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Fire & Fuels Management

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Prefire Drought Intensity Drives Postfire Recovery and Mortality in *Pinus monticola* and *Pseudotsuga menziesii* Saplings

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Abstract

Increasing frequency of droughts and wildfire are sparking concerns that these compounded disturbance events are pushing forested ecosystems beyond recovery. An improved understanding of how compounded events affect tree physiology and mortality is needed given the reliance of fire management planning on accurate estimates of postfire tree mortality. In this study, we use a toxicological dose-response approach to quantify the impact of variable-intensity drought and fire on the physiology and mortality of *Pinus monticola* and *Pseudotsuga menziesii* saplings. We show that the dose-response relationship between fire intensity and mortality shifts toward increased vulnerability under drought, indicating higher mortality with increasing drought at any fire intensity. The trajectory we observed in postfire chlorophyll fluorescence, an indicator of photosynthetic efficiency and stress, was an effective early warning sign of impending tree death. Postfire mortality modeling shows that accurate mortality classification can be achieved using prefire physiology and morphology metrics combined with fire intensity. Variable importance measures indicate that physiological condition and fire intensity have greater influence on the classification accuracy than morphological metrics. The wide range in drought and fire responses observed between this study and others highlights the need for more research on compound disturbance effects.

Study Implications: An improved understanding of how drought and fire affect tree physiology and mortality is needed by natural resource managers looking to predict postfire tree mortality. This study advances our compound disturbance understanding by subjecting conifer saplings to variable drought and fire intensities and quantifying and modeling moderate-term recovery and mortality. The results show reduced physiological recovery and amplified mortality in saplings exposed to greater drought and fire intensity. Overall, this study highlights the importance of physiological condition when modeling tree mortality and could potentially be used to inform current postfire tree mortality models.

Keywords: drought, fire, fire severity, compound disturbances, recovery, mortality, chlorophyll fluorescence

Natural disturbances such as drought, fire, and insects are pivotal in shaping forest ecosystem composition, structure, and productivity by injuring and killing individual trees and altering forest succession (Paine et al. 1998; Turner 2010). The degree of disturbance-induced change largely depends on the intensity, frequency, and extent of the disturbance and can vary significantly between disturbance types (Dale et al. 2001). Compound disturbances, or disturbances occurring simultaneously or rapidly in sequence, can create greater ecosystem change than individual disturbance events alone, and can contribute to reduced forest resilience, or the time it takes a forest to recover to a predisturbance state (Kleinman et al. 2019; Millar and Stephenson 2015; Paine et al. 1998). Compound disturbances represent a growing threat to western United States forests given projected increases in both drought and fire activity (Abatzoglou et al. 2021; Anderegg et al. 2022; Dai 2013), however, the extent and severity of this threat is largely unknown given that trees of differing species, sizes, and ages can have widely different physiological and mortality responses to drought and fire (Adams et al. 2017; Hood et al. 2018; McDowell et al. 2018). An improved understanding of the effects of simultaneous drought and fire stress is needed to inform natural resource managers on actions that could mitigate any amplified detrimental impacts.

The combined effects of drought and fire on tree physiology, recovery, and mortality are poorly understood (Kleinman et al. 2019; Millar and Stephenson 2015; Sturtevant and Fortin 2021). Drought can prompt trees to

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close stomata to limit water loss, which reduces carbon assimilation via photosynthesis and increases dependence on nonstructural carbohydrate (NSC) stores for cellular maintenance and repair (McDowell et al. 2011, 2022). Drought also depletes tree water content, increasing flammability (Ruffault et al. 2023; Weir and Scasta 2014), and if persistent, can result in xylem hydraulic dysfunction and eventual phloem transport failure (McDowell et al. 2022). Fires can exacerbate the stress of droughted trees by damaging critical tissues and organs necessary for NSC production and transport (Hood et al. 2018; Partelli-Feltrin et al. 2023). Depending on the fire intensity and presence or absences of fire-resistant tree traits (e.g., bark thickness, crown height above ground), and strategies (e.g., NSC storage belowground, serotiny), fire can damage sensitive foliage and buds in the crown (Michaletz and Johnson 2006; Smith et al. 2017; Sparks et al. 2023) and stem/branch phloem that are necessary for the translocation of NSC from the crown to the roots (Partelli-Feltrin et al. 2023). Because drought reduces the NSC stores that a tree needs for repairing fire-damaged tissues, drought is hypothesized to increase postfire tree mortality, especially for trees exposed to higher-intensity fires (figure 1) (Smith et al. 2017; Sparks et al. 2018; van Mantgem et al. 2018). Several studies have provided evidence in support of this hypothesis in *Pinus ponderosa* and *Larix occidentalis* saplings, where mortality generally increased with increasing drought and fire intensity (Partelli-Feltrin et al. 2020; Sparks et al. 2018). Similarly, others have shown that drought stress and associated reductions in tree vigor (e.g., reduced growth rate) in mature conifers increased vulnerability to fire-induced mortality (Slack et al. 2016; van Mantgem et al. 2013, 2018). Conversely, others have observed no or very low levels of mortality in resprouting *Quercus* spp. and *Pinus palustris* that were subjected to drought and surface fires (Chiatante et al. 2015; Di Iorio et al. 2011; Wilson et al. 2022). Although these studies have advanced our understanding of drought and fire effects, some are limited, as they did not have a drought-only treatment to isolate drought and combined drought and fire effects (Sparks et al. 2018). Others did not test severe drought intensities that could cause even nonburned trees to die (Partelli-Feltrin et al. 2020; Wilson et al. 2022) or did not quantify the fire intensity (Chiatante et al. 2015; Di Iorio et al. 2011; van Mantgem et al. 2013, 2018).

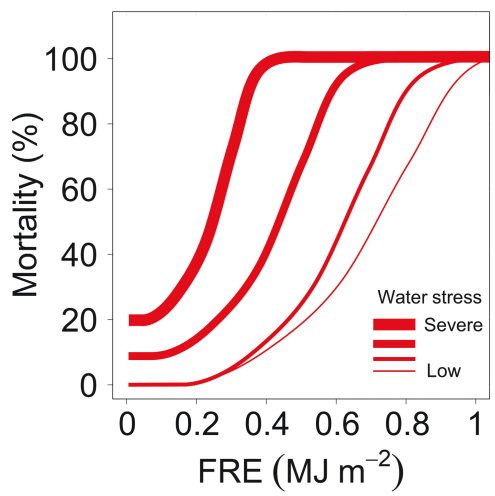

Figure 1 Hypothesized leftward shift of increased vulnerability in the relationship between fire intensity, reported here as fire radiative energy (FRE; units: MJ m^{-2}), and conifer sapling mortality as water stress increases (adapted from Sparks et al. 2018). At severe water stress levels, mortality will occur even in trees exposed to very low-intensity fires or no fire and is denoted by the upward shift of the FRE-mortality relationship. The "Low" water stress line represents the average mortality observed across FRE doses from 0 to 1 MJ m^{-2} for well-watered conifer saplings of similar size and age to those in this study (Smith et al. 2017; Sparks et al. 2023; Steady et al. 2019).

Understanding how trees respond to drought and fire is important for tree mortality modeling and identifying early warning signs of tree mortality. Tree mortality models underlie software tools used in fire management planning (e.g., First Order Fire Effects Model, Lutes 2020; FFE-FVS, Rebain 2022), and thus their accuracy is of critical importance (Hood et al. 2018; Woolley et al. 2012). Few equations used within these models focus on smaller trees (Battaglia et al. 2009), which represents a considerable knowledge gap given that prescribed burning commonly includes objectives to purposefully kill, or reduce the mortality of, smaller trees (Hood et al. 2018). Furthermore, climate change is predicted to decrease the time between fires in the western United States (Abatzoglou et al. 2017; Bowman et al. 2017) and this region is also expected to need a higher frequency of prescribed fires to reduce wildfire hazard (Voelker et al. 2019), compounding to increase the occurrence of fires on younger cohorts of trees. Many models use prefire morphological attributes (e.g., bark thickness and crown base height) and postfire injury (e.g., crown scorch and stem charring) to predict postfire mortality (Ryan and Reinhardt 1988; Shearman et al. 2019; Stephens and Finney 2002), but it is not well understood whether using only prefire physiological and morphological characteristics and fire intensity can provide accurate mortality predictions. Prefire morphology could potentially improve mortality prediction given that prior observations have shown size-dependent relationships, where smaller trees are killed at higher proportions than larger trees at a given fire intensity (McDowell et al. 2018; Stephens and Finney 2002). Inclusion of morphology may be advantageous, given that some metrics can be accurately quantified (e.g., total height, crown base height) or modeled (e.g., diameter) at the individual tree level across large spatial scales using airborne laser scanning (Hyyppa and Inkinen 1999; Popescu 2007; Popescu and Zhao 2008; Sparks et al. 2022), whereas estimates of crown scorch and stem char are difficult to collect at large scales, as they need to be assessed by ground observation personnel (Varner et al. 2021). Other studies have shown that prefire physiological condition, including minimal water stress (Partelli-Feltrin et al. 2020; Sparks et al. 2018), greater photosynthetic efficiency (expressed as chlorophyll fluorescence) (Smith et al. 2017), and increased growth rate (van Mantgem et al. 2003) increase the probability of postfire tree survival. Remotely sensed observations of chlorophyll fluorescence, which provide information on the efficiency of leaf photochemistry (Maxwell and Johnson 2000; Murchie and Lawson 2013), could provide a mechanistic and scalable metric of postfire tree physiological condition. Chlorophyll fluorescence is highly sensitive to plant stress (e.g., water, cold, heat) (Ač et al. 2015; Guadagno et al. 2017), which suggests that it could provide an early warning sign and predictor variable in postfire mortality modeling, but limited research has assessed this potential (Smith et al. 2017; Sparks et al. 2023).

The objective of this study was to quantify the impact of variable-intensity drought and fire on *Pinus monticola* var. *minima* Lemmon and *Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco sapling physiology and mortality. We specifically address the following questions:

(1) How does increasing drought stress and fire intensity affect sapling postfire recovery?
(2) How does increasing sapling drought stress affect the fire intensity-mortality dose-response relationship?
(3) Can we accurately model postfire sapling mortality using prefire physiological and morphological characteristics and fire intensity?

To answer these questions, we used a controlled dose-response approach (Smith et al. 2016; Sparks et al. 2023) where *P. monticola* and *P. menziesii* saplings were subjected to varying drought and surface fire intensities and monitored for up to 10 weeks postfire. Prefire sapling physiological condition and morphology observations were used as inputs in a random forest classifier to assess the accuracy and relative importance of these attributes when predicting sapling mortality.

Materials and Methods

Pinus monticola and *P. menziesii* Saplings and Study Treatments

Pinus monticola and *P. menziesii* saplings ($N = 64$ per species) were acquired from the Franklin H. Pitkin Forest Nursery at the University of Idaho and were grown in 9.5 L pots through two-and-a-half growing seasons under natural light conditions in a climate-controlled greenhouse in Moscow, Idaho, USA (N 46.73° W 117.00°). During this period, saplings were watered to field capacity daily to minimize water stress. Prior to drought and fire treatments, the mean (±SE) diameter at root collar (DRC) was 1.7 ± 0.03 cm and 2.1 ± 0.05 cm and mean height was 0.82 ± 0.02 m and 1.0 ± 0.02 m for *P. monticola* and *P. menziesii*, respectively. The mean height to live crown was 13.6 ± 0.71 cm and 6.8 ± 0.53 cm and number of live branches was 17 ± 0.7 and 34 ± 0.9 for *P. monticola* and *P. menziesii*, respectively.

We conducted a pilot drought to determine the length of time and foliar moisture content (FMC) at which the saplings would start dying during drought. Three saplings of each species had water withheld until mortality was determined. Mortality was defined as the death of all foliage and the inability to regenerate shoots. A stem cambium scratch test was also used to confirm mortality, where living cambium is green and dead cambium is brown. Mature needles produced in the previous year were collected from each sapling every ~7 days and were used to calculate FMC. At each sampling date, ~5 g of needles were collected randomly throughout the top third of each sapling crown and had their fresh sample weight recorded (± 0.01 g). These foliar samples were then oven dried for 24 hours at 100°C and weighed again to acquire their dry weight. Foliar moisture content (FMC, %) was calculated on a dry weight basis. After 21 days without water, all trees were dead except one *P. monticola* sapling.

Following the pilot drought, *P. monticola* and *P. menziesii* saplings were randomly divided into one of four drought groups and one of three fire treatment groups (Table 1). The most severe drought treatment was slightly longer than the pilot drought to ensure some drought-induced mortality. Starting at 25 days prefire, the three drought groups had water withheld for progressively shorter intervals while the control was watered to field capacity daily. After the drought treatments were complete, the saplings in the drought and fire treatment groups were subjected to surface fires with a known fire intensity dose (Table 1), reported as fire radiative energy (FRE, in MJ m^{-2}), or the total radiative heat flux. Surface fires were conducted at the Idaho Fire Initiative for Research and Education (IFIRE), a climatically controlled indoor combustion laboratory. We used FRE as the dose metric, given that prior studies have shown that pure fuel beds with the same mass and moisture content produce consistent and repeatable quantities of FRE (Smith et al. 2013, 2016; Wooster et al. 2021). We used FRE doses of 0 MJ m^{-2} (i.e., no fire), 0.4 MJ m^{-2}, and 0.6 MJ m^{-2}, as these doses are known to result in low-to-moderate mortality levels in saplings with minimal water stress (Sparks et al. 2023). The specific FRE doses were created by burning fuel beds of pure *P. monticola* needles at <1% moisture content. The relationship between fuel load and FRE reported in Smith et al. (2017) was used to calculate the necessary fuel load for each dose group, where the needle fuel load (kg) = 2.679/FRE. Before burning each sapling, ~5 g of needles were collected randomly throughout the top third and bottom third of each sapling crown for FMC estimation. Saplings in each dose group were burned individually and were inserted into a custom-cut concrete board so that the soil surface of the sapling pot was level with the board. The corresponding fuel load of dry needles was evenly distributed in a 1 m^2 circular area surrounding each sapling and ignited on one side to produce a surface fire with a uniform flaming front (figure 2). After the fire treatments, all saplings, including those in unburned treatment groups, were watered to field capacity daily.

