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Ponderosa pine hydraulic stress predicts more extreme wildfire behavior under future conditions in Bandelier National Monument, New Mexico

Zachary Robbins^{1*} , Westin Guthrie¹, Adam Killebrew¹, Luz Salinas¹, Ashley M. Matheny², Suvan Cabraal², Maria Ulatowski², Laura Trader³, Adam Atchley¹, Rod Linn¹, Chonggang Xu¹, Julia Oliveto¹ and L. Turin Dickman¹

Abstract

Background Live fuel moisture contributes to wildfire spread and reflects plant stress and physiological traits. The anticipated change in live fuel moisture under future conditions is likely non-linear, owing to physiological plant thresholds in water hydraulics. We constructed a mechanistic model of live fuel moisture's response to water stress to understand the impact of future climate on live fuel moisture. We first gathered data on plant physiology and live fuel moisture for *Pinus ponderosa* at Bandelier National Monument, NM, USA, and modeled their relationship. We then parameterized a mechanistic plant hydrodynamics model (FATES-HYDRO) to simulate changes in plant stress and a statistical model to simulate the resulting impact on live fuel moisture. We then simulated FATES-HYDRO under future climate anomalies (SSP2-4.5 and SSP5-8.5: 2080–2100) to understand the change in plant stress and estimate its impact on live fuel moisture.

Results We found that the number of days below crucial thresholds of live fuel moisture (100% and 79%) increased from contemporary levels (< 100%: 72 days, < 79%: 1.4 days) under SSP2-4.5 (< 100%: 185 days, < 79%: 10.2 day) and increased exponentially under SSP5-8.5 (< 100%: 215 days, < 79%: 65 days). We found that gross primary productivity decreased under both future climate scenarios (contemporary: 336 g C m⁻², SSP2-4.5: 203 g C m⁻², SSP5-8.5: 243 g C m⁻²); however, spring productivity increased under SSP5-8.5, potentially altering fuel loading. We additionally see a potentially lethal loss of conductivity in hydraulic *P. ponderosa* under SSP5-8.5.

Conclusions The overall increase in plant water stress (as represented by loss of hydraulic conductivity and leaf water potential) and lower live fuel moisture appear to be driven by reduced precipitation during late summer monsoons typical of the region, extending the fire season later in the year. We predict increasing variability in the *P. ponderosa* wildfire regime under both climate projections driven by changing productivity, rising mortality, and an overall decrease in live fuel moisture.

Keywords Live fuel moisture, Plant physiology, Ponderosa pine, Bandelier National Monument

*Correspondence:

Zachary Robbins
zjrobbins@lanl.gov

Full list of author information is available at the end of the article

Resumen

Antecedentes La humedad del combustible vivo contribuye a la propagación de los incendios y refleja el estrés de las plantas y sus características fisiológicas. El cambio anticipado en el contenido de humedad bajo condiciones futuras es probablemente no lineal, debido a los límites fisiológicos de las plantas en la hidráulica del agua. Construimos un modelo mecanístico del contenido de humedad del combustible vivo en respuesta al estrés hídrico, para entender el impacto del clima futuro en la humedad del combustible vivo. Primeramente tomamos datos sobre la fisiología de las plantas y sobre la humedad del combustible vivo de pino ponderosa en el Monumento Nacional de Bandelier en Nuevo México, EEUU, y modelamos sus relaciones. Luego parametrizamos un modelo mecanístico de la hidrodinámica de las plantas (FATES-HYDRO), para simular cambios en el estrés de las plantas y en el contenido de humedad del combustible vivo. Simulamos luego FATES-HYDRO bajo las anomalías de cambio climático a futuro (SSP2-4.5 y SSP5-8.5: 2080-2100) para entender los cambios en el estrés de las plantas y estimar el impacto en sobre el contenido de humedad del combustible vivo.

Resultados Encontramos que el número de días por debajo de los límites cruciales de humedad del combustible vivo (100% y 79%) se incrementaron desde valores contemporáneos (< 100%: 72 días, < 79%: 1.4 días), bajo el SSP2-4.5 (< 100%: 185 días, < 79%: 10.2 días), y se incrementaron exponencialmente bajo el SSP5-8.5 (< 100%: 215 días, < 79%: 65 días). Encontramos que la productividad primaria total decrecía bajo los dos futuros escenarios climáticos (contemporáneo: 336 g C m⁻²; 203 g C m⁻² en SSP2-4.5, y 243 g C m⁻² en SSP5-8.5). Sin embargo, la productividad primaveral se incrementaba bajo el escenario SSP5-8.5, alterando potencialmente la carga de combustible. Vimos adicionalmente una potencialidad letal de la conductividad hidráulica de pino ponderosa bajo el escenario SSP5-8.5.

Conclusiones El aumento generalizado del estrés hídrico en plantas (representado por una pérdida en la conductividad hidráulica y en el potencial agua de las hojas) y una menor humedad del combustible vivo, parece ser conducido debido a la reducción en la precipitación por los monzones típicos durante el verano tardío en la región, extendiendo la estación de incendios por más tiempo en el año. Predicimos una variabilidad incremental en el régimen de incendios de pino ponderosa bajo ambas proyecciones de cambio climático, motivados por cambios en la productividad, el incremento en la mortalidad, y un generalizado decremento en la humedad del combustible vivo.

Background

Future climate presents a unique challenge to the prediction of wildfire behavior, as fuel (the combustible material in wildfire) and its characteristics (e.g., flammability) are a product of complex interactions between plant demographics, plant physiology, and environmental conditions (Littell et al. 2016; Higuera et al. 2015). Warming, drought, and increased CO₂ levels may all have independent effects on plant physiology and can result in different vegetative assemblages, both of which affect fuel quantity and moisture (Swann et al. 2023; Flannigan et al. 2016; Abatzaglou et al., 2018). The impact of a future climate on fire risk may also depend on precipitation timing and amount (King et al. 2013; Westerling et al., 2006). For example, greater rainfall before the fire season and increased warming could contribute to a greater accumulation of fuel that can ultimately increase fire spread (Dennison & Moritz 2009). Meanwhile, warming could also cause earlier snowmelt and increase water deficits, causing fuels to dry more readily and decreasing fuel moistures during fire season (Westerling 2016).

Live fuel moisture content (LFMC) is the amount of water in living plant tissues (i.e., the ratio of removable water compared to dry weight) and is crucial to the

prediction of climate impacts on fire regimes. Higher LFMC typically corresponds to lower flammability due to the energy required to evaporate the moisture before biomass can reach combustion temperatures (Rossa et al., 2016). LFMC has been shown to be a key predictor of fire spread and ignition, contributing exponentially to fire spread both in field and laboratory settings in fuel beds with large live fuel fractions (Dennison & Moritz 2009; Rossa et al., 2016; Chuvieco et al. 2009). Traits related to water acquisition, storage, and use within plants (i.e., minimum and predawn leaf water potential (LWP), and cuticular conductance, the water loss when stomata are closed) have been shown to correlate with LFMC in terminal shoots in semi-arid plants (Pivovarov et al. 2019). Differences in rooting depth and xylem architecture can also influence plant water storage and LFMC (Agee et al. 2021). Thus, various species with unique drought adaptations and hydraulic strategies may have varied LFMC responses to climate, resulting in varied LFMC under the same meteorological conditions (Pivovarov et al. 2019; Matheny et al. 2017). Traditional fire risk indices are calculated through empirical relationships derived exclusively from weather and seasonal timing (cFWI: Van Wagner, (1974); GSI: Jolly et al. 2005); while these have

been used to estimate the change in future fire risk, they do so without considering the crucial thresholds that plants may cross (Bobribb and Holbrook et al., 2003; Nolan et al., (2020). Key to predicting fire behavior is an understanding of how the plant carbon and water cycles alter fuel availability (live or dead vegetation available to burn) under non-analog climate conditions (Jolly and Johnson 2018; Dickman et al. (2023).

The temporal response of plants to weather, soil conditions, and the resulting soil water availability is non-linear owing to plant physiological response. Plant traits can determine when plants close their stomata, how they draw down water from their leaves, and their thresholds for mortality (McDowell et al. 2008a, b). Plants respond non-linearly to changes in precipitation, temperature, and vapor pressure deficit (VPD) from the atmosphere, increasing transpiration but also by closing their stomata, limiting transpiration (Grossiord et al. 2020; Novick et al. 2024). Further, an increase in drought stress results in greater plant mortality which can lower overall fuel moisture both in the short and long term (Ruffault, et al. 2022).

Due to the complex interactions between future climate and plant physiology, we need mechanistic models of plant physiology to capture changes in LFMC and predict the impact of future conditions on fire spread. The use of mechanistic models can provide methods by which to project LFMC while accounting for species-specific responses to soil water deficits (Cakpo et al. 2024, Ruffault et al., 2023; Ma et al., (2020), warming temperature, and increases in atmospheric CO₂ levels (Balaguer Romano et al., 2023). The addition of species-specific traits is crucial as they control water maintenance and thus the water content and necrosis of live fuels (creating dead fuels; Ruffault et al., 2023).

To understand one driver of future fire behavior under future conditions, we collected data on the change in LFMC as a function of physiological conditions and then simulated how LFMC would change under future climate. Throughout one growing season (March–October 2023), we examined *Pinus ponderosa* forests in Bandelier National Monument. *P. ponderosa* is a useful indicator species as it is widespread throughout the Rocky Mountains, ranging from Montana to northern Mexico and east to Texas (Oliver et al., 1990), with sub-species found throughout the Eastern Cascades of Washington, Oregon, California, and British Columbia. *P. ponderosa* is classified as being fire dependent due to being light intolerant (Arno et al. 1995) and as fire adapted with thick bark, self-pruning limbs, and an expected 5–20-year fire return interval. *P. ponderosa* is an isohydric species (McDowell et al. 2008a, b), which maintains relatively constant minimum LWP by reducing

stomatal conductance under elevated temperature and drought conditions to minimize water loss. This strategy is thought to reduce the risk of hydraulic failure, though more recent work suggests that stomatal behavior may not be a reliable indicator of embolism resistance (Garcia-Forner et al. 2016). *P. ponderosa* is also thought to demonstrate enhanced capacity for water storage (Carnwath et al. 2012; Stout and Sala (2003) and has been shown to use hydraulic redistribution to move water from lower to upper soil layers under drought (Warren & Meinzer, 2006), further limiting its exposure to hydraulic failure. However, cuticular conductance (Kerstiens 1996, Running, (1976) and leaky roots (as evidenced through hydraulic redistribution; Caldwell et al. (1998) may contribute to increased water stress following stomatal closure. Generally, the growing season predawn LWP is between −0.5 and −2.0 MPa (O'Hara and O'Hara, (2002). Assimilation and stomatal conductance are typically higher during the early part of the growing season and diminish in the later growing season (Grulke and Rezlaff, 2001). Average water-use efficiency in *P. ponderosa* forests is between 4.4 and 4.7 mmol CO₂ per mol H₂O (O'Hara and O'Hara, 2002).

LFMC samples were collected monthly, along with plant physiological parameters that are indicators of change in LFMC (minimum and predawn LWP and stomatal conductance (G_s)). We used this data to constrain the parameters of a plant hydrodynamic model, FATES-HYDRO (Xu et al. 2023). We then modeled the plant physiology of *P. ponderosa* under two future climate scenarios (shared socioeconomic pathway: SSP2-4.5 and SSP5-8.5; years 2080–2100) to understand how future plant stress will be altered and the subsequent impact on LFMC.

Methods

Field site and sampling

Data was collected at Bandelier National Monument in Northern New Mexico, USA (Fig. 1). The study was performed on four plots selected near long-term Bandelier Fire Ecology plots (Walker et al. 2018). Historically, fire regimes in the southern Rockies and New Mexico typically occur early in the growing season, after snowmelt and prior to the summer monsoons (July to August, Touchan et al., 1996). Lightning ignitions peak in June and July, with 72% of burned area in New Mexico corresponding to the June lightning ignitions (Touchan et al., 1996). Large wildfire seasons often require correct climatic sequencing, with a prior wet year providing sufficient fuel and subsequent dry conditions leading to fire spread (Margolis et al. 2017, 2017a). Monsoon-season drought during the fire year is significantly associated with large late-season fire occurrence (Margolis et al. 2017, 2017a).

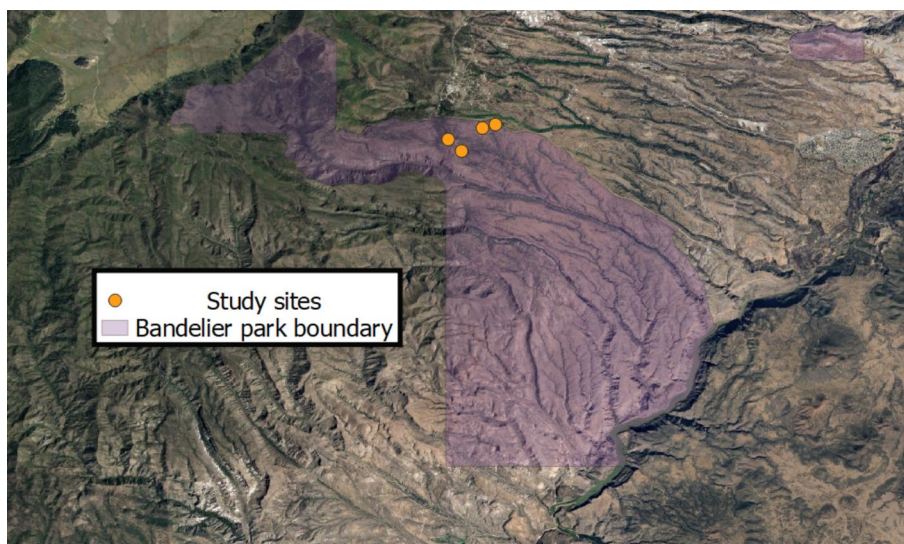


Fig. 1 Study sites in Bandelier National Monument, NM, USA

Within each of the four plots, we selected four *P. ponderosa* trees for intensive measurement. Samples of LWP, G_s , and LFMC measurements were retrieved from the canopies of mature *P. ponderosa* trees five times over the course of the 2023 growing season. Predawn samples were collected before civil twilight (4:00–7:00 MDT) and midday samples were collected within approximately 1 h of maximum diurnal temperature (11:00–14:00 MDT). We used a Big Shot arbor slingshot (Notch Equipment, Greensboro, NC, USA) to collect samples. Sampling was targeted toward the mid-canopy to provide an intermediate measure between lower LMA bottom-canopy leaves and higher LMA upper-canopy leaves. A rope saw was used to harvest a sun-exposed (at midday), south-facing branch, and two terminal shoot samples were collected immediately or after G_s measurement (LI-600 Porometer/Fluorometer, LI-COR Environmental, Lincoln, NE, USA) and placed in zip-top cooler bags to prevent moisture loss prior to LWP and LFMC measurement. Samples were transported to the lab for LWP measurement with a Scholander-type pressure chamber (Kaufmann, Merrill & Thor 1982; pressure chamber Model 1005, PMS Instrument Company, Albany, OR, USA) within 2 hours of sampling. Following midday LWP measurement, ~20 g of needles were weighed and dried in an oven at 65 °C to weight constancy and then reweighed (Stonex et al., 2004; Zahn and Henson 2011). We obtained LFMC percentage using Eq. 1.

Fuel moisture modeling

Using field measurements, a statistical model of LFMC was fit to represent the change in *P. ponderosa* LFMC as a function of measured physiology. The statistical model was fit using a general linear model of the predawn and midday LWP and the midday G_s . Analysis was conducted using AIC, RMSE, and R^2 comparison within the sklearn (Virtanen et al., 2020) and the statistical models packages in Python 3.11 to select the most parsimonious and predictive model with the lowest error (Table S.4).

The FATES-HYDRO model is a hydrodynamic sub-model with the E3SM-FATES model to simulate the relationship between water content and water potential (a continuous porous media approach) between four tissue types within plants (absorbing roots, transporting roots, stem, and branches). It uses this relationship to simulate the relationship between water potentials, hydraulic conductivity, and stomatal conductance. It scales these calculations to the whole tree by accounting for the branching structure and height to tissue. It further allows for direct comparison to common measurements of LWP and stomatal closure. The water potentials for specific tissues are calculated from relative water content based on three stages of water tissue drainage. Stage one represents the water drawn from capillary reserves when the tissue is at or above full turgor. The second stage represents the stage between full turgor and the turgor loss point when the total water

$$\text{LFMC} = 100 * \frac{\text{Water Mass}}{\text{Dry Mass}} = 100 * \frac{\text{Initial needle weight} - \text{Dried needle weight}}{\text{Dried needle weight}} \quad (1)$$

potential is a function of the solute and pressure water potential (elastic cell drainage). The third stage is after the turgor loss point but above the point of residual water content, where the water potential is only a function of the solute water potential. Stomatal reduction is based on a Ball Berry model which includes LWP, base cuticular conductance, CO_2 levels, and atmospheric pressure at the leaf surface which act to adjust the photosynthetic rate within the FATES model and has been shown to be the most appropriate stomatal model for use in *P. ponderosa* (Misson et al. 2004). FATES-HYDRO additionally accounts for root water loss under prolonged drought conditions. For equations used to govern these processes, please see Christoffersen et al. (2016) and Xu et al. (2023).

The FATES-HYDRO model has more model parameters than could be directly measured in this study (Xu et al. 2023); we instead use measurements to filter the total trait space. In this process, we start with a range of observable traits from observational studies that are fit to statistical distributions. From these distributions, we draw a large number of feasible trait combinations (in this case 1000 simulations). These are then compared to site-specific data gathered for the study. Models that best represent the observations (in this case the top 1% of models as assessed by normalized root mean square error) are selected for hypothesis testing.

The FATES-HYDRO was initialized for Bandelier sites using temperature ($^{\circ}\text{C}$), precipitation (mm), relative humidity (%), and solar radiation from ERA5 (2010–2024; Hersbach et al., (2020)). The soil texture was initialized using the USGS soil survey (Soil Survey Staff, 2023) using % sand (0–100 cm), % clay (0–100 cm), organic matter (0–100 cm), and runoff coefficients (stand level). Stand densities (number of trees per meter at various diameters) for the area were determined from the USFS Forest Inventory and Analysis program beginning in 2010 (Gray et al., 2012).

Initial *P. ponderosa* parameter ranges were gathered through the TRY database (Kattge et al., 2020); these include leaf water content apoplastic fraction, leaf elastic modulus, osmotic potential at full turgor, xylem water potential at which 50% of conductivity is lost (P_{50}), vulnerability shape, photosynthesis carboxylation capacity per leaf area at 25 $^{\circ}\text{C}$ ($V_{c_{\max}}$; Farquhar model), stem specific density, and maximum hydraulic conductance ($K_{\max}$). Additional values were found through literature review: in this case, the water potential at which 50% of stomatal closure occurs ($p_{50_{gs}}$). We got initial ranges of fraction of water in capillary reserve, xylem taper exponent for sapwood, and specific leaf area from prior FATES-HYDRO sensitivity analyses (Xu et al. 2023). Turgor loss point is constructed within the exercise as the

product of the osmotic potential at full turgor and the bulk elastic modulus per Xu et al. (2023). See Table S.1 for explanation and Fig. S.1 for ranges tested and values selected. These parameter distributions were then sampled to construct 1000 parameter sets.

Each parameter set was run in FATES-HYDRO 2010–2024 and compared to observations from 2023–2024. These observations include field data (LWP and G_s), as well as remotely sensed measurements of gross primary productivity (GPP: MOD17AH2; Zhao et al. 2011) and soil moisture (ERA5; Hersbach et al., (2020)). These were then compared with the observational data for G_s , predawn and midday LWP, ERA5 soil moisture, and GPP. Some model bias exists for seasonal changes in productivity and LWP. We used total normalized RMSE used as a loss function to equally weight the leaf measured observations (LWP, G_s , GPP) with overall ecosystem water use (soil water balances). The top 1% of models were selected as a representative trait ensemble for future simulation based on total normalized RMSE.

Given that there are uncertainties in model parameterization from existing databases, we used this trait filtering approach to select trait combinations that are consistent with observed GPP, leaf water potential, and soil moisture. Given the limited observations, we do acknowledge that these combinations may not represent the “true” trait combinations; however, we believe these are all plausible combinations given the observed constraints and acknowledge this as a source of uncertainty in our representation of traits in the model system.

Climate modeling

To simulate future plant stress, we constructed temperature, precipitation, and relative humidity anomalies using CMIP6 model runs (Masson-Delmotte et al. 2021), from select models (ACCESS-CM2, GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, UKESM1-0-LL), under SSP2-4.5 and SSP5-8.5. These models were selected as they approximately span (2–5 $^{\circ}\text{C}$) the very likely range of equilibrium climate sensitivities (ECS, see Supplementary Table S2), represented in the 2021 IPCC report (2021 IPCC). For each model and scenario, the mean difference in weekly precipitation, temperature, and relative humidity between 1986–2006 and 2080–2100 were calculated. These anomalies were then applied to the initial contemporary climate driver used in calibrating the model, which was then rerun for each of the trait ensembles selected for the years 2010–2024. CO_2 concentrations under contemporary climate were set to 367 ppm, while SSP2-4.5 and SSP5-8.5 were projected with CO_2 concentrations at 603 and 1059 ppm, respectively.

Data analysis

Simulations were then analyzed for change in LWP, Gs, GPP, and percentage loss of hydraulic conductivity (PLC) for the years 2014–2024 to allow for model spin-up. These analyses were used to infer changes in LFMC based on the statistical model. We analyzed the number of days under critical fire spread LFMC thresholds of 100% (likely to burn: Jolly (2007) and 79% (rapid fire spread: Dennison & Moritz 2009), along with changes in GPP, and risk of hydraulic failure ($PLC > 60\%$: Adams et al. 2017 and $PLC > 88\%$: Choat et al., (2012) and thus mortality. Using the stand level productivity and water loss outputs from FATES-HYDRO, we additionally calculated the water-use efficiency (mmol carbon/mol water; Briggs and Shantz, 1913) for each scenario to understand the relative contribution of rising CO_2 levels in concert with altered temperature and precipitation. The growing season for analysis was defined as the months in which 80% of modeled GPP occurs (March–October).

Results

LFMC model fitting

Our statistical model of *P. ponderosa* LFMC was fit using AIC as an inverse Gaussian function (Wald function: $LFMC \sim (\mu, \lambda)$, where μ is a function of predawn LWP (LWP_{pd} , MPa), midday LWP (LWP_{md} , MPa), and Gs ($mol\ H_2O\ m^{-2}\ s^{-1}$; Table S.3) and showed general agreement with observations ($R^2 = 0.31$; Fig. 2), comparable to previous models of LFMC (Nolan et al., 2020). None of

the predictive variables shows strong correlation among them (Fig. S.3). The final model had an MAE of 7.03% and a RMSE of 9.13%. Mean residual is +0.21%, indicating very little overall model bias toward underprediction (Fig. S.3, Table S.4). Given the limited data we collected for this study, we chose to fit the model with all data points. To understand prediction outside of training, we did a bootstrap analysis where 30% of the data is withheld from the fitting process and tested against a model fit with the remainder. This was iterated with partitions equal to the number of observations ($n = 38$). The average R^2 for the models fit using this process was 0.316.

FATES-HYDRO model fitting

We selected the top 1% FATES-HYDRO trait ensembles (Table S.2) for future simulations based on the minimum sum of normalized RMSE for monthly GPP, predawn and midday LWP, midday G_s , and soil water content at three layers (0–7 cm, 7–28 cm, 28–100 cm; Fig. 3, Fig. S.1). Mean RMSE were $90.52\ g\ C\ m^{-2}\ month^{-1}$ for GPP, 0.71 MPa for predawn LWP, 0.41 MPa for midday LWP, $0.078\ mol\ H_2O\ m^{-2}\ s^{-1}$ for midday G_s , 0.06 m/m for 0–7 cm soil water, 0.04 m/m for 7–28 cm soil water, and 0.03 m/m for 28–100 cm soil water (Fig. 3).

Future climate projections

The CMIP6 climate projections for Bandelier National Monument indicate rising VPD, temperature, and a reduction in precipitation (Fig. 4, Table S.5). The

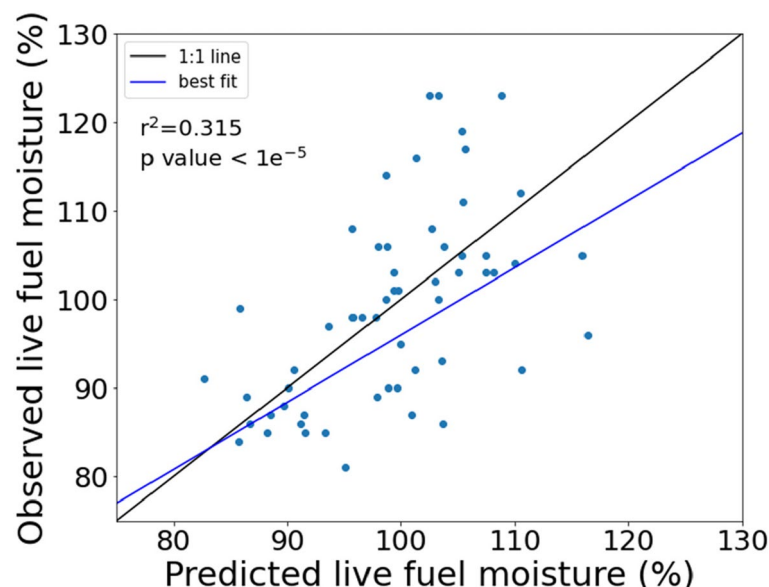


Fig. 2 Live fuel moisture content (LFMC) model output compared to field observed LFMC measurements for *P. ponderosa* in Bandelier National Monument using a linear statistical model fit (blue line) from predawn LWP (MPa), midday LWP (MPa), and stomatal conductance ($mol\ H_2O\ m^{-2}\ s^{-1}$). Black line represents the one-to-one line between observations and predictions

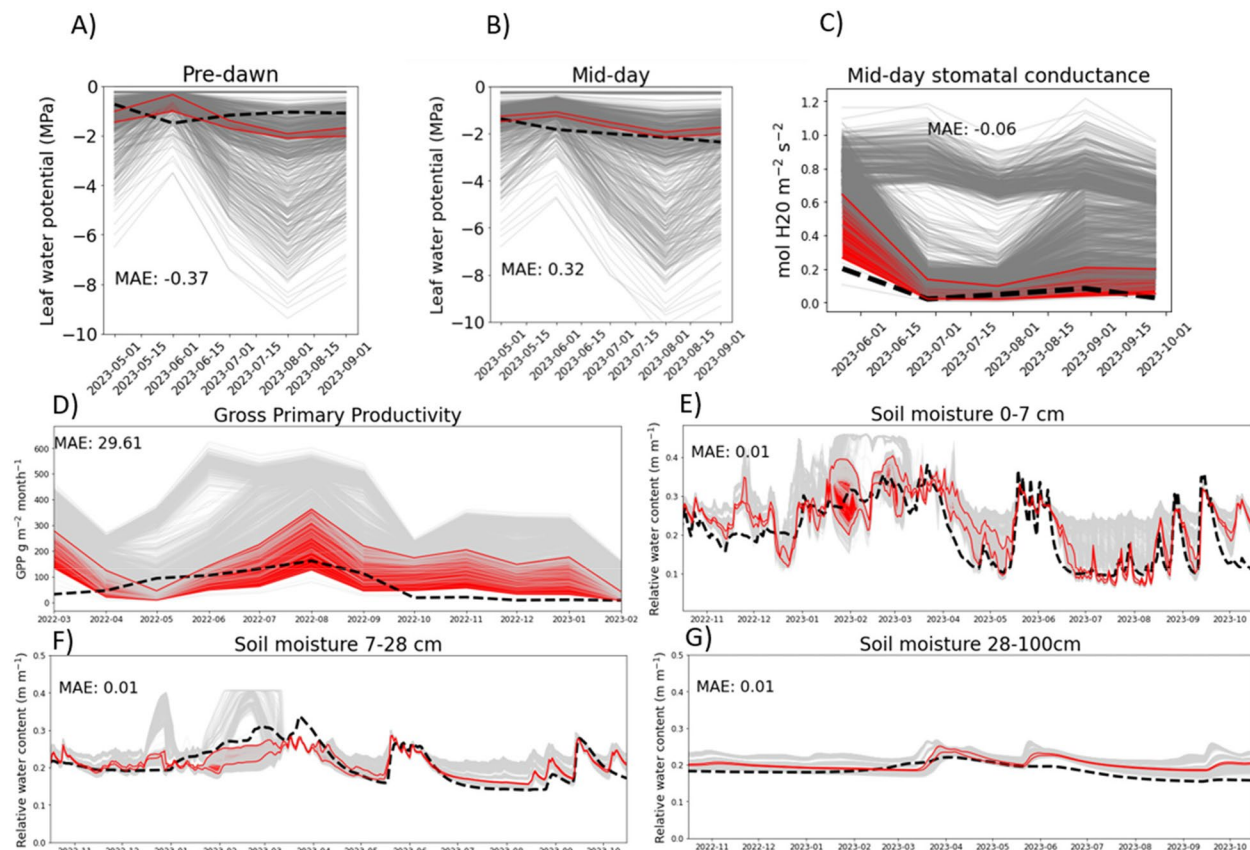


Fig. 3 Model (solid lines) and observation (dashed line) comparison for FATES-HYDRO at Bandelier National Monument 2023: **A** predawn leaf water potential (MPa), **B** midday leaf water potential (MPa), **C** midday stomatal conductance ($\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$), **D** gross primary productivity ($\text{g C m}^{-2} \text{month}^{-1}$), **E** soil water potential 0–7 cm (m m^{-1}), **F** soil water potential 7–28 cm (m m^{-1}), **G** soil water potential 28–100 cm (m m^{-1}). All model runs are shown in light gray, observations are shown in dotted black lines, and selected trait ensembles are denoted in red

mean temperature increased ~ 2.1 °C under SSP2-4.5 and ~ 4.1 °C under SSP5-8.5. The mean VPD increased 15.3% under SSP2-4.5 and 33.4% under SSP5-8.5. Precipitation decreased by 42.6% (395 mm a year) under SSP2-4.5 and by 47% (430 mm per year) under SSP5-8.5. Temperature change appears uniform throughout the year; however, the biggest change in VPD occurs during the summer months, which is also when precipitation decrease is the greatest.

Anticipated change in live fuel moisture

The contemporary climate simulations (2014–2024) have higher LFM in all parts of the year, suggesting drier future live fuels under both future climate scenario simulations. Mean monthly LFM of *P. ponderosa* ranged from 97 to 223% under contemporary climate simulations, 79 to 220% under SSP2-4.5, and 74 to 228% under SSP5-8.5 (Fig. 5). Under contemporary climate, 1.4% of the simulated days (averaging 5 per year) were spent under the critical threshold of 79% LFM, while 19.8% of days (72 per year) were below the threshold of 100%

LFMC (Table 1; Fig. 6). In the SSP2-4.5 climate scenario, *P. ponderosa* spent 10.2% of days (37 per year) below the 79% threshold and 42% of days (185 per year) below the 100% threshold. In the SSP5-8.5 climate projections, *P. ponderosa* saw 17.8% of simulated days (65 per year) under 79% LFM and 58.6% of days (215 per year) under 100% LFM.

Future plant stress projections

Much of the change in live fuel moisture in our simulations is driven by increased plant water stress as seen in the decline in midday LWP (Fig. 7). *P. ponderosa* in the contemporary climate scenario had a minimum LWP of -3.41 MPa across 10 years. Under the SSP2-4.5 climate simulation, *P. ponderosa* has a minimum LWP of -3.51 MPa. In comparing 2023, under the contemporary climate, only 1 month had monthly mean midday LWP < -2.0 MPa (August) while SSP2-4.5 had 4 months (February and July–September) and SSP5-8.5 had 6 months (January and July–December). We further see lower levels of G_s in both future scenarios,

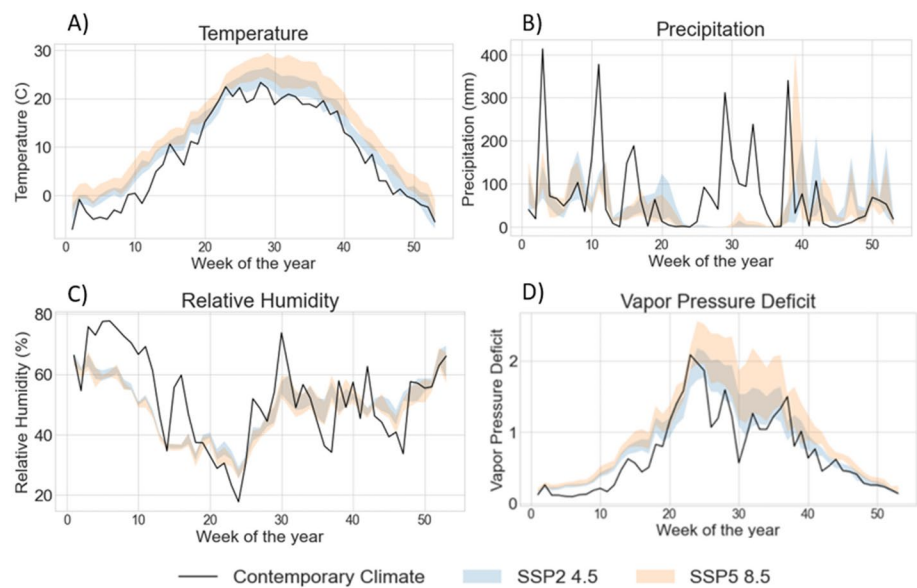


Fig. 4 Comparison of weekly climate at Bandelier National Monument under contemporary conditions (black line) and with SSP2-4.5 (blue) and SSP5-8.5 (orange) CMIP6 (Masson-Delmotte et al. 2021) climate anomalies: **A** temperature (°C), **B** precipitation (mm), **C** relative humidity (%), and **D** VPD (kPa). Bands on SSP2-4.5 and SSP5-8.5 represent the range of climate models evaluated. SSP2-4.5 and SSP5-8.5 climate simulations represent end of century anomaly projections (CMIP6) overlaid upon our contemporary climate drivers

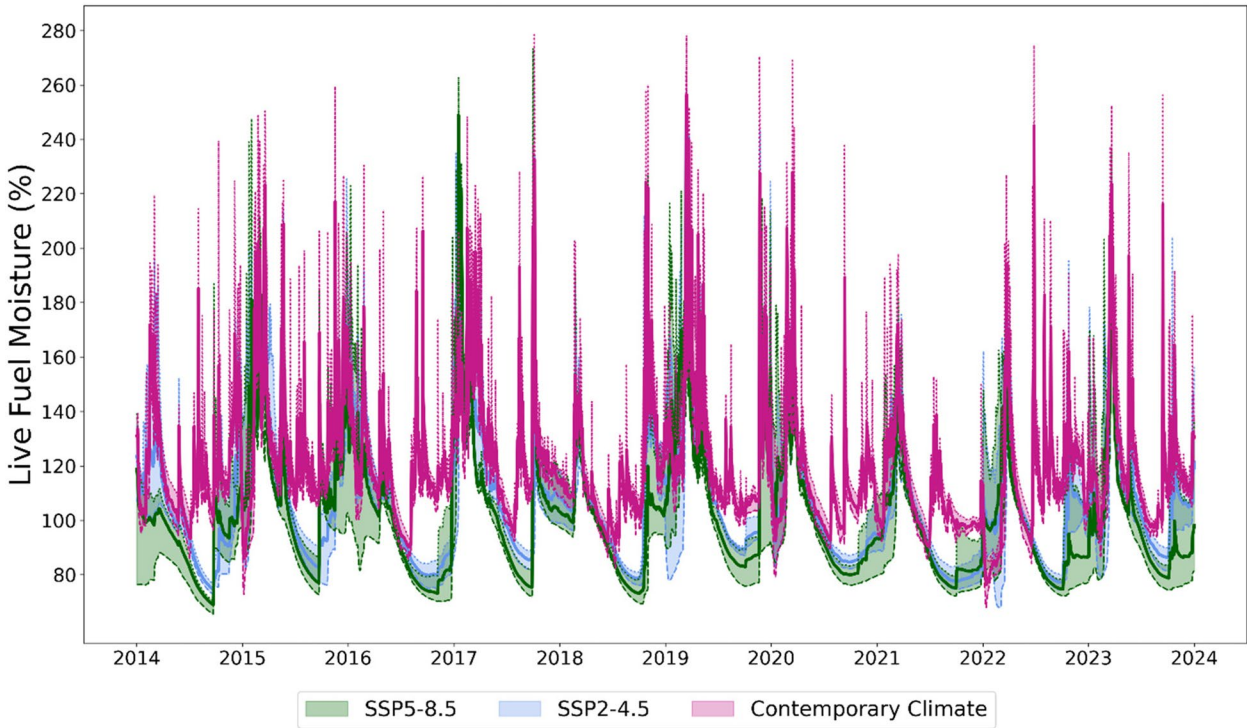


Fig. 5 *P. ponderosa* percent live fuel moisture simulated using FATES-HYDRO under different climate anomalies for 2014–2024 in Bandelier National Monument. Across the three scenarios, the solid line represents the mean and the colored bands represent variability from ten replicate simulations for each scenario. SSP2-4.5 and SSP5-8.5 climate simulations represent end of century anomaly projections (CMIP6) overlaid upon our contemporary climate drivers

Table 1 Summary of leaf water potential (LWP) and live fuel moisture content (LFMC) simulated using the FATES-HYDRO model for Bandelier National Monument, NM, USA, under contemporary and CMIP6 (shared socioeconomic pathway 2-4.5 and 5-8.5). SSP2-4.5 and SSP5-8.5 climate simulations represent end of century anomaly projections (CMIP6) overlaid upon our contemporary climate drivers. LFMC is summarized by annual percent and number of days below fire risk thresholds of 100% and 79%

Climate scenario	Lowest mean LWP (MPa)	Percent days < 100% LFMC (average days per year per run)	Percent days < 79% LFMC (average days per year per run)
Contemporary climate	−3.41	19.8% (72 days)	1.4% (5 days)
SSP2-4.5	−3.51	42.00% (185 days)	10.2% (37 days)
SSP5-8.5	−4.13	58.6% (215 days)	17.8% (65 days)

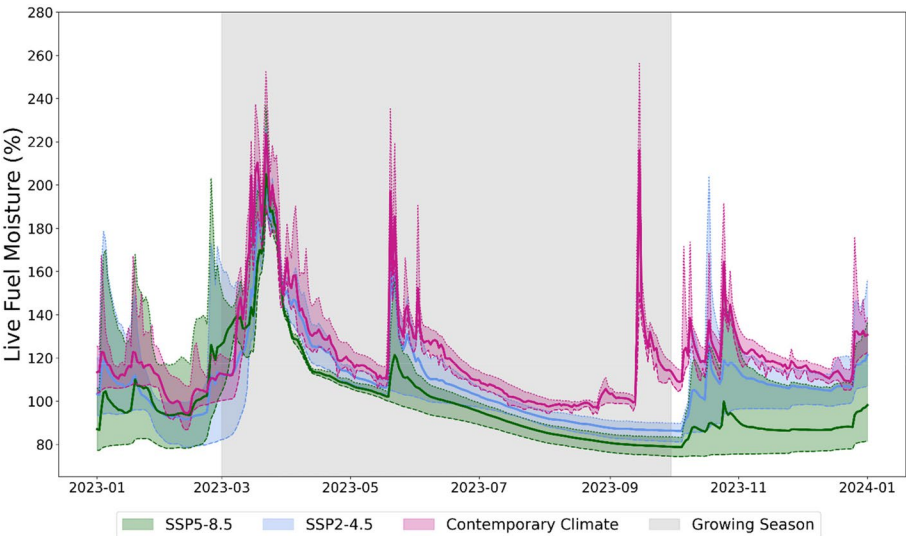


Fig. 6 *P. ponderosa* percent live fuel moisture simulated using FATES-HYDRO under different climate anomalies for 2023 in Bandelier National Monument. Across the three scenarios, the solid line represents the mean and the colored bands represent variability from ten replicate simulations for each scenario. SSP2-4.5 and SSP5-8.5 climate simulations represent end of century anomaly projections (CMIP6) overlaid upon our contemporary climate drivers. The gray shaded area represents the growing season (March–October: representing roughly 80% of gross primary productivity) in northern New Mexico

indicating a greater period of stomatal closure (Fig. 8A). The maximum contemporary monthly mean G_s of $0.019 \text{ mol m}^{-2} \text{ s}^{-1}$ is observed in March (Fig. 9A). During the growing season, contemporary G_s averaged $0.006 \text{ mol m}^{-2} \text{ s}^{-1}$, with greater activity than SSP2-4.5 and SSP5-8.5. The highest SSP2-4.5 monthly mean G_s of $0.07 \text{ mol m}^{-2} \text{ s}^{-1}$ is recorded in March. Overall, the mean growing season G_s within SSP5-8.5 is low, averaging at $0.0009 \text{ mol m}^{-2} \text{ s}^{-1}$. During the growing season (March–October), contemporary simulations show only 1 month (June) that averages below $0.005 \text{ mol m}^{-2} \text{ s}^{-1}$ while SSP2-4.5 and SSP5-8.5 both have seven (March–October). This suggests severe limitations in gas exchange during the warmer months, likely due to increased VPD and soil moisture stress.

Future change in productivity

Contemporary climate scenarios have generally higher monthly GPP than end-of-century climate scenarios, even with higher levels of CO_2 . Annual productivity (Table 2) fell in both future scenarios (SSP2-4.5: $202.77 \text{ g C m}^{-2}$, SSP5-8.5: $242.23 \text{ g C m}^{-2}$) compared to contemporary simulations ($336.80 \text{ g C m}^{-2}$). Peak contemporary monthly GPP (51.09 g C m^{-2}) occurs in March (Fig. 8B). SSP2-4.5 scenarios show a similar seasonal pattern with a maximum GPP of 48.00 g C m^{-2} observed in March (Table 2; Fig. 9B). Under scenario SSP5-8.5, the highest monthly mean GPP of 55.17 g C m^{-2} occurs in March, an increase in productivity compared to the contemporary scenario. SSP5-8.5 has higher early season productivity (Jan–Apr: $116.92 \text{ g C m}^{-2}$) than the contemporary scenario (94.54 g C m^{-2}), while the SSP2-4.5 scenario has comparable productivity (95.52 g C m^{-2}). Water-use efficiency

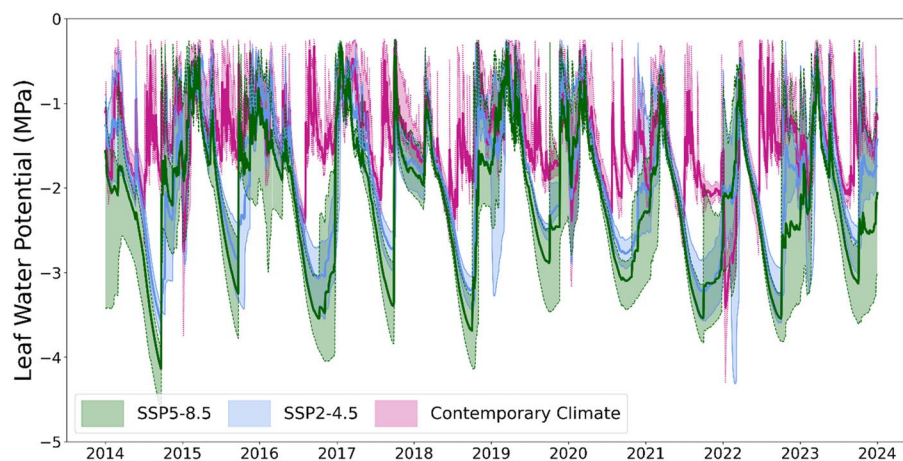


Fig. 7 *P. ponderosa* midday leaf water potential (MPa) under different climate anomalies for 2014–2024 in Bandelier National Monument simulated using the FATES-HYDRO model. Across the three scenarios, the solid line represents the mean and the colored bands represent variability from ten replicate simulations for each scenario SSP2-4.5 and SSP5-8.5 climate simulations represent end of century anomaly projections (CMIP6) overlaid upon our contemporary climate drivers

was calculated at the stand level (mmol carbon/mol water) based on the photosynthetic and transpiration rates. The contemporary simulation had an average water-use efficiency of 3.45 mmol C per mol H₂O, the SSP2-4.5 scenario had an average water-use efficiency of 4.47 mmol C per mol H₂O, and the SSP5-8.5 scenario had a water-use efficiency of 4.83 mmol C per mol H₂O.

Future change in risk of hydraulic failure

The contemporary climate scenario showed low PLC throughout the year (Fig. 10). The contemporary scenarios suggest little likelihood of hydraulic failure and mortality, as PLC does not approach either a mortality threshold of 60% (Adams et al. 2017) or 88% (Choat et al., 2012). SSP2-4.5 scenarios show higher PLC than contemporary climate, spending 11.5% of days above PLC 60%, though zero above PLC 88%, suggesting the potential for some mortality. SSP5-8.5 scenarios show 20.5% of days spent above the PLC 60% but none above the PLC 88% threshold.

Discussion

Changes in seasonal live fuel moisture

The seasonality and absolute values of LFMF could radically shift as water-use thresholds in plants are crossed under warmer summers with increased VPD and lower precipitation. This change in canopy moisture will impact future crown fire behavior as the relative rate of spread of canopy fire accelerates exponentially with declining LFMF, particularly below 79% (Rossa et al. 2016). Our results indicate a greater number of days below the 100% and 79% LFMF thresholds, suggesting a prolonged fire season and greater potential for extreme fire (Table 1).

These findings show a greater increase in the length of the fire season than described by Ma et al. (2020) who saw an increase of 10–20 days below 79% LFMF under SSP5-8.5, and 8–11 days under SSP2-4.5 in the chaparral ecosystem in California as compared to our increase of 65 days under SSP5-8.5 and 35 days under SSP2-4.5. For context, the length of the fire season is estimated to have expanded on average by 20 days in the last 25 years in the contiguous USA (Cattau et al., 2020). The most considerable change in LFMF in our study area occurs primarily from summer to fall, coinciding with periods of elevated VPD under future climate scenarios (Fig. 4). Under SSP2-4.5, the additional fire season (below 100% LFMF) is between August and October (Fig. 6), while under SSP5-8.5, it extends from July through the end of the year, with periods from August on showing high fire risk (below 79% LFMF).

The combination of higher VPD and lower precipitation (Fig. 4) puts increased stress on the plant water continuum (Figs. 7 and 8). Studies of US Southwest (Arizona and New Mexico) fire occurrence suggest that the VPD has been rising over the 30-year period between 1984 and 2015 and is the climatic variable most associated with increases in burned area and fire severity, with a much stronger association than either temperature or precipitation (Mueller et al. 2020). In the same study, annual minimum VPD had the highest correlation to fire regime, suggesting that the inability for hydraulic recharge contributed to these more extensive and more severe fires. Historical (1599–1899) reconstruction of the fire regime by Margolis et al. (2017, 2017a) suggests that the most extensive fire seasons within the Jemez Mountains (including

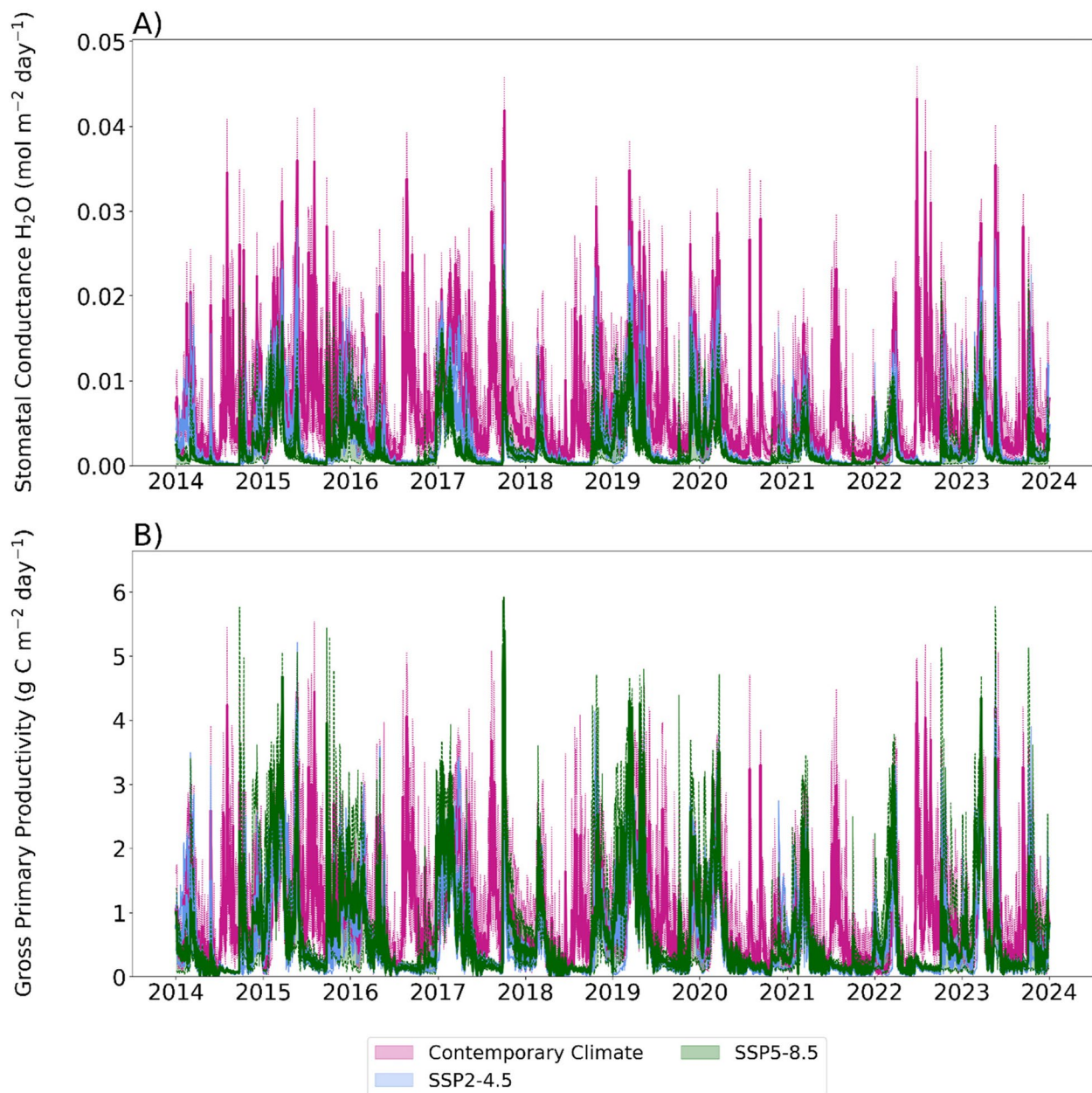


Fig. 8 **A** Daily *P. ponderosa* stomatal conductance (average mol m⁻² s⁻¹) and **B** gross primary productivity (g C m⁻²) under different climate anomalies for 2014–2024 in Bandelier National Monument. Across the three scenarios, the solid line represents the mean and the colored bands represent variability from ten replicate simulations for each scenario. SSP2-4.5 and SSP5-8.5 climate simulations represent end of century anomaly projections (CMIP6) overlaid upon our contemporary climate drivers

this study area) are associated with cool season (October–April) drought and the prior 2–3 years precipitation driving fuel accumulation. However, they additionally find late summer fires appear to be driven by declines in monsoon season precipitation (North American Monsoon (NAM), typically from July to

September; Adams and Comrie, 1997). This is where our projections predict the greatest change in LFMCI. Other southwestern fire patterns have been shown to correlate with consecutive days without rain (Holden et al. 2007).

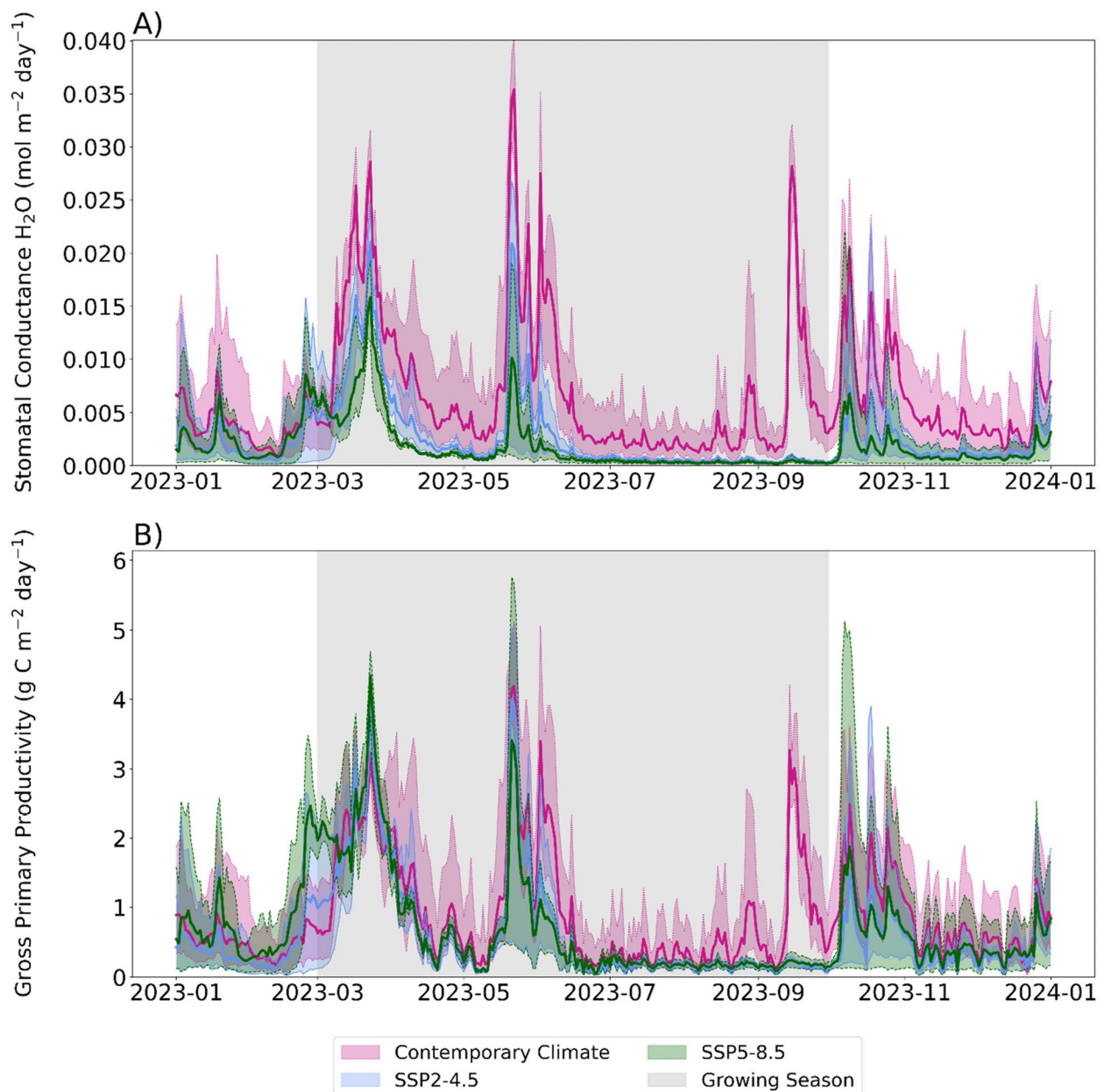


Fig. 9 **A** Daily *P. ponderosa* stomatal conductance (average $mol\ m^{-2}\ s^{-1}$) and **B** gross primary productivity ($g\ C\ m^{-2}$) under different climate anomalies for 2023 in Bandelier National Monument. Across the three scenarios, the solid line represents the mean and the colored bands represent variability from ten replicate simulations for each scenario. The gray shaded areas represent the growing season in northern New Mexico (March–October). SSP2-4.5 and SSP5-8.5 climate simulations represent end of century anomaly projections (CMIP6) overlaid upon our contemporary climate drivers

Effects on plant physiology drive exponential increase in dry live fuels

Our model results show warmer temperatures and drought leading to increased plant water stress and thus decreased LFMC. While contemporary simulations show *P. ponderosa* rarely exceeding its turgor loss point (TLP ~ -2.0 MPa), future simulations regularly

show $LWP < -2.5$ MPa and prolonged periods of stomatal closure, driven by extended periods of high VPD and reduced late summer precipitation (weeks 25–35 2023, Figs. 4). It is hypothesized that future conditions would increase stomatal closure, thus minimizing water loss and declines in LWP and LFMC. Within SSP2-4.5 and SSP5-8.5 scenarios, however, we see continued decline

Table 2 Quarterly and annual gross primary productivity (GPP, g C m⁻²) for 2014–2024 simulated by FATES-HYDRO for Bandelier National Monument under future climate scenarios (CMIP6: shared socioeconomic pathways 2-4.5 and 5-8.5). SSP2-4.5 and SSP5-8.5 climate simulations represent end of century anomaly projections (CMIP6) overlaid upon our contemporary climate drivers

Scenario	Q1 (Jan–Mar)	Q2 (Apr–Jun)	Q3 (July–Sep)	Q4 (Oct–Dec)	Mean Annual Total
Contemporary	94.54	72.24	91.12	79.88	336.80
SSP2-4.5	95.27	46.00	13.84	47.64	202.77
SSP5-8.5	116.92	46.45	17.69	61.16	242.23

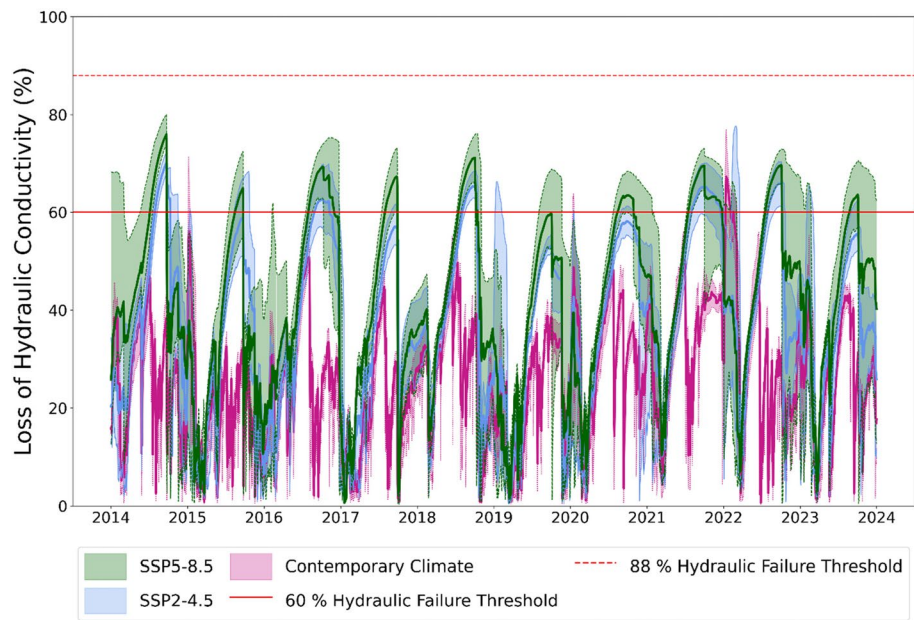


Fig. 10 Daily percentage loss of hydraulic conductivity (PLC) for *P. ponderosa* under different climate anomalies for 2014–2024 in Bandelier National Monument. Across the three scenarios, the solid line represents the mean and the colored bands represent variability from ten replicate simulations for each scenario. SSP2-4.5 and SSP5-8.5 climate simulations represent end of century anomaly projections (CMIP6) overlaid upon our contemporary climate drivers. Hydraulic failure threshold at 60% from Adams et al. (2017) and 88% from Choat et al. (2012)

in LWP past the point of stomatal closure, even while FATES-HYDRO stimulates stomatal closure and thus water conservation. The FATES-HYDRO model includes minimum conductance (water loss through the cuticle and incompletely closed stomata) as recommended by Duursma et al. (2019), and thus water lost from the above ground portion of the plant is never zero. Additionally, FATES-HYDRO includes root water efflux under conditions where the rhizosphere water potential is more negative than root water potential (Caldwell et al. 1998) as documented for *P. ponderosa* (Warren et al., 2011). Stomatal closure prevents decline in midday LWP relative to predawn; however, if soil water availability (~predawn LWP) declines below the stomatal closure point for a prolonged period, midday LWP will equilibrate with predawn (soil) and decline in concert despite stomatal closure (Plaut et al. 2012).

Experimental data suggests that trees experience more significant physiological stress under the same drought conditions at warmer temperatures (Allen et al. 2015) and that the effect of CO₂ on increasing water-use efficiency is minimal under these conditions (Birami et al. 2020). Our simulations show increased plant stress (decreased LWP and greater loss of conductivity) under future precipitation patterns and climate scenarios, even with increased water-use efficiency (3.45 mmol C per mol H₂O, SSP2-4.5: 4.47 mmol C per mol H₂O, SSP5-8.5: 4.83 mmol C per mol H₂O) under rising CO₂. Changes in LFMC in *P. ponderosa* appear to be driven by prolonged periods of more negative LWP, driven, presumably by cuticular conductance or root leakage (i.e., non-stomatal water loss; Duursma et al., 2019). Increasing atmospheric dryness (VPD) aligns with rapidly decreasing LWP under SSP5-8.5, even while G_s is near zero (Figs. 6 and 7). A rise in water loss, even as G_s decreases, is seen currently in

P. ponderosa forests in the neighboring areas that do not experience the NAM (Strange et al. 2023).

Increased gross primary productivity antecedent to fire season

In the US SW, future fire seasons may be dependent on spring rain providing adequate fuel to burn during the summer months, as is seen in lower elevations (Keely and Syphard et al., 2015) and high climatic water deficit areas (Abatzoglou et al. 2018). Our SSP5-8.5 results suggest the possibility for both an expansion in the amount of spring fuel generated and the rapid drying of fuel during the summer months, as seen in the increased spring GPP and the reduction in LPMC during the summer months, expanding both conditions necessary for fire. In the spring and early summer (where precipitation persists), we see increased growth, likely due to higher water-use efficiency and increased early spring temperature conducive to an earlier growing season. However, when aggregated across the growing season, the future climate scenarios show reduced GPP. This could have important implications for the regional carbon cycles, where reduced carbon sink from terrestrial ecosystems could exacerbate future CO₂ concentrations. While we cannot interpret our findings in the context of multiple years of fuel accumulation, the increased spring GPP and a decline in late-season LWP suggest the opportunity for two of these fire-driving events to become more frequent.

Implications of demographic change

Changes in mortality rates, as suggested by the higher PLC values under future climate (SSP5-8.5), and a transition in forest demographics may further alter the fuel profile of these forests. Our results suggest that our study area (at the lower *P. ponderosa* elevation range) may experience increased mortality due to hydraulic failure, potentially driving this change (Fig. 10). Other studies have found Utah *P. ponderosa* begins to experience hydraulic failure at an exponential rate after water potential exceeds −2.0 MPa and reaches 50% loss of conductivity around −3 MPa (Koepke & Kolb 2013). Only in our SSP5-8.5 scenarios is LWP projected this low (Fig. 7). We see simulated percent loss of conductivity >60% in some trait ensembles in both SSP2-4.5 and SSP5-8.5, suggesting that at least some mortality might occur in these scenarios. It should be noted that *P. ponderosa* may experience mortality prior to this, either through biotic agents or carbon starvation (Hubbard et al. 2001).

P. ponderosa may also be replaced by oak (*Quercus* spp.) and/or New Mexico locust (*Robinia neomexicana*), which would further alter the fire fuel profile (Strom & Fule, 2007). Gambel oak (*Quercus gambelii*) has the potential to significantly shift fire behavior in Northern

New Mexico by altering the landscape's fuel profile—what biomass is available, the sensitivity to fire, the spatial pattern of that biomass, and litter profiles. Compared to the more open and discontinuous fuels in *P. ponderosa* forests, Gambel oak tends to form dense, clonal thickets that increase horizontal fuel continuity and promote higher-severity fires. These shrub fields burn with similar frequency and seasonal timing as mixed conifer forests, but their structure supports more intense fire behavior. High-severity fire, coupled with changing environmental conditions, limits *P. ponderosa* regeneration and promotes the expansion of Gambel oak across the region (Guiterman et al. 2018; Woolman et al. 2022). As these shrub fields replace conifer stands, they shift not only what biomass is available to burn but also how that biomass is arranged in space and how it responds to changing moisture conditions. Our findings, which suggest lower LPMC in *P. ponderosa* under future climate scenarios may further enable the high-severity disturbances that drive type conversion reinforcing a feedback loop that favors Gambel oak while limiting conifer recovery. However, long-term projections of ecotones in response to climate suggest that Southern Rocky Mountain *P. ponderosa* woodland may occupy a similar total area by the end of the century, moving up in elevation and latitude, with the more southern portion of the range transitioning out of *P. ponderosa* (Harris et al. 2023).

The fire and fuel implications of massive, large-scale die-off in *P. ponderosa* have been studied extensively due to the occurrence of bark beetle outbreaks and may provide insight into how the fuel loads of these forests may be altered. After bark beetle outbreaks, researchers find a doubling of fine (non-woody) and 1–1000 h fuels (woody fuels) in the short term (~5 years; Hoffman et al. 2011). In the long term (≥5 years), bark beetle impacted stands have lower surface fuel loads with increasing larger fuels (1–100 h) and sapling live fuels, increasing the rate of passive crown fire and decreasing active crown and surface fire behavior (Hansen et al., 2015). However, these studies do not account for future changes in LPMC within the regenerating understory. A crucial dynamic will be whether *P. ponderosa* regeneration persists and how the physiology of these regenerating pines may be affected by increased aridity.

Loss of North American Monsoon

Key to the change in the LPMC we observe is the projected collapse of the NAM season during the late summer months (weeks 22–38, Fig. 4). Bandelier National Monument experiences the NAM and regularly sees 40% of annual rain in the late summer following a dry summer period (Reneau 2000). The future climate projections show greatly reduced precipitation during the summer

and monsoon seasons but increased precipitation later in the year (weeks 40–50). The return of the rains in October under SSP2-4.5 reduces plant water stress (Figs. 4 and 7); however, under SSP5-8.5, we see insufficient precipitation to return LWP to levels above the TLP (−2.0 MPa). These projections are consistent with a general reduction in later summer NAM and an increase in fall precipitation under CMIP6 (though not under CMIP5 models; Hernandez & Chen 2022). Decrease in specific humidity and lower evapotranspiration and soil moisture may contribute to the lack of summer rains, as hot days become drier (McKinnon, 2021). Monsoons have been shown to be a significant buffer of drought mortality historically, and our results concur with prior studies showing that increasing CO₂ (and thus increased water-use efficiency) is likely not sufficient to mitigate the loss of monsoons (Strange et al. 2023).

Caveats and future work

It is important to note that retrospective studies have found climate variation to account for only a portion of the change in the fire regime, as management, fire exclusion, successional pattern, and land use likely all play an important role (Abatzoglou et al. 2018; Keely and Syphard et al., 2015). One main concern with LFMC is the difficulty in estimating its effect on larger scales to understand retrospective fire occurrence and determine fire risk (Rossa & Fernandes 2018). Disentangling the effect of LFMC, dead fuel moisture content, and other drivers of fire is complex, often owing to limited sample size and climate covariance (Pimont et al. 2019). Similar to other recent models, our efforts tend to overpredict LFMC during periods of ready water availability (Balaguer Romano et al., 2022) and would benefit from inclusion of maximum saturated water content if used in real-time fire simulations (as was done in Rufault et al., 2023). Our work does not include increased leaf necrosis and thus changes in the total fuel moisture profile, an important consideration in total plant flammability (Cakpo et al. 2024). Our empirical model using midday Gs and predawn and midday LWP was similarly predictive of LFMC as prior models using turgor loss point and midday LWP (Figs. S.6, S.7; Nolan et al., (2020), providing a more scalable methodology due to efficiency and potential for remote collection of Gs data. Our work highlights the predictive capacity of these models in arid field deployment.

In our study, improvements could be made to account for tree size, tree density, aspect, and slope and its effect on plant water stress. This could improve the correlation between plant stress and live fuel moisture, and FATES-HYDRO's representation of LWP and Gs. It is also important that NAM dynamics within the CMIP suite of

models may not currently be fully resolved and exhibit biases due to resolution (Hernandez & Chen (2022). Our sampling represents the lower elevation range of *P. ponderosa* in the Jemez Mountains and, as such, may not represent the drought resilience of higher elevation *P. ponderosa*, as in the mountains of Arizona, where lower elevation *P. ponderosa* had a lower drought tolerance than higher elevation *P. ponderosa* (Kilgore et al. 2021). Future FATES-HYDRO simulations examining the dynamic competition of oak and *P. ponderosa* will be useful to understand the change in proportional biomass and its effect on overall LFMC and fire behavior.

While our model successfully captures the observed benchmarking variables, however, model–data discrepancies remain even after ensemble filtering. Identifying the sources of these discrepancies, whether from uncertainties in plant traits, climate inputs, soil parameterization, or model structural limitations, is scientifically important. Unfortunately, the current lack of site-specific measurement of plant traits, soil properties, and climate data prevents us from attributing these uncertainties. Future studies aimed at disentangling these sources could significantly enhance our predictive understanding.

Conclusions

The seasonality and absolute values of LFMC could radically shift as water-use thresholds in plants are crossed under warmer summers with increased VPD and lower precipitation. This change in canopy moisture will impact future crown fire behavior, expanding the potential for extreme wildfires and longer fire seasons. We predict increasing variability in the *P. ponderosa* wildfire regime under both climate projections, driven by changing productivity, rising mortality, and an overall decrease in live fuel moisture. The overall increase in stress and lower live fuel moisture is driven by reduced precipitation during late summer monsoons typical of the region, extending the fire season later in the year. Our work emphasizes the need for including plant physiology models in fire risk forecasts.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42408-025-00412-0>.

Supplementary Material 1

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Authors' contributions

A.M.M., S.C., M.U., L.T., and L.T.D. designed and implemented monitoring. Z.J.R., W.G., A.K., L.S., M.U., and L.T.D. collected and analyzed field data. Z.J.R., W.G., and

J.O. designed and conducted modeling simulations. Z.J.R., W.G., and L.T.D. analyzed model outputs and generated results. Z.J.R., W.G., A.A., R.L., J.O., A.M.M., S.C., M.U., L.T., and L.T.D. drafted and revised the article.

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Data availability

The FATES model is available at <https://github.com/NGEET/fates> and the E3SM model at <https://github.com/E3SM-Project/E3SM>. Data and scripts specific to recreate the figures and results of this paper will be published in a GitHub repository following acceptance.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

All authors consent to the material in this manuscript.

Competing interests

The authors state no conflict of interests.

Author details

¹Earth and Environmental Sciences Division, Los Alamos National Laboratory, Los Alamos, NM, USA. ²Department of Earth and Planetary Sciences, Jackson School of Geosciences, University of Texas at Austin, Austin, TX, USA. ³National Park Service, Bandelier National Monument, Los Alamos, NM 87544, USA.

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