

Wildfire and drought dynamics destabilize carbon stores of fire-suppressed forests

J. MASON EARLES,^{1,4} MALCOLM P. NORTH,^{1,2} AND MATTHEW D. HURTEAU³

¹Graduate Group in Ecology, University of California, One Shields Avenue, Davis, California 95616 USA

²USFS Pacific Southwest Research Station, Davis, California 95618 USA

³Ecosystem Science and Management, Pennsylvania State University, State College, Pennsylvania 16803 USA

Abstract. Widespread fire suppression and thinning have altered the structure and composition of many forests in the western United States, making them more susceptible to the synergy of large-scale drought and fire events. We examine how these changes affect carbon storage and stability compared to historic fire-adapted conditions. We modeled carbon dynamics under possible drought and fire conditions over a 300-year simulation period in two mixed-conifer conditions common in the western United States: (1) pine-dominated with an active fire regime and (2) fir-dominated, fire suppressed forests. Fir-dominated stands, with higher live- and dead-wood density, had much lower carbon stability as drought and fire frequency increased compared to pine-dominated forest. Carbon instability resulted from species (i.e., fir's greater susceptibility to drought and fire) and stand (i.e., high density of smaller trees) conditions that develop in the absence of active management. Our modeling suggests restoring historic species composition and active fire regimes can significantly increase carbon stability in fire-suppressed, mixed-conifer forests. Long-term management of forest carbon should consider the relative resilience of stand structure and composition to possible increases in disturbance frequency and intensity under changing climate.

Key words: carbon; climate change; drought; fire; fire suppression; forest; wildfire.

INTRODUCTION

Forests store more than twice as much carbon (C) as Earth's atmosphere and continue to be a significant sink, taking up 2.4 ± 1.0 Pg C/yr (Pan et al. 2011). While international efforts have focused on increasing and maintaining C through incentives to increase afforestation/reforestation and reduce deforestation, the influence of changing climate has largely been left out of management, model, and market analyses. Changing climate may alter disturbance regimes and abiotic stress, influencing forest C stock stability and carrying capacity. Managed as offsets, forests can sequester additional C and maintain it long enough to mitigate anthropogenic emissions, a concept referred to as permanence. Yet these stocks are sensitive to changes in disturbance patterns associated with increased fire size and severity (California's recent Rim Fire) and drought intensity and duration (Schwalm et al. 2012, van Mantgem et al. 2013). Climate change is likely to affect both of these traits by altering disturbance regimes and differentially changing species-specific growth and mortality rates. Effective assessments of carbon permanence and pricing will only be possible after ecologists help quantify the

risk and stability of different forest stocks (Hurteau et al. 2013).

In many of the world's drier forests, tree growth and mortality are strongly influenced by drought, fire, and forest conditions resulting from fire suppression. Recent research has focused on the effects of fire suppression, wildfire, and whether efforts to restore forest structure and reduce fuel loads in fire-prone forests are a net C gain or loss. Results suggest that fuels treatments may reduce wildfire emissions and enhance C permanence, but the total C loss (treatment + moderate wildfire emissions) can be higher than severe wildfire in the absence of treatments (North and Hurteau 2011). Given the relative infrequency of fire at the landscape scale because of suppression, only about one in ten treated forests burn, increasing the ratio of treatment-induced C removals to reduced wildfire emissions. Campbell et al. (2012) found that simulated fire-suppressed forests, experiencing infrequent high-severity fire, store more C than treated forests that burn more frequently. They suggest this negative relationship between fire frequency and average landscape C storage always holds unless treatment, wildfire, or their interaction changes a forest's maximum biomass potential. In many dry forests, however, a significant change in biomass potential has already occurred as fire suppression and timber harvest have altered species composition and seral patterns affecting forest carbon storage and stability.

Manuscript received 2 October 2013; revised 26 November 2013; accepted 10 December 2013. Corresponding Editor: B. P. Wilcox.

⁴ E-mail: jmearles@ucdavis.edu

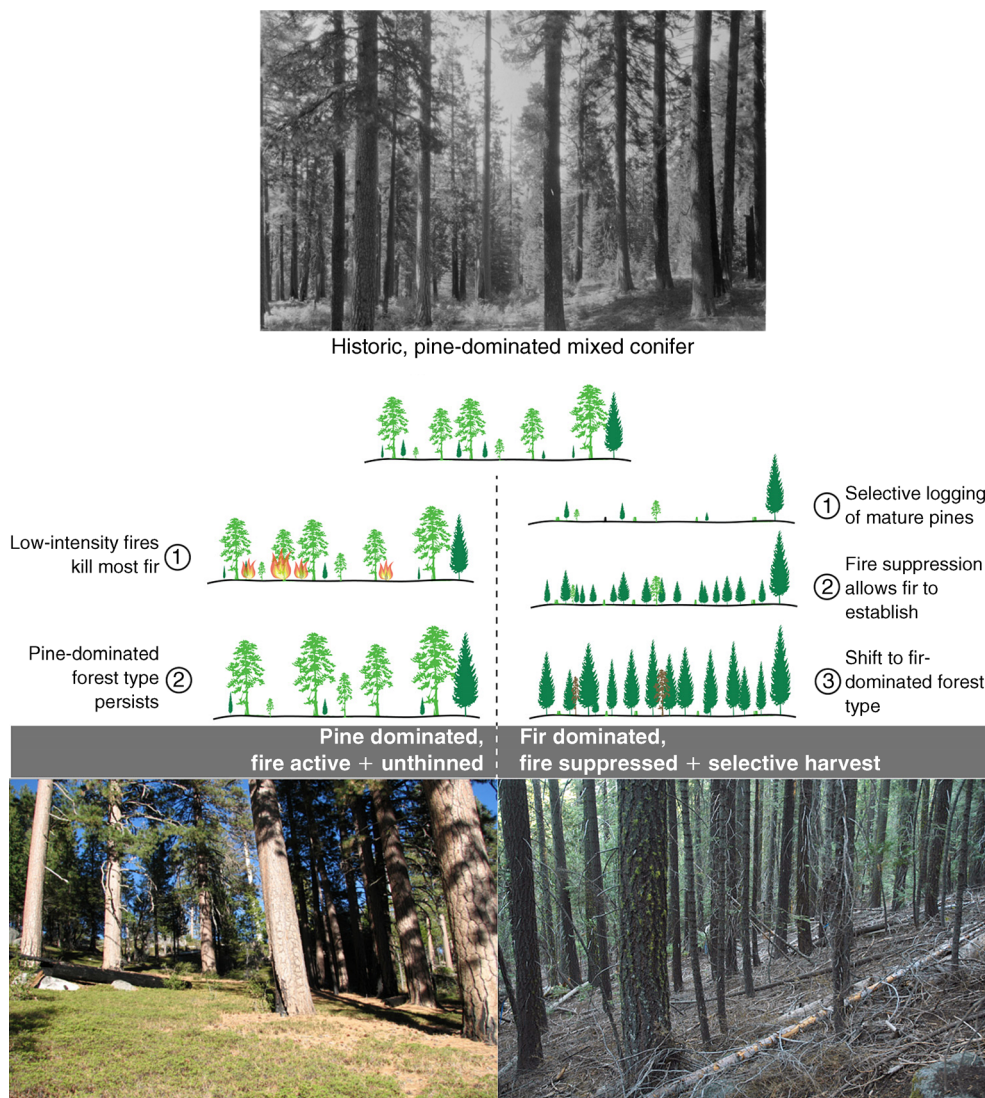


FIG. 1. Historic mixed-conifer forests and two generalized successional trajectories for contemporary forests conditions. The photos are of three mixed-conifer stands with similar site conditions (same elevation and within 50 km of each other in California, USA) in 1925 before logging (top), in 2009 following pine removal in the 1930s and fire suppression on the Sierra National Forest (lower right), and in 2009 unlogged with a restored fire regime in Yosemite National Park (lower left).

Forests that historically had frequent fire regimes (i.e., <30 years) make up 26% of temperate forests globally (Archibald et al. 2013), and within the United States, most are in an altered or degraded condition due to fire exclusion (Stephens and Ruth 2005). Following European settlement, many forests were logged of the most valuable trees (often large pines) and fires were largely eliminated across the western United States. These factors have shifted the structure and composition of many dry forests from a relatively low density of large fire-resistant species to a high density of smaller fire-sensitive species (Fig. 1), conditions that are prone to drought stress and higher fire-induced mortality. How does this altered forest succession affect carbon carrying capacity and permanence compared to historic condi-

tions that evolved with active fire regimes? How will stand conditions produced by this change respond to increased drought and fire projected by most global climate change models?

To investigate these questions, we modeled growth and mortality for historic pine-dominated (i.e., fire active) and modern fir-dominated (i.e., fire suppressed and selectively logged), mixed-conifer forest under different fire and drought frequencies. We compared carbon carrying capacity simulated over a 300-year period using stochastic fire and drought events to quantify how these disturbances interact with forest type to influence carbon dynamics. While important to ongoing climate change mitigation, currently there is little information to evaluate potential effects of

different forest management practices on C stability and carrying capacity under a range of plausible future fire and drought conditions.

MATERIALS AND METHODS

Mixed-conifer forests are widely distributed across the western United States, have been extensively impacted by timber harvest, and have both shade-intolerant/fire-resistant and shade-tolerant/fire-sensitive species that characterize many fire-dependent forests. For a model system, we used the extensively researched mixed conifer in the Sierra Nevada Mountains of California. Sierran mixed-conifer forests comprise nearly 1.7 million ha and range from 300 to 2200 m in elevation depending on latitude. As a legacy of past land use and management, these forests are dominated by white fir (*Abies concolor*) or ponderosa pine (*Pinus ponderosa*), among other species (Fites-Kaufman et al. 2007). Historically, low-intensity fire burned in these forests with a median return interval of 4–22 years (Fites-Kaufman et al. 2007, North et al. 2005), commonly creating a low-density forest dominated by large-diameter, fire-tolerant pine (Fig. 1). Fires ceased in many Sierran forests around 1880, leading to a significant increase in shade-tolerant, fire-sensitive fir regeneration, fuel loading, and continuous canopy cover. Many mixed-conifer forests were selectively logged in the 20th century, which removed the forest's overstory canopy of large pines, releasing the shade-tolerant fir that established in the absence of fire (Fig. 1).