Chlorophyll Fluorescence Measurements

Chlorophyll fluorescence is the re-emission of light absorbed by chlorophyll molecules associated with photosystem II (PSII). Fluorescence represents one of three fates of harvested light energy, including energy used to drive photosynthesis and energy dissipated as heat. Because fluorescence occurs in competition with these other processes, fluorescence can provide useful information on the efficiency of leaf photochemistry (Maxwell and Johnson 2000; Murchie and Lawson 2013). A commonly used chlorophyll fluorescence metric is the maximum quantum yield of PSII (F_v/F_m), calculated following Genty et al. (1989):

Table 1. Sample size for each treatment group for each species ($N = 64$ per species). FRE, fire radiative energy.

Drought treatment group (days without water)	Number of saplings at each FRE dose		
	0 (no fire)	0.4 MJ m^{-2}	0.6 MJ m^{-2}
0	4	6	6
14	4	6	6
19	4	6	6
25	4	6	6

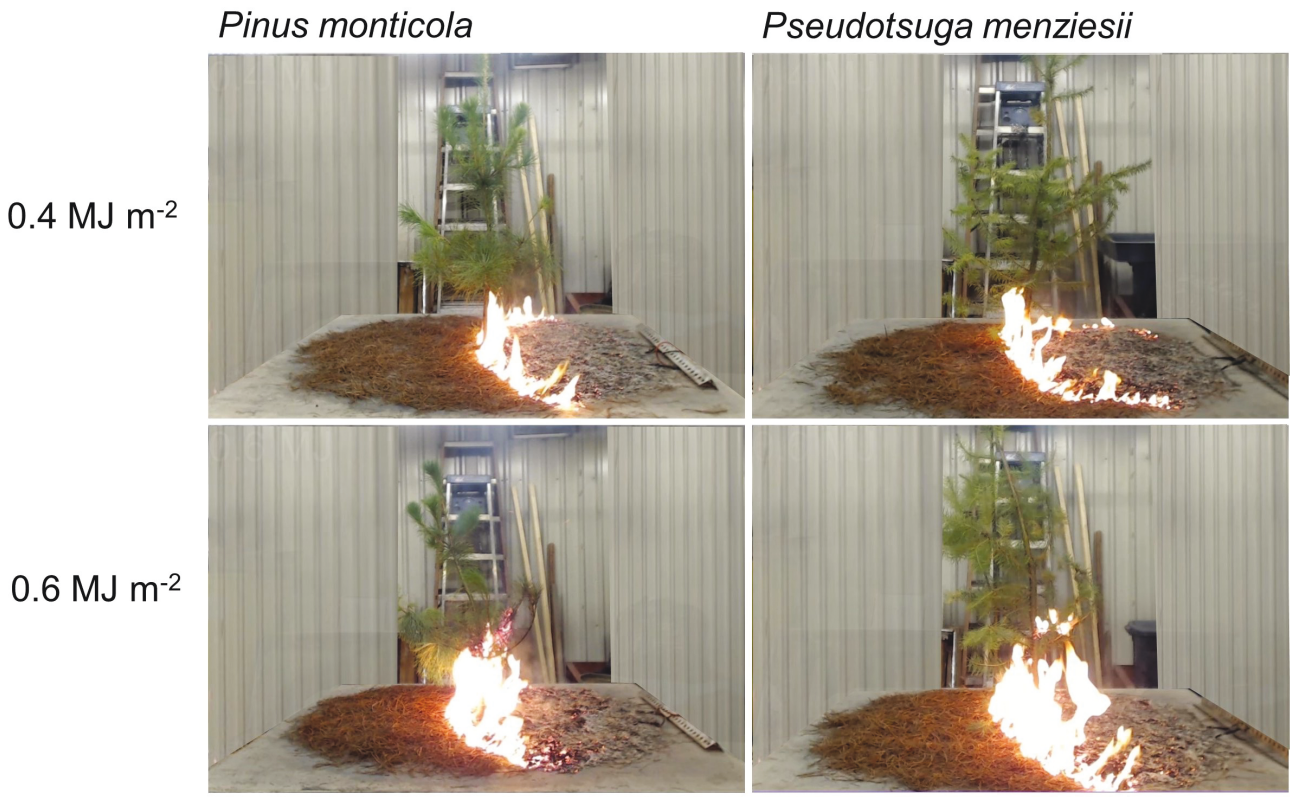

Figure 2 Experimental burn setup for representative *Pinus monticola* (left column) and *Pseudotsuga menziesii* (right column) saplings subjected to surface fires with fire radiative energy of 0.4 MJ m^{-2} (top row) and 0.6 MJ m^{-2} (bottom row).

$$\frac{F_v}{F_m} = \frac{F_m - F_o}{F_m} \quad (1)$$

where F_v is the difference between the maximum fluorescence (F_m) and the minimum fluorescence (F_o). Subjecting a dark-adapted leaf to a saturating pulse of light energy induces maximum fluorescence, as there is assumed to be little to no heat dissipation (Murchie and Lawson 2013). Likewise, minimal fluorescence can be measured by subjecting a dark-adapted leaf to a weak pulse of light energy. Generally, stressed plants will have F_v/F_m values less than 0.8 (Maxwell and Johnson 2000). Water stress, in particular, impedes electron donation in PSII and is reflected in decreases in F_v (Downton et al. 1981).

Chlorophyll fluorescence measurements were acquired weekly on all study trees from 1 week prefire to 4 weeks postfire and then biweekly until 8 weeks postfire using an OS30p+ fluorometer (Opti-Sciences, Hudson, NH). Measurements were acquired at night, at least 1 hour after sunset, so that needles could dark adapt. Measurements were taken on needles with minimal visible damage or discoloration in the top one-third of each sapling crown. Minimal fluorescence (F_o) was measured, and maximum fluorescence (F_m) was measured after a short saturation pulse (3500 µmol m^{-2} s^{-1}) of red light centered at 660 nm.

Morphological Measurements and Mortality Assessment

Total sapling height and DRC were measured at weekly intervals starting from 1 week prefire to 4 weeks postfire. The height to live crown and number of live branches were also measured for each sapling prior to the start of the drought treatments. Fire-induced crown scorch was not measured, as it was impossible to visually differentiate foliage killed by the fire and dying or killed foliage due to the prefire drought. Mortality was assessed at 1 day prefire and 10 weeks postfire.

Analysis and Mortality Modeling

Differences in prefire physiology and foliar moisture content among drought treatments were compared with ANOVA, and if significant (α = .05), a Tukey's honest significant difference test. We quantified the effect of FMC and FRE dose on sapling mortality using logistic regression in R statistical software (R Core Team 2023). Logistic regression models were fit separately for each FRE dose group and were used to determine the lethal threshold of FMC at which 50% of saplings died.

A random forest classification approach was used to model postfire mortality. Random forest is an ensemble learning algorithm that uses bootstrap samples of the training data to train each tree in an ensemble of n trees (Breiman 2001). Trees are assigned live or dead classification by a majority vote of the ensemble of trees and cross-validated against the data not included in the bootstrap samples, referred to as the "out-of-bag observations." Random forest classification does not make distributional assumptions about the data and is insensitive to collinearity among predictor variables (Cutler et al. 2007). It has also been shown to be superior to other modeling approaches, such as logistic regression, when using unbalanced datasets such as tree mortality datasets (Shearman et al. 2019).

Random forest classification was conducted using the 'randomForest' (Liaw and Wiener 2002) R package in R statistical software (R Core Team 2023). The classifier was trained with $n = 500$ 'trees', and the number of variables at each split was set to the square root of the total number of predictor variables. We split each species dataset into training and validation datasets using an 80:20 ratio. To avoid the large variability in classification accuracy that arises by doing a single split of data into training and validation datasets, we repeatedly split each dataset into training and validation sets using bootstrapping following Lyons et al. (2018). In total, one hundred different sets were generated, and a classification was performed using each set. Predictor variables included prefire F_v/F_m, FMC, FRE dose, height, DRC, number of live branches, and height to live crown. Predictor variable importance was calculated as the mean decrease in classification accuracy or the normalized difference in the misclassification rate between the original and modified classifications where values of the predictor variable of interest were randomly permuted in the out-of-bag observations.

Validation was performed for each classification iteration using confusion matrices calculated between the predicted live or dead classification and the reference observations. These confusion matrices were used to calculate average overall accuracy, omission and commission errors, and associated 95% confidence intervals (Story and Congalton 1986). The overall accuracy is the percentage of correctly classified saplings divided by the total number of saplings. Commission error is calculated as 1 minus user's accuracy, where user's accuracy represents the proportion of saplings classified as class *i* that have reference class *i*. Omission error is calculated as 1 minus producer's accuracy, where producer's accuracy represents the proportion of saplings of reference class *j*, classified as class *j*.

Results

Drought Impacts on Prefire Sapling Physiology

The conifer saplings' FMC declined with lengthening drought treatments (figure 3). At the end of the drought period, *P. monticola* 0–19 day drought groups did not have significant differences in their FMC, whereas the 25 day drought group was significantly lower ($P < .001$) (figure 3). *Pinus menziesii* drought groups were more variable, with progressively lower FMC ($P < .001$) in the 19–25 day drought groups than the 0–14 day drought groups. Although not significantly different, the lower crown FMC was 9% and 12% lower than upper crown FMC, on average, for *P. monticola* and *P. menziesii*, respectively.

For both species, F_v/F_m followed the same pattern as FMC. At the end of the drought period, the average F_v/F_m for *P. monticola* in the 0–19 day drought groups were not significantly different, and the 25 day drought group was lower ($P < .001$) (figure 4). Although not significantly different, the average F_v/F_m for *P. monticola* in the 19 day drought group was 7.5% lower than in the 0–14 day drought groups. The average F_v/F_m for *P. menziesii* was progressively lower in the 19–25 day drought groups than in the 0–14 day drought groups ($P < .001$) (figure 4).

Drought and Fire Impacts on Sapling Physiology and Mortality

F_v/F_m displayed differing temporal trajectories from 1 week prefire to 8 weeks postfire for saplings that lived versus those that died by 10 weeks postfire (figures 5 and 6). Generally, saplings alive at 10 weeks postfire maintained high F_v/F_m (>0.6) throughout the monitoring period. A majority of saplings (~82%) in the 0–14 day drought groups that were subjected to surface fires experienced an immediate 1 week postfire decline in F_v/F_m, followed by a slight increase 2–3 weeks postfire. The average magnitude of the F_v/F_m loss was greater for *P. menziesii* saplings in the 0- and 14-day drought groups subjected to 0.6 MJ m^{-2} fires (-41% and -35%, respectively) than those subjected to 0.4 MJ m^{-2} fires (-23% and -14%, respectively). Conversely, there was no difference in the magnitude of the F_v/F_m loss for *P. monticola* saplings in the 0- and 14-day drought groups subjected to 0.4 MJ m^{-2} fires (-7% and -8%, respectively) and those subjected to 0.6 MJ m^{-2} fires (-7% and -8%, respectively). Saplings that lived were able to maintain F_v/F_m recovery (figures 5b and c and 6b and c), whereas saplings that died displayed decreasing F_v/F_m for the remainder of the monitoring period (figures 5e and f and 6e and f). Saplings that recovered their F_v/F_m to prefire levels were generally in less severe drought groups (≤14 days drought) and lower FRE groups (≤0.4 MJ m^{-2}).

For both species, there was a leftward shift in the dose-response relationship between FRE and mortality for saplings in more severe drought groups (figure 7). In other words, more severely water-stressed saplings had higher mortality rates than less water-stressed saplings when exposed to the same FRE dose. For *P. monticola*, the FRE dose at which some mortality occurred decreased from 0.6 MJ m^{-2} for the 14 day drought group to 0.4 MJ m^{-2} for the 19 day drought group to 0 MJ m^{-2} for the 25 day drought group (figure 7a). *Pinus monticola* in the 0 day drought group exhibited 0% mortality across all FRE doses. For *P. menziesii*, the FRE dose at which some mortality occurred decreased from 0.6 MJ m^{-2} for the 0 and 14 day drought groups to 0.4 MJ m^{-2} for the 19 day drought group to 0 MJ m^{-2} for the 25 day drought group (figure 7b). Mortality in unburned saplings occurred in the 25 day drought group for both *P. monticola* (75% mortality, figure 7a) and *P. menziesii* (100% mortality, figure 7b).

The 50% lethal FMC (LD50) for both *P. monticola* and *P. menziesii* increased with greater FRE (figure 8). The LD50 for *P. monticola* increased from 88.2% for unburned saplings to 152.5% for saplings in the 0.6 MJ m^{-2} FRE dose group. Likewise, the LD50 for *P. menziesii* increased from 37.1% for unburned saplings to 136.5% for saplings in the 0.6 MJ m^{-2} FRE dose group. All unburned saplings that died had an FMC lower than 50%, whereas trees that died in the 0.4 and 0.6 MJ m^{-2} FRE dose groups had a wider range of FMC, with some mortality occurring in saplings with FMC greater than 150%.

Postfire Sapling Mortality Prediction

The overall accuracy for the random forest live or dead classification, averaged over the one hundred dataset iterations, was moderately high for both *P. monticola* (82.0%) and *P. menziesii* (78.5%) (Table 2). For both species, omission errors for dead sapling classification were higher than commission errors, and commission errors for live saplings were higher than omission errors. These patterns indicate that the classifier tended to misclassify dead saplings as live.

Our assessment of predictor variable importance shows that for both species, prefire physiological condition (e.g., water stress and F_v/F_m) is more important than FRE dose for predicting mortality at 10 weeks postfire (figure 9).

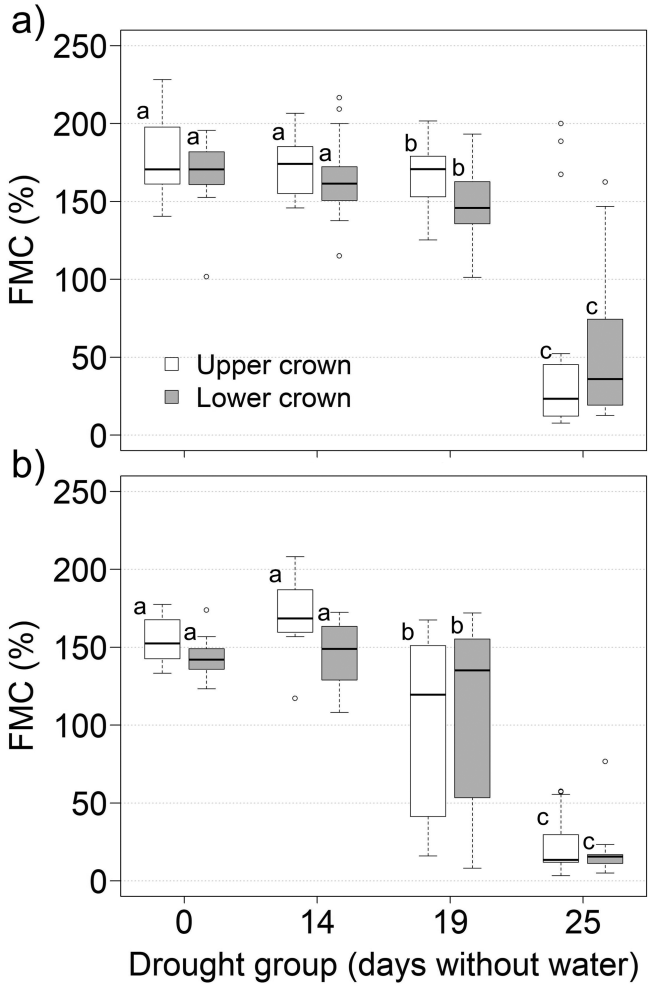

Figure 3 Foliar moisture content (FMC) for the upper and lower crown needles for (a) *Pinus monticola* and (b) *Pseudotsuga menziesii* prior to fire treatments. Mean values sharing the same letter are not significantly different ($P < .05$).

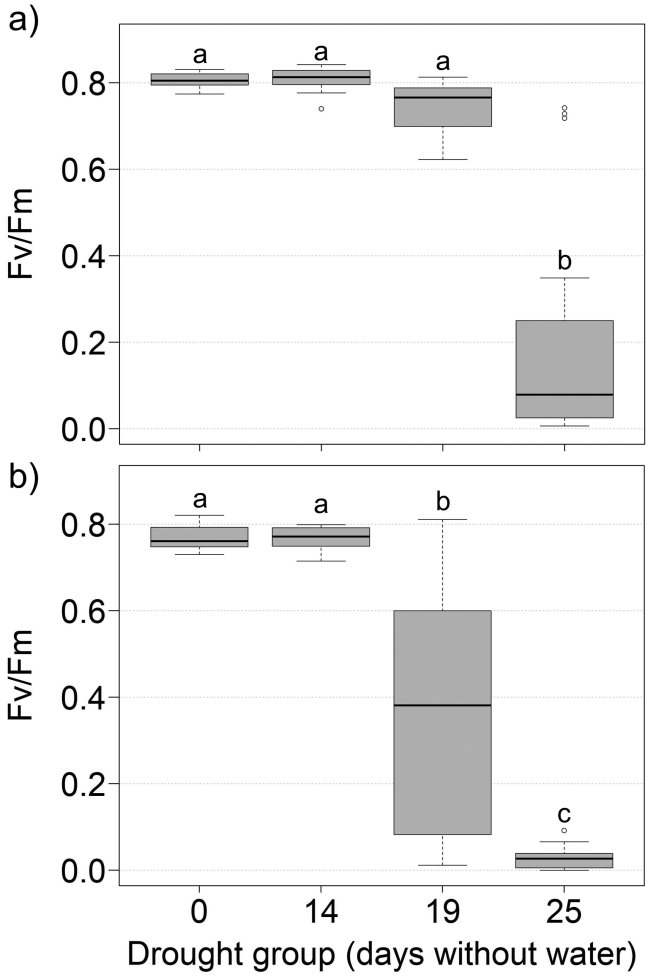

Figure 4 Chlorophyll fluorescence (F_v/F_m) across drought groups for (a) *Pinus monticola* and (b) *Pseudotsuga menziesii* saplings prior to fire treatments. Mean values sharing the same letter are not significantly different ($P < .05$).

Morphological metrics were generally not as important for predicting tree mortality; however, height was the most important morphological variable for both species.

Discussion

This study used a toxicological dose-response approach to assess how compound disturbances, specifically drought and fire, affect tree physiology, recovery, and mortality. In general, we observed an amplified response, where *P. monticola* and *P. menziesii* saplings subjected to higher intensity drought and fire treatments showed reduced capacity to recover photosynthetic capacity after the treatments. Likewise, mortality also increased with greater drought and fire intensity. As hypothesized by Smith et al. (2017) and Sparks et al. (2018) (figure 1), the FRE-mortality dose-response relationship shifted leftward and upward (figure 7), and the most severe drought treatments were sufficient to cause mortality in the absence of fire. Similarly, the LD50, the FMC at which it is more likely for trees to die than survive at each FRE dose, increased with increasing FRE (figure 8), demonstrating the shifting vulnerability of trees with varying compound disturbance intensity. Overall, *P. monticola* generally maintained higher FMC and F_v/F_m and had lower mortality than *P. menziesii* across most treatment intensities, indicating a higher drought-fire resistance. Mortality was accurately predicted in both species using prefire physiological status, morphological attributes, and surface fire intensity. Physiological status in terms of FMC and F_v/F_m and fire intensity were the most important predictor variables, and morphological variables were the least important (figure 9). It is important to note that these findings may not translate to older and larger trees that have more developed morphological features, such as thicker bark and a higher crown base height, that would increase their probability of survival. Numerous studies have observed that bark thickness, coupled with postfire injury observations such as crown scorch, can accurately predict tree mortality across a range of species (Cansler et al. 2020; Ryan and Reinhardt 1988; Stephens and Finney 2002). However, the findings of this study and others in mature trees (Furniss et al. 2018; Shearman et al. 2023), suggest that modeling systems reliant on deriving fire-induced tree mortality from tree morphological traits should explore including physiological traits and parameters associated with fire-resistant mechanisms to improve prediction accuracy when dealing with fire-drought scenarios.

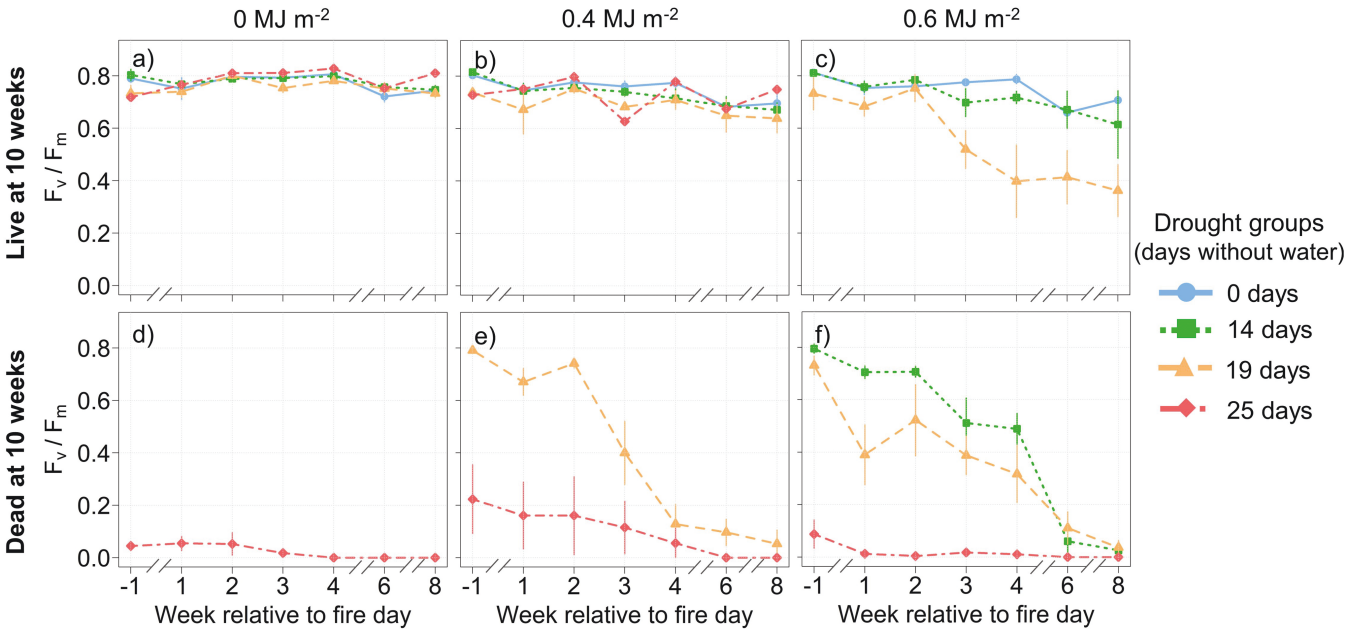

Figure 5 Temporal trajectories of average (±SE) *Pinus monticola* sapling chlorophyll fluorescence (F_v/F_m) from 1 week prefire to 8 weeks postfire for living (a–c) and dead (d–f) saplings at 10 weeks postfire. Panes show saplings in the 0 MJ m^{-2} (left), 0.4 MJ m^{-2} (center), and 0.6 MJ m^{-2} (right) fire radiative energy (FRE) dose groups.

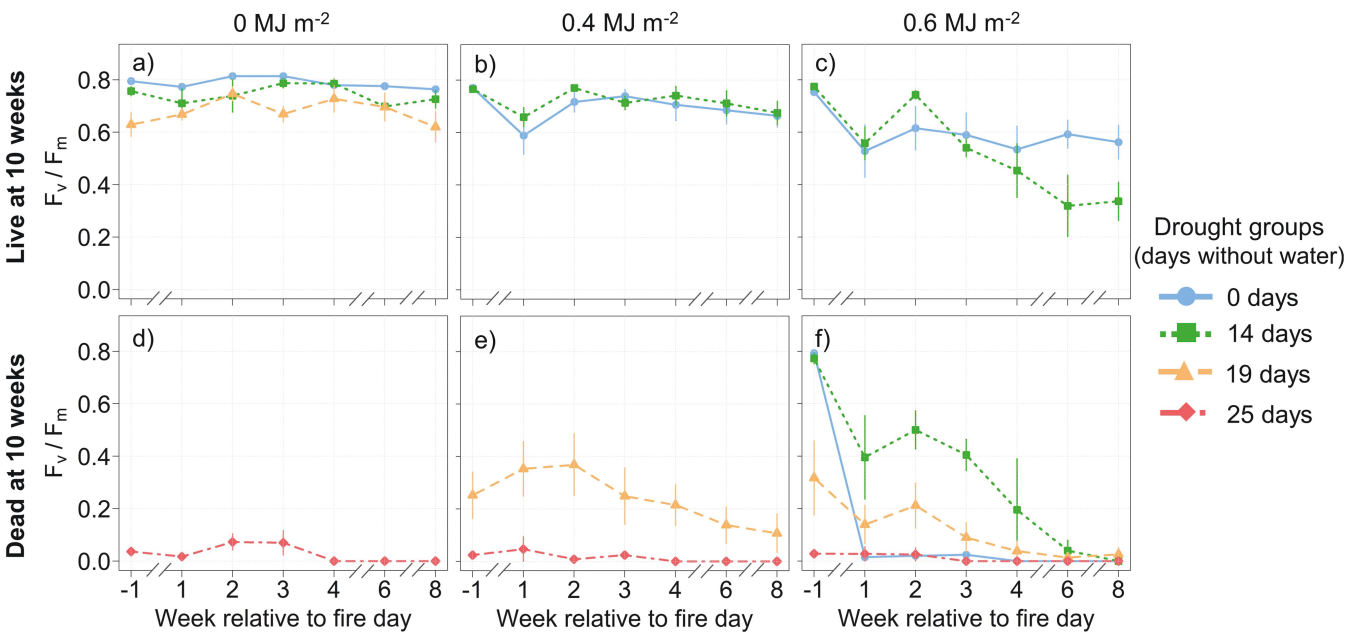

Figure 6 Temporal trajectories of average (±SE) *Pseudotsuga menziesii* sapling chlorophyll fluorescence (F_v/F_m) from 1 week prefire to 8 weeks postfire for living (a–c) and dead (d–f) saplings at 10 weeks postfire. Panes show saplings in the 0 MJ m^{-2} (left), 0.4 MJ m^{-2} (center), and 0.6 MJ m^{-2} (right) fire radiative energy (FRE) dose groups.

There were some key similarities and differences in the physiological response of *P. monticola* and *P. menziesii* saplings to the drought and fire treatments. Prior to the fire treatments, FMC for both species was higher in the 0–14 day drought groups and lower in the 19–25 day drought groups (figure 3). The substantial reduction in FMC for saplings droughted beyond 19 days for *P. monticola* and 14 days for *P. menziesii* is likely associated with increased water loss after loss of cell turgor pressure (Nolan et al. 2018, 2020; Tyree and Hammel 1972). *P. monticola* maintained higher FMC across all groups and had a longer drought length until a significant decrease in FMC (~19 days) compared with *P. menziesii* (14 days). This may be partially owing to the higher stomatal sensitivity of *P. monticola* during the onset of drought stress, as closing stomata reduces water loss due to evapotranspiration. For example, Lopushinsky and Klock (1974) observed a steeper decline in transpiration for *Pinus* spp. seedlings versus *P. menziesii* seedlings as water stress increased, indicating higher stomatal sensitivity in *Pinus* spp. seedlings. Differences in FMC during the course of our drought treatment may also

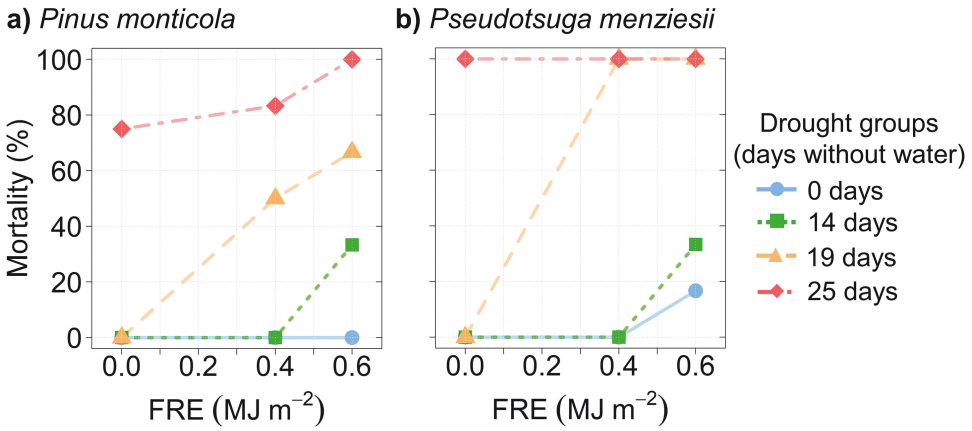

Figure 7 Dose-response relationships between fire radiative energy (FRE) and mortality at 10 weeks postfire for (a) *Pinus monticola* and (b) *Pseudotsuga menziesii* across the four drought groups.

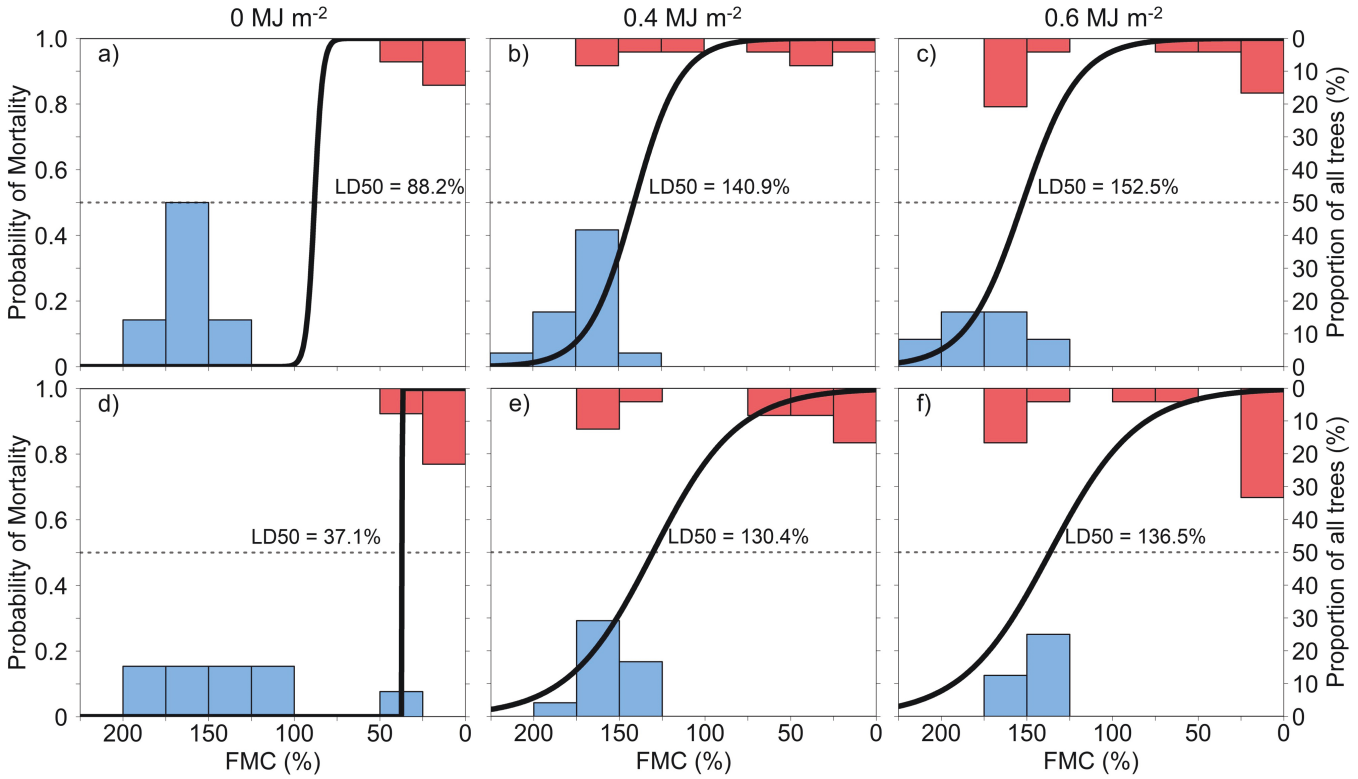

Figure 8 The 50% lethal foliar moisture content (FMC LD50, dashed line) increased for *Pinus monticola* (a–c) and *Pseudotsuga menziesii* (d–f) at 10 weeks postfire as fire radiative energy (FRE) increased from 0 MJ m^{-2} (left column) to 0.6 MJ m^{-2} (right column). Bars represent the proportion of living (blue) and dead (red) trees in each 25% FMC bin for each FRE dose group and the solid black line is the logistic regression fit.

have been driven by differences in minimum leaf conductance after stomatal closure (Duursma et al. 2019). Prefire F_v/F_m in both species mirrored FMC, where F_v/F_m was higher in the 0–14 day drought groups and lower in the 0–14 day drought groups (figure 4). As water limitation in plants impedes electron donation in PSII, resulting in lower F_v (Downton et al. 1981), it is consistent that F_v/F_m was lower in more severely droughted saplings.

Multitemporal observations of F_v/F_m provided useful information on the damage, repair, and recovery trajectory of PSII in both species. F_v/F_m in both species declined at 1 week postfire, followed by an increase at 2–3 weeks postfire, likely indicating damage to and subsequent repair of the photosynthetic apparatus. Although not statistically significant, *P. menziesii* saplings exposed to the highest FRE dose (0.6 MJ m^{-2}) generally had a greater F_v/F_m dip than those exposed to lower doses ($P = .26$). This damage-then-repair pattern has also been observed in non-water-stressed *P. monticola* saplings (Sparks et al. 2023) and *Pinus contorta* var. *latifolia* saplings (Smith et al. 2017) exposed to low intensity fires, where F_v/F_m recovered within several weeks postfire and then declined until sapling death. Other studies have observed similar short-term F_v/F_m dips after heat stress. For example, Marias et al. (2017) observed a significant decrease (~50% reduction)

in F_v/F_m in 1 year old *Pinus ponderosa* and *Pseudotsuga menziesii* seedlings for 1–2 days after exposure to 45°C air temperature for 1 hour. Generally, saplings in the current experiment with a low prefire F_v/F_m (<0.5) or a decreasing F_v/F_m trajectory after 2 weeks postfire were observed to be dead at 10 weeks postfire (figures 5 and 6). These results suggest that repeated chlorophyll fluorescence observations could be used as an early warning sign of death in these species. For example, dying trees could potentially be identified as those with a negative postfire chlorophyll fluorescence trajectory.

Table 2. Confusion matrix results showing live or dead classification accuracy for *Pinus monticola* and *Pseudotsuga menziesii*, averaged across the 100 classification iterations. Accuracy metrics report the mean (±95% confidence interval).

Live or dead classification	Accuracy metric	*P. monticola*	*P. menziesii*
Dead	Producer's accuracy	58.9 (5.3)	68.8 (4.0)
	Omission error	41.1 (5.3)	31.1 (4.0)
	User's accuracy	82.4 (4.9)	79.3 (3.6)
	Commission error	17.6 (4.9)	20.7 (3.6)
Live	Producer's accuracy	93.4 (1.7)	86.2 (2.3)
	Omission error	6.5 (1.7)	13.8 (2.3)
	User's accuracy	82.7 (2.2)	79.1 (2.8)
	Commission error	17.3 (2.2)	20.8 (2.8)
	Overall accuracy	82.0 (1.9)	78.5 (1.9)

Amplified mortality in drought-stressed saplings subjected to low intensity surface fires appears to be highly dependent on species. Our observations of greater mortality in *P. monticola* and *P. menziesii* saplings exposed to greater drought and surface fire intensity match some prior studies but not others. Similar to our observations, Partelli-Feltrin et al. (2020) observed greater mortality in water stressed ($\Psi_{predawn}$: -0.84 MPa) *P. ponderosa* saplings subjected to low intensity surface fire (FRE = 0.7 MJ m^{-2}) (100% mortality) than in well-watered saplings (~25% mortality). Likewise, Sparks et al. (2018) observed greater mortality (86%) in water-stressed ($\Psi_{predawn}$: -1 to -1.75 MPa) *Larix occidentalis* saplings subjected to low-intensity surface fires (0.4 MJ m^{-2}) compared with well-watered saplings (14% mortality). Notably, severely water-stressed ($\Psi_{predawn}$: -2 to -2.75 MPa) *L. occidentalis* saplings whose foliage senesced prior to the surface fires displayed lower mortality (14%) than saplings that did not senesce (86%). These mortality patterns are in stark contrast to observations of species that can resprout from insulated buds near or below the soil surface. Wilson et al. (2022) observed less than 10% mortality in water-stressed ($\Psi_{predawn}$: -2.4 MPa) *P. palustris* seedlings that were subjected to surface fires with a FRE of ~5 MJ m^{-2}. However, it should be noted that these seedlings were in their highly fire-resistant "grass stage," where seedlings only have a tuft of needles and a few centimeters of stem above the soil surface. Similarly, other studies have observed no mortality in water-stressed *Quercus* spp. saplings that were top killed in surface fires (Chiatante et al. 2015; Di Iorio et al. 2011). Clearly, the observed variability in drought and fire responses among

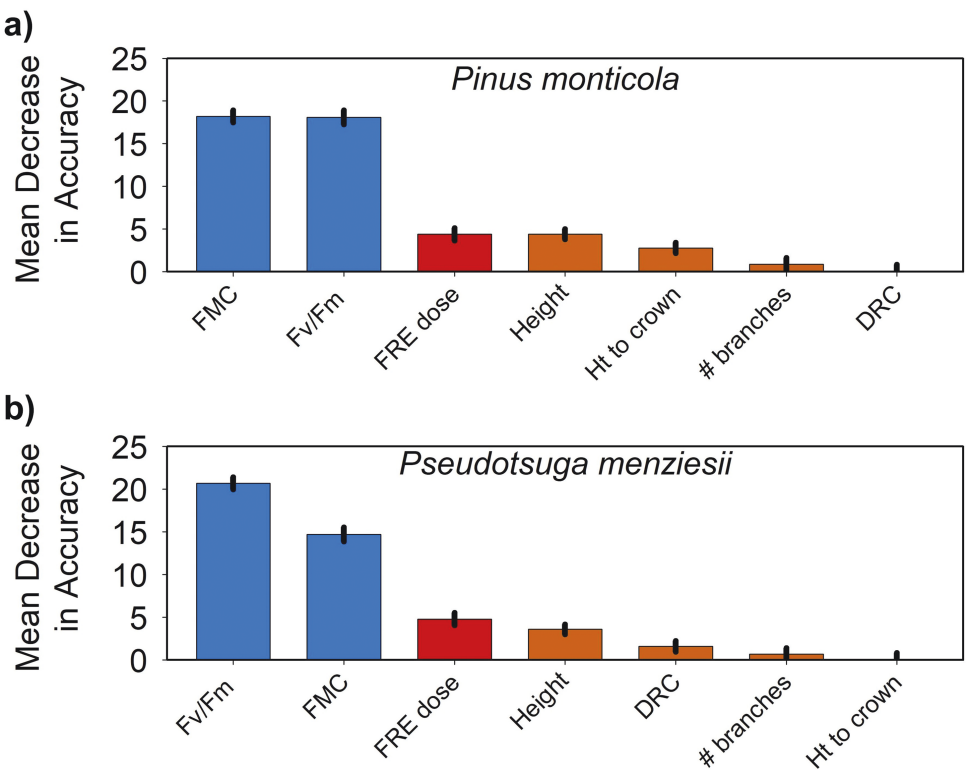

Figure 9 Predictor variable importance reported as the mean (±95% confidence interval) decrease in live or dead classification accuracy for (a) *Pinus monticola* and (b) *Pseudotