yield. Biogeochemistry-based simulation models (e.g., CENTURY) predict increases in plant productivity under increasing atmospheric CO_2 (transpiration decreases thus improving water use efficiency).

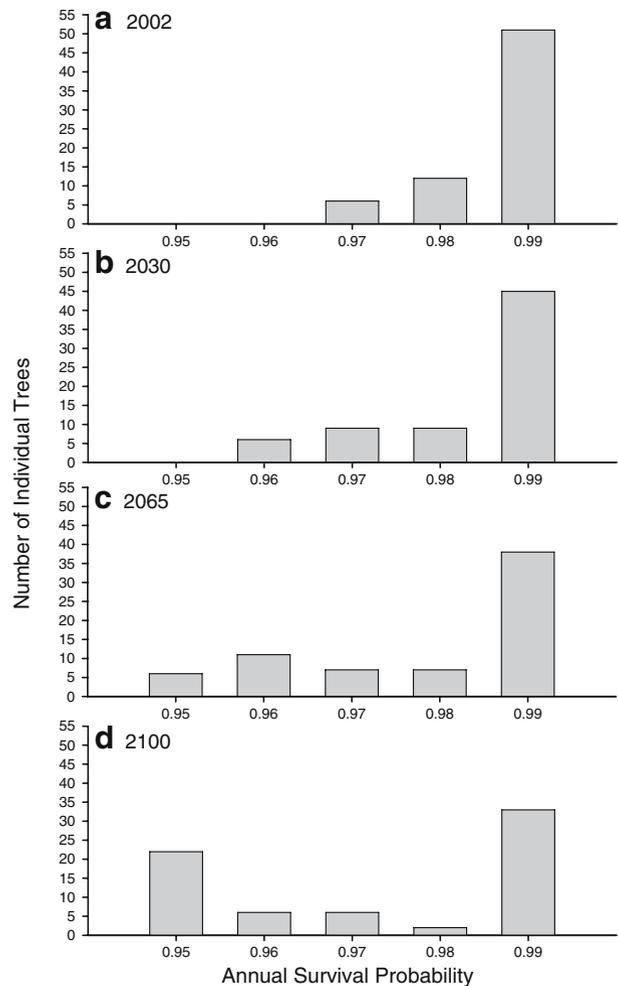
Table 5 Annual survival probabilities for 69 *Abies concolor* trees sampled from the reserve stands at Blodgett Forest

aProjection scenario	Target year			
	2002	2030	2065	2100
GFDL A2				
Mode	0.999 (48%)	0.999 (45%)	0.999 (39%)	0.956 (29%)
25th	0.989	0.983	0.971	0.956
50th	0.998	0.997	0.993	0.983
75th	1.000	1.000	1.000	0.999
GFDL B1				
Mode	0.999 (48%)	0.999 (48%)	0.999 (39%)	0.999 (39%)
25th	0.991	0.987	0.976	0.973
50th	0.998	0.997	0.994	0.994
75th	1.000	1.000	1.000	1.000
BFRS (current)				
Mode	0.999 (48%)	–	–	–
25th	0.987	–	–	–
50th	0.997	–	–	–
75th	1.000	–	–	–
PCM A2				
Mode	0.999 (48%)	0.999 (48%)	0.999 (46%)	0.999 (39%)
25th	0.988	0.989	0.985	0.967
50th	0.998	0.998	0.997	0.992
75th	1.000	1.000	1.000	0.999
PCM B1				
Mode	0.999 (48%)	0.999 (45%)	0.999 (46%)	0.999 (48%)
25th	0.991	0.987	0.986	0.988
50th	0.998	0.997	0.997	0.998
75th	1.000	1.000	1.000	1.000

^aProjections based on absolute growth during the five years preceding the target year. Dendrochronologies were adjusted for each climate scenario using the growth residual equations from Yeh and Wensel (2000). Mortality models fit for *Abies concolor* from growth and demography data from Sequoia Kings Canyon National Park. Vulnerability profiles summarized using modal values and quantile distributions.

Lenihan et al. (2003, 2006) include this CO₂ fertilization-effect in their state-wide analysis of climate change effects on California vegetation. However growth chamber studies of plant physiological response to increased CO₂ routinely report photosynthetic acclimation implying that any increases in productivity will be short-lived (Long et al. 2004). Results from the free air CO₂ enrichment (FACE) experiments parallel some of the findings from enclosure studies (Long et al. 2004) but a recent meta-analysis of FACE experiments support the contention that tree productivity does respond to CO₂ enrichment (Ainsworth and Long 2005). For example in one of the longest FACE experiments with trees, Wittig et al. (2005) found significant increases in gross primary productivity for poplar coppice plantations grown for three years in CO₂ enriched environment. However, the increased productivity declined exponentially with time. By year three, gross productivity gains ranged from 5 to 19% (species-dependent) of the control. Interestingly Wittig et al. (2005) attributed the declines in productivity to light limitation (i.e., canopy closure) and not down-regulation of photosynthesis. In contrast to the FACE meta-analysis, results from a web-FACE study in a mature natural forest, where pure CO₂ is released via a fine web of tubes woven into the tree canopies, showed no persistent stimulation in tree stem growth

Fig. 8 a–d Shifts in annual survival probability for 69 white fir trees in the mature mixed conifer forest in El Dorado county. Survival probabilities based on parameterized mortality function using the last five years of growth (i.e., standard model, see text). Changes in tree growth based on climate-related growth residuals; projected climate using GFDL downscaled predictions under A2 emission scenario

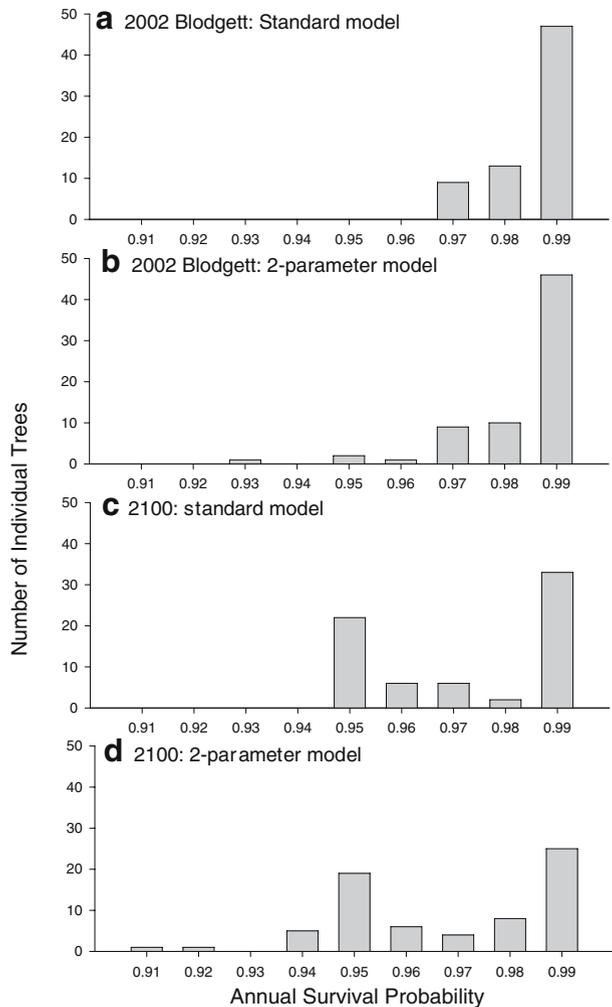


(Korner et al. 2005). Thus it remains an unresolved question whether the observed increases in tree production under enriched CO_2 translates into sustained increases in stem growth (Norby et al. 2005). Given our focus on wood production (i.e., stem growth) and the 30-year time frame adopted for this study, we did not include any CO_2 fertilization effect in our models. Clearly a better understanding of the long-term effects of climate change and atmospheric CO_2 concentrations on tree water relations, forest productivity, and carbon allocation is crucial to improving projections of future forest conditions.

4.2 Tree mortality and forest health

No combination of climate scenarios and mortality models produced dramatic increases in white fir mortality (Table 5, Figs. 8 and 9). However the projected changes in climate could exacerbate ongoing forest health concerns. The predicted reductions in growth increased the number of susceptible trees in the forest. Weak trees are less able to resist pathogen infections and insect attacks, regardless of whether the pests are native or recently arrived.

Fig. 9 Comparison of vulnerability profiles for 69 white fir trees in the mature mixed conifer forest in El Dorado County. Profiles calculated from two different growth mortality functions. The standard growth-mortality function is based on the last 5 years of growth. The two-parameter function uses growth during the previous 25 years and the number of abrupt changes in growth in the previous 25 years. **a, b** Comparison of vulnerability profiles in 2002 for the observed chronologies. **c, d** Comparison of vulnerability profiles in 2100 for reconstructed chronologies. Changes in tree growth based on climate-related growth residuals; future climate projected using GFDL downscaled model under the A2 emission scenario



Our model only considered non-catastrophic mortality, yet there are clear linkages to fire risk, disease epidemics, and insect outbreaks. One preventative response is to retain a mixture of species and ages in the mixed-conifer forests. Designing diverse forest structures with multiple species can alleviate some risk associated with even-aged, single species stands. Monodominant stands (i.e., forests where one tree species constitutes more than 50% of the stand) are at most risk. A spatially mixed forest limits the spread of both pathogens and insects. Another effective adaptation would be to maintain lower tree densities. By reducing fuel loads and competition, lower density stands provide structures that are more resilient to catastrophic events like fire and epidemics.

We recognize that a significant challenge in predicting the impact of climate change on managed forests in California will be anticipating the biological interactions that accompany that change. Some of the most important interactions will include forest insects and diseases. These pests have complex interactions with hosts, vectors, and natural enemies. Moreover the ecology of all of these organisms is likely to be affected by a

changing climate. Currently we are not capable of quantifying these crucial interactions. However we can discuss the most relevant issues for California's forests.

Pest organisms have the ability to adapt much faster than their host trees, thereby increasingly the likelihood of severe pest impact. Problems encountered with pest introductions via global trade provide a cautionary example. As organisms move into new but favorable habitats, potential for widespread damage is high because trees do not adapt quickly. Thus if a changing climate enables a pest to expand its range, the impact could be similar to the introduction of an exotic pest. For example, pine pitch canker (an introduced pathogen caused by *Fusarium circinatum*), once limited to coastal areas of California, has expanded to the El Dorado National Forest in the Sierra Nevada (Vogler et al. 2004; Gordon 2005). If climate change results in more favorable environmental conditions in the Sierra Nevada Mountains for pitch canker (e.g., milder winter minimum temperatures), it could result in increased disease severity (all of the pine species in the mixed-conifer forest are susceptible) and economic loss. In addition to the arrival of new pests, extant native organisms that rely on host stress may become more prevalent due to the greater proportion of stressed trees (e.g., Fig. 8) in the population (Lonsdale and Gibbs 1996). Specific examples relevant to California's conifer forests include root diseases caused by *Armillaria* spp. and certain wood or twig boring insects (*Ips* spp.).

4.3 Implications for timber management

All climate scenarios considered here were associated with decreasing volume growth and timber yield. The responses available to offset declining yields in any specific region fall into three categories. The most obvious is cutting more acreage to maintain constant total yields. However, there are California regulatory restrictions on state and private lands that propose to cut more timber than can be replaced by growth. Any long term increases in harvest volume would need to come from federal lands which have been largely removed from the commercial timber base over the past decade or from other lands that have not traditionally yielded timber products. Another response is to reduce investment in timber management in order to increase net financial return. This strategy results in less intensive forest management (e.g., reductions in shrub control, longer intervals between non-commercial thinning) that has implications for both forest health and fire risk. Alternatively, silvicultural treatments could be designed to compensate growth losses from climate change with improvements in stand conditions. Planting mixtures of species, maintaining several age classes, reducing tree density, and pruning trees at strategic intervals are examples of cultural practices that could improve timber values but not necessarily timber yields.

4.4 Study limitations

All case studies are limited by the specificity of the particular case. In return, more detailed, and perhaps more reliable, information is obtained. However even for this site in El Dorado County where we had proven models and extensive data, we could only evaluate climate change impacts on key forest parameters in isolation. But the processes of growth and mortality are fundamentally linked and the interaction will have direct effects on the forest's susceptibility to disease and insect attacks. Thus these processes must be studied in concert in order to properly forecast their role under a changed climate. Even within the modeling framework we defined, there are uncertainties in our projections. All results are limited by the applicability of the CACTOS growth and yield model and the efficacy of the statistically-fitted climate-growth residuals (Wensel et al. 1986, Yeh and Wensel 2000).

In addition, our implementation strategy had direct effects on our findings. On the one hand, we did not propagate through time the CACTOS_{clim} results for the reserve stand. By constraining forest composition and structure, we potentially underestimated the consequences of climate change. On the other hand, we explicitly excluded CO₂ fertilization effects – a decision that potentially leads to overestimates of productivity declines. We also used simulated stands to evaluate growth in pine plantations. A better alternative would be to ground the climate growth projections for pine plantations in inventory data as we did for the reserve and single-tree analyses.

Modeling specific impacts of future climate on California's forests is a precarious undertaking. In particular, we are concerned about the consequences of unanticipated events. We have only modeled the direct effects of climate change and not considered potential indirect effects on the disturbance regime (*sensu* Aber et al. 2001). Fire is an obvious concern. Insect outbreaks or pathogen irruptions also have the potential to entirely swamp climate-related growth effects on forest yield and tree mortality. The nature, magnitude, and timing of these transforming events are difficult to predict. Unfortunately we will likely gain experience with these climate-driven transformations, and these events will provide crucial learning opportunities if we have built the informational and computational infrastructure needed to study them.

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