General modeling framework

We identified Forest Inventory and Analysis (FIA) plots on the western slope of the Sierra Nevada that spanned a continuum of mixed-conifer stand conditions from low-density, pine-dominated to high-density, fir-dominated stands. We simulated growth and mortality of these stands under various drought and fire scenarios, using a modified version of the Western Sierra variant of the Forest Vegetation Simulator (FVS). FVS is an individual-tree, distance-independent growth and yield model developed and widely used by the U.S. Forest Service (Crookston and Dixon 2005). Periodic diameter and height growth increments are modeled as a function of species, stand, and site-specific variables. Competition-based mortality is driven primarily by stand density, a tree's size relative to others in the stand, and species. FVS is widely used and has been validated for a range of species across the United States (e.g., Froese and Robinson 2007, Leites et al. 2009, Hummel et al. 2013). We did not adjust future tree growth rates because of the uncertainty regarding the effect and long-term sustainability of increasing CO₂ fertilization (Luo et al. 2004, Norby et al. 2010, Peñuelas et al. 2011).

Sapling regeneration

The Western Sierra variant lacks a regeneration module in FVS, so we derived a sapling regeneration

(diameter <12.7 cm) module using FIA data stratified by forest type and location. To account for the relative scarcity of saplings in plot data, making our data zero-inflated, we utilized a two-stage modeling process. We fit a binomial model that best predicted presence/absence of saplings based on available stand variables (e.g., quadratic mean diameter, stand density index, elevation, slope, aspect, and so on). We used the Akaike information criterion (AIC) to rank the models based on the maximized likelihood of the posterior density function. Because sapling data were over-dispersed, we then fit a negative binomial model that best predicted the number of saplings based on available stand variables. Again, AIC was used for model selection, and all analyses were performed using R statistical software (R Development Core Team 2013). We determined regeneration in FVS by modeling the expected number of saplings for a species and comparing the estimate to the number present in FVS for a given year. The difference between these values was then added to the stand. The regeneration module is available upon request.

Forest condition

Simulations of 43 FIA plots across a gradient of forest conditions resulted in stands converging into either a pine- or fir-dominated structure within the first 100 years of the 300-year simulations. This is consistent with previous research suggesting mixed conifer becomes dominated by pine or fir depending on fire history and overstory composition, which serves as the seed source (Zald et al. 2008). Direct comparison of the two different compositions was confounded by individual plot differences in elevation, aspect, and productivity (as measured by site index) that affect FVS. To facilitate a more robust comparison, we selected pine- and fir-dominated stands with similar structural conditions using selection criteria based on studies that characterized conditions of unlogged, fire-active mixed-conifer forest (North et al. 2007, Collins and Stephens 2010, Taylor 2010, Lydersen and North 2012) and modern fire-suppressed forests that were selectively harvested (Table 1; Appendix: Table A1; Parsons and DeBenedetti 1979).

Fire events

We modeled stochastic fire events based on historic and modern fire frequencies. Twentieth-century Sierran fire rotations have increased from an historical range of 12–15 years to 185 and 644 years for pine- and fir-dominated stands, respectively (McKelvey et al. 1996). Given projected increases in wildfire frequency (Westerling et al. 2011), we modeled a 250-year fire frequency as a conservative estimate of future fir-dominated stands. Warming and water deficit in the western United States are driving greater wildfire activity (Westerling et al. 2006). If warming continues, the area burned in California is projected to increase 41–69% by 2085 (Westerling et al. 2011). To simulate projected wildfire

increases, we included a 50% increase in fire frequency (125 years) for fir-dominated stands. To simulate the shorter fire return interval required to maintain pine-dominated stands, we used a 40-year fire return interval. While longer than the historic interval, this frequency is realistic given current regulatory constraints on burning. We included a 25-year fire return interval to simulate proactive fire-based management.

Fire behavior and intensity were modeled using the FVS Fire and Fuels Extension. For the pine-dominated forest, we used weather conditions from two prescribed fires implemented in the vicinity of our FIA data that included variable wind speeds of 1.8–5.3 m/s, afternoon temperatures between 20°C and 28°C, and dry to very dry fuel moistures. Since only extreme fire events tend to escape suppression, we used weather records for the 1999 “Bucks” fire that burned >14 000 ha near the fir-dominated site (FRAP 2013). During the most active period, wind speeds were 6.7–11.1 m/s, afternoon temperatures were 24°–28°C, and fuel moistures were very dry. For both stands, fires were modeled as occurring in the late summer/early fall, when wildfire and prescribed fire are most likely.

Drought events

The Sierra Nevada Mountains are semiarid and characterized by frequent drought. Periods of prolonged drought (2–5 years) are correlated with increased mortality events in mixed-conifer forests (Guarín and Taylor 2005). We simulated stochastic drought events based on prolonged drought frequency, defined here as three or more years in which the Palmer Drought Severity Index (PDSI) was negative. PDSI is a relative measure of moisture stress where 0 is average precipitation, +6 is very wet, and –6 is very dry (Cook et al. 2004). We used a historical record of PDSI, calculated from a network of 835 tree ring data sets (Cook et al. 2004). Since 1960, 31 of 54 years scored negatively on the PDSI for California climate region 5, which includes much of the Sierra Nevada. Historically, prolonged drought of three or more years occurred about every 25 years. Using these records, we modeled two drought frequencies, 50 and 25 years. These data suggest a 50-year period is conservative, while a 25-year frequency may be more representative of historical conditions, but is still probably conservative given projected increases in temperature (Cayan et al. 2008).

During prolonged drought, mortality was determined by one of three drought mortality response functions (Fig. 2). We modeled species-specific percent mortality logistically as a function of the percentage of maximum stand density index (SDI). Stand density is a function of trees per hectare (TPH) and quadratic mean diameter (QMD), or

$$\text{SDI} = \text{TPH} \left(\frac{\text{QMD}}{10} \right)^{1.605}$$

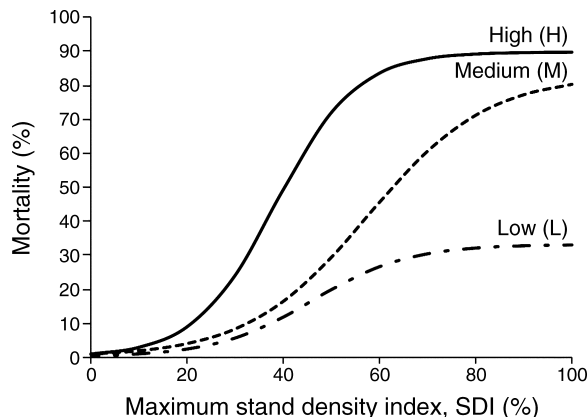


FIG. 2. Three generalized drought mortality response curves used in our Forest Vegetation Simulator (FVS) modeling. Mortality in response to decreased water potential varies by species resulting from the physiological strategy used to cope with drought. The curves vary by the rate (rise steepness) at which they approach the percentage of maximum mortality (upper asymptote).

(Reineke 1933). For a given location, FVS calculates a maximum SDI and models tree mortality as a function of the ratio of current to maximum SDI. The three drought mortality response curves vary by percent maximum mortality and the rate at which they approach this maximum. Drought-induced mortality is negatively related to soil water potential (McDowell et al. 2008), which decreases with greater water demand present at higher stand densities. Mortality driven by decreased water potential varies by species resulting from the physiological strategy used to cope with drought (McDowell et al. 2008). We chose the three drought curves to represent a range of potential mortality outcomes (see Fig. 2) because, although models have improved (McDowell et al. 2013), substantial uncertainties remain in how to best predict drought-induced mortality (McDowell et al. 2011).

Carbon calculations

Forest C estimated by FVS includes above- and belowground live- and dead-wood pools using allometric relationships between tree diameter and biomass (Jenkins et al. 2003) and understory plant C. In addition to characterizing forest C dynamics, we examine time-averaged C storage, or carbon carrying capacity (CCC) as described by Keith et al. (2009). CCC captures periodic reductions in C storage due to mortality events, like fire and drought. By comparing CCC across fire and drought scenarios, we identify the long-term capacity of a forest to store C. Since we were interested in net changes in a forest's capacity to store C, we did not estimate emissions due to decomposition and combustion. However, changes in C stock reflect such processes.

Model simulations

In total, we examined 12 scenarios for each stand condition, each with two fire frequencies, two drought frequencies, and three drought mortality responses. Scenarios were each simulated 100 times, and we examined variation in C dynamics and CCC over a 300-year period (see Appendix: Fig. A1 for mean and variance from all runs). Although we focused on stand-level response, multiple simulations and the range of responses from stochastic processes provide insight into the range of expected outcomes at a landscape scale. While drought effects are experienced at a regional scale, wildfires typically occur at scales smaller than the landscape. Our simulation results capture fire variability and its effects on carbon dynamics that would occur across a forested landscape because in any given year only a fraction of the stand-level simulations are burning. Thus, the range of carbon outcomes represents both burned and unburned conditions in any given time step.

RESULTS

Among all scenarios, fir-dominated forest had higher maximum (600 Mg/ha) and lower minimum (50 Mg/ha) C stocks than pine-dominated forest (Fig. 3). Median CCC values varied by forest type, fire frequency, drought frequency, and mortality response (see Fig. 3). Fir-dominated forest stored a higher fraction of C in dead wood compared to pine-dominated forest, where most C is in live trees, due largely to the effect of density on drought-induced mortality. This difference accounts for the much lower variance in CCC in pine-dominated forest where C storage is more stable and “permanent.”

Drought mortality response and fire/drought frequency determine CCC (Fig. 3). Holding drought frequency and response constant, CCC drops as fire becomes more frequent (Fig. 3a, b). When fir-dominated and pine-dominated forests have a fire frequency of 250 years and 40 years, respectively, a drought frequency of 50 years, and an intermediate drought mortality response, the fir-dominated forest has a higher median CCC (474 Mg C/ha) compared to the pine-dominated forest (323 Mg C/ha). Increasing fire frequency to 125 years and 25 years for fir-dominated and pine-dominated forests resulted in a median CCC of 272 Mg C/ha and 313 Mg C/ha, respectively. In fir-dominated forest, CCC variability increased with increasing fire frequency, whereas increased fire yielded minimal CCC changes in pine-dominated forest.

As drought frequency and tree mortality increases, the amount of C stored decreases (Fig. 3c–f). While mortality is relatively insensitive to drought frequency, CCC is highly sensitive to the drought mortality function. High drought mortality substantially reduces CCC for both stands (fir-dominated = 348 Mg C/ha; pine-dominated = 216 Mg C/ha).

For the fir-dominated system, CCC varied as a function of fire and drought frequency and drought

mortality response. The best case scenario (S1), with low fire and drought frequency and medium drought mortality, yielded 474 Mg C/ha (95% CI 225–573 Mg C/ha). The worst case (S2), with high fire and drought frequency and high drought mortality, yielded 236 Mg C/ha (95% CI 120–352 Mg C/ha). Both scenarios included substantial dead C (Fig. 3g). For the pine-dominated system, CCC ranged from scenario S3 at 363 Mg C/ha (95% CI 335–389 Mg C/ha) to S4 at 285 Mg C/ha⁻¹ (95% CI 257–317 Mg C/ha). Increasing fire (40 to 25 years) and drought (50 to 25 years) frequency and drought mortality response (low to medium) yielded a much smaller decrease in CCC for this fire-active condition (Fig. 3h). Consistent with previous trends, fire-active stands tend to store a higher percentage of C in live biomass.

DISCUSSION

Fire-suppressed, fir-dominated forests have higher carbon stocks under current climate and fire conditions. However, a change in any one of the factors we simulated (e.g., fire/drought frequency, drought mortality response) led to a substantial increase in carbon stock variability. When fire and drought effects were simulated simultaneously, the interaction of increasing drought and fire frequency resulted in substantial destabilization of carbon stocks and a drop in the carbon carrying capacity for the forest type (e.g., Fig. 3g). When a fire-maintained, pine-dominated forest is subjected to increasing drought or fire frequency, it has greater resistance to carbon stock changes as evidenced by a much smaller range of variability relative to the fir-dominated condition (Fig. 3).

While infrequent, high-severity fire increases C for a forest undergoing a given successional trajectory (see Campbell et al. 2012), fire suppression typically alters species composition and structural condition, changing forest response to abiotic stress. Our modeling suggests fire suppression provides fire-intolerant fir the opportunity to establish, but physiological differences and increased forest density make fir-dominated forests less drought tolerant. This shift in mixed-conifer structure and composition illustrates how fire suppression can decrease CCC and C permanence, especially if changing climate conditions increase drought stress and the risk of stand-replacing fire. This tree species shift toward shade tolerance and drought intolerance following fire suppression may be a general pattern, as shade and drought tolerance are negatively correlated for many species (Niinemets and Valladares 2006). For example, fire suppression in southeastern U.S. *Pinus palustris* forests yielded increased establishment of shade-tolerant broad-leaved species (Daubenmire 1990). Immediate research is needed in other moisture limited, fire-dependent forests to assess whether these forest's substantial carbon stores and offset potential may be destabilized by changing climate conditions.

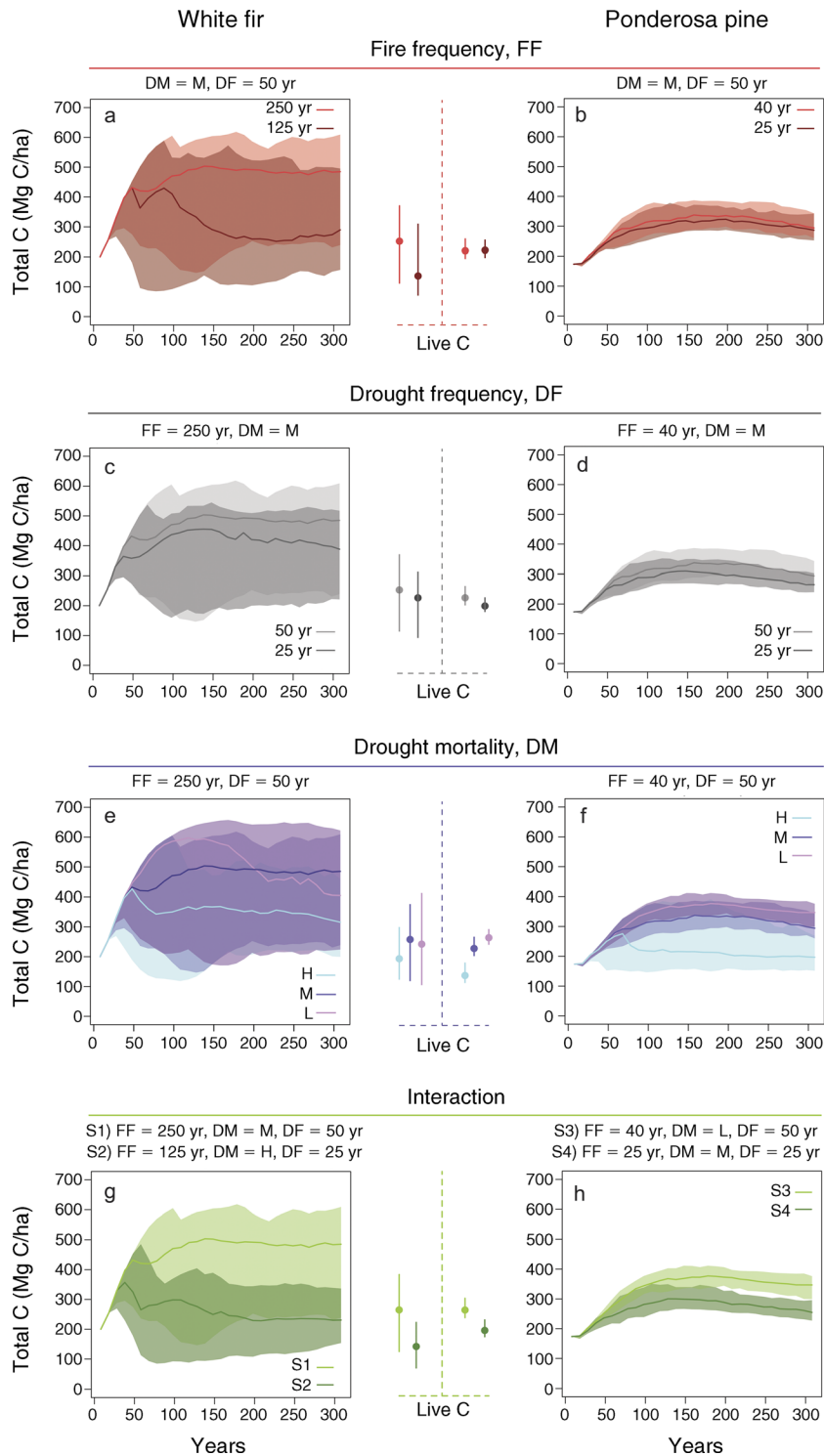


FIG. 3. Median line and 95th percentile for total (live plus dead) carbon (Mg/ha). Dot and whisker plots are the median and 95th percentile of live C only for each scenario. Panels summarize simulations when only (a and b) fire frequency (FF), (c and d) drought frequency (DF), and (e and f) drought mortality (DM) response are varied. Drought mortality is defined as: H, high mortality response curve; M, medium mortality response curve; and L, low mortality response curve (see Fig. 2). The bottom panels (g and h) summarize two combinations (scenarios 1 and 2 [S1 and S2] and scenarios 3 and 4 [S3 and S4]) of fire frequency, drought frequency, drought mortality response that may represent lower and upper bounds of likely future conditions.

Our results are built from model projections and should be interpreted cautiously. Growth and mortality rates in FVS are based upon many empirical studies that incorporate regional and site differences (Crookston and Dixon 2005). Yet these rates may change under shifting climate conditions affecting CCC estimates and altering stand development dynamics. Our use of multiple simulations, a range of drought mortality responses and variable drought and fire frequencies are an effort to bracket potential forest responses and explore how sensitive carbon stores are to changes in these parameters. Using the same model and similar site conditions allows for consistent, relative model comparisons of CCC in pine- and fir-dominated mixed conifer. Greater estimate precision, however, is difficult given current uncertainties in future abiotic conditions and how different tree species will respond.

Globally, wildfire is expected to become more frequent in temperate forests under future climate (Moritz et al. 2012), a trend observed since the mid-1980s for the western United States (Westerling et al. 2006). Continued fire suppression and the resulting species shift may lead to more frequent turnover of C stored in forests historically dependent on frequent fire. Even with moderate assumptions about drought frequency and mortality, our modeling suggests increasing fire frequency could dramatically reduce C storage in mixed-conifer forests now dominated by fir (see Fig. 3a). Fire-tolerant species like ponderosa pine, however, may buffer stored C against more frequent fire, particularly if fire actively maintains forest structure. As fire frequency increases, CCC of fir-dominated forests is substantially more uncertain than pine-dominated forests, leading to greater risks of large-scale C losses due to combined fire and drought-induced mortality.

Climate projections indicate that more prolonged and severe drought will occur in most of North America, along with many other regions globally (Dai 2011). If frequency and severity worsens, drought may exert stronger control on tree mortality; a pattern already observed in the western United States (van Mantgem et al. 2009). Based on our simulations, shifting dominance to more drought-sensitive species substantially reduces CCC in mixed-conifer forests, especially at higher drought and fire frequency (see Fig. 3c, g). Drought mortality response for mature individuals of most species is not well established at ecological or physiological scales. While drought may increase stress, mortality also depends on the presence of insects and pathogens whose success increases with tree stress (McDowell et al. 2011). Improved predictions of forest CCC in response to climate change and human impacts depend on advancement in our understanding of drought response and factors influencing insect/pathogen success.

Climate change is likely to have significant impacts on several processes we could not include in our model. In some places, forest regeneration may repeatedly fail or

undergo significant changes in species composition (Anderson-Teixeira et al. 2013, Loudermilk et al. 2013); while in other locations, changing climate may provide opportunities for forest expansion (Lenihan et al. 2008). Interactions between fire and climate have the potential to influence the postfire successional pathway and resultant vegetation type at a given location (Hurteau and Brooks 2011, Loudermilk et al. 2013). Pests and pathogens have a strong influence on tree vigor and mortality, yet models of how changing temperature and precipitation patterns may affect their population distribution and abundance are still in early stages of development (Bentz et al. 2010). Our simulations did not capture the potential complex interactions of these dynamics because we sought to isolate the effects of changes in drought and fire frequency and their interactions with species composition. Fully accounting for the range of potential outcomes from interactions of climate, disturbance, and species composition will require a diversity of approaches at different scales of investigation to improve our understanding of how these factors will influence future forest dynamics.

Management practices can fundamentally shift the forest's CCC and stability due to changes in disturbance resilience. Selective logging coupled with fire suppression allowed fir to establish dominance where fire-tolerant pine historically dominated mixed conifer. Continued suppression reinforces this altered state, perpetuating a condition that is less fire and drought tolerant (i.e., lower disturbance resilience). Fire actively maintains the dominance of a fire- and drought-tolerant species, providing a more stable and permanent C sink. In these forests, ecologically appropriate fire may benefit C stability and permanence. Efforts to manage forests as long-term C sinks need to weigh the relative resilience of different structures and compositions to likely increases in disturbance frequency and intensity under changing climate conditions.

ACKNOWLEDGMENTS

J. M. Earles received funding through the U.S. Environmental Protection Agency STAR fellowship program.

LITERATURE CITED

- Anderson-Teixeira, K. J., A. D. Miller, J. E. Mohan, T. W. Hudiburg, B. D. Duval, and E. H. Delucia. 2013. Altered dynamics of forest recovery under a changing climate. *Global Change Biology* 19:2001–2021.
- Archibald, S., C. E. R. Lehmann, J. L. Gómez-Dans, and R. A. Bradstock. 2013. Defining pyromes and global syndromes of fire regimes. *Proceedings of the National Academy of Sciences USA* 110:6442–6447.
- Bentz, B. J., J. Régnière, C. J. Fettig, E. M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. F. Negrón, and S. J. Seybold. 2010. Climate change and bark beetles of the Western United States and Canada: direct and indirect effects. *Bioscience* 60:602–613.
- Campbell, J. L., M. E. Harmon, and S. R. Mitchell. 2012. Can fuel-reduction treatments really increase forest carbon storage in the western US by reducing future fire emissions? *Frontiers in Ecology and the Environment* 10:83–90.

- Cayan, D., E. Maurer, M. Dettinger, M. Tyree, and K. Hayhoe. 2008. Climate change scenarios for the California region. *Climatic Change* 87:21–42.
- Collins, B., and S. Stephens. 2010. Stand-replacing patches within a 'mixed severity' fire regime: quantitative characterization using recent fires in a long-established natural fire area. *Landscape Ecology* 25:927–939.
- Cook, E. R., C. A. Woodhouse, C. M. Eakin, D. M. Meko, and D. W. Stahle. 2004. Long-term aridity changes in the Western United States. *Science* 306:1015–1018.
- Crookston, N. L., and G. E. Dixon. 2005. The forest vegetation simulator: a review of its structure, content, and applications. *Computers and Electronics in Agriculture* 49:60–80.
- Dai, A. 2011. Drought under global warming: a review. *Wiley Interdisciplinary Reviews: Climate Change* 2:45–65.
- Daubenmire, R. 1990. The *Magnolia grandiflora-Quercus virginiana* forest of Florida. *American Midland Naturalist* 123:331–347.
- Fites-Kaufman, J., P. Rundel, N. Stephenson, and D. Weixelman. 2007. Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges. University of California Press, Berkeley, California, USA.
- FRAP [Fire Resource and Assessment Program]. 2013. California fire perimeter data. California Department of Forestry and Fire Protection, Sacramento, California, USA.
- Froese, R. E., and A. P. Robinson. 2007. A validation and evaluation of the Prognosis individual-tree basal area increment model. *Canadian Journal of Forest Research* 37:1438–1449.
- Guarin, A., and A. H. Taylor. 2005. Drought triggered tree mortality in mixed conifer forests in Yosemite National Park, California, USA. *Forest Ecology and Management* 218:229–244.
- Hummel, S., M. Kennedy, and E. A. Steel. 2013. Assessing forest vegetation and fire simulation model performance after the Cold Springs wildfire, Washington USA. *Forest Ecology and Management* 287:40–52.
- Hurteau, M., and M. Brooks. 2011. Short- and long-term effects of fire on carbon in US dry temperate forest systems. *BioScience* 61:139–146.
- Hurteau, M. D., B. A. Hungate, G. W. Koch, M. P. North, and G. R. Smith. 2013. Aligning ecology and markets in the forest carbon cycle. *Frontiers in Ecology and the Environment* 11:37–42.
- Jenkins, J. C., D. C. Chojnacky, L. S. Heath, and R. A. Birdsey. 2003. National-scale biomass estimators for United States tree species. *Forest Science* 49:12–35.
- Keith, H., B. G. Mackey, and D. B. Lindenmayer. 2009. Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proceedings of the National Academy of Sciences USA* 106:11635–11640.
- Leites, L. P., A. P. Robinson, and N. L. Crookston. 2009. Accuracy and equivalence testing of crown ratio models and assessment of their impact on diameter growth and basal area increment predictions of two variants of the Forest Vegetation Simulator. *Canadian Journal of Forest Research* 39:655–665.
- Lenihan, J. M., D. Bachelet, R. P. Neilson, and R. Drapek. 2007. Response of vegetation distribution, ecosystem productivity, and fire to climate change scenarios for California. *Climatic Change* 87(S1):215–230.
- Loudermilk, E. L., R. M. Scheller, P. J. Weisberg, J. Yang, T. E. Dilts, S. L. Karam, and C. Skinner. 2013. Carbon dynamics in the future forest: the importance of long-term successional legacy and climate–fire interactions. *Global Change Biology* 19:3502–3515.
- Luo, Y., et al. 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *Bioscience* 54:731–739.
- Lydersen, J., and M. North. 2012. Topographic variation in structure of mixed-conifer forests under an active-fire regime. *Ecosystems* 15:1134–1146.
- McDowell, N. G., D. J. Beerling, D. D. Breshears, R. A. Fisher, K. F. Raffa, and M. Stitt. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology and Evolution* 26:523–532.
- McDowell, N., R. Fisher, and C. Xu. 2013. Evaluating theories of drought-induced vegetation mortality using a multimodel-experiment framework. *New Phytologist* 200:304–321.
- McDowell, N., et al. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist* 178:719–739.
- McKelvey, K. S., C. N. Skinner, C. Chang, D. C. Erman, S. J. Husari, D. J. Parsons, J. W. van Wagendonk, and C. P. Weatherspoon. 1996. An overview of fire in the Sierra Nevada. Pages 1033–1040 in D. C. Erman and the SNEP Team, editors. *Sierra Nevada Ecosystem Project: Final report to Congress, volume II*. University of California, Davis, California, USA.
- Moritz, M. A., M.-A. Parisien, E. Batllori, M. A. Krawchuk, J. Van Dorn, D. J. Ganz, and K. Hayhoe. 2012. Climate change and disruptions to global fire activity. *Ecosphere* 3:art49.
- Niinemets, Ü., and F. Valladares. 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecological Monographs* 76:521–547.
- Norby, R. J., J. M. Warren, C. M. Iversen, B. E. Medlyn, and R. E. Mcmurtrie. 2010. CO₂ enhancement of forest productivity constrained by limited nitrogen availability. *Proceedings of the National Academy of Sciences USA* 107:19368–19373.
- North, M. P., and M. D. Hurteau. 2011. High-severity wildfire effects on carbon stocks and emissions in fuels treated and untreated forest. *Forest Ecology and Management* 261:1115–1120.
- North, M., M. Hurteau, R. Fiegner, and M. Barbour. 2005. Influence of fire and El Nino on tree recruitment varies by species in Sierran mixed conifer. *Forest Science* 51:187–197.
- North, M., J. Innes, and H. Zald. 2007. Comparison of thinning and prescribed fire restoration treatments to Sierran mixed-conifer historic conditions. *Canadian Journal of Forest Research* 37:331–342.
- Pan, Y., et al. 2011. A large and persistent carbon sink in the world's forests. *Science* 333:988–993.
- Parsons, D. J., and S. H. DeBenedetti. 1979. Impact of fire suppression on a mixed-conifer forest. *Forest Ecology and Management* 2:21–33.
- Peñuelas, J., J. G. Canadell, and R. Ogaya. 2011. Increased water-use efficiency during the 20th century did not translate into enhanced tree growth. *Global Ecology and Biogeography* 20:597–608.
- R Development Core Team. 2013. R: a language and environment for statistical computing. Version 3.0.2. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Reineke, L. H. 1933. Perfecting a stand-density index for even-aged forests. *Journal of Agricultural Research* 46:627–638.
- Schwalm, C. R., C. A. Williams, K. Schaefer, D. Baldocchi, T. A. Black, A. H. Goldstein, B. E. Law, W. C. Oechel, U. K. T. Paw, and R. L. Scott. 2012. Reduction in carbon uptake during turn of the century drought in western North America. *Nature Geoscience* 5:551–556.
- Stephens, S. L., and L. W. Ruth. 2005. Federal forest-fire policy in the United States. *Ecological Applications* 15:532–542.

- Taylor, A. H. 2010. Fire disturbance and forest structure in an old-growth *Pinus ponderosa* forest, southern Cascades, USA. *Journal of Vegetation Science* 21:561–572.
- van Mantgem, P. J., J. C. B. Nesmith, M. Keifer, E. E. Knapp, A. Flint, and L. Flint. 2013. Climatic stress increases forest fire severity across the western United States. *Ecology Letters* 16:1151–1156.
- van Mantgem, P. J., et al. 2009. Widespread increase of tree mortality rates in the western United States. *Science* 323:521–524.
- Westerling, A. L., B. P. Bryant, H. K. Preisler, T. P. Holmes, H. G. Hidalgo, T. Das, and S. R. Shrestha. 2011. Climate change and growth scenarios for California wildfire. *Climatic Change* 109:445–463.
- Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science* 313:940–943.
- Zald, H. S. J., A. N. Gray, M. North, and R. A. Kern. 2008. Initial tree regeneration responses to fire and thinning treatments in a Sierra Nevada mixed-conifer forest, USA. *Forest Ecology and Management* 256:168–179.

SUPPLEMENTAL MATERIAL

Appendix

A table depicting stand characteristics of modeled mixed-conifer conditions and a figure showing carbon carrying capacity for 24 scenarios examined ([Ecological Archives A024-043-A1](#)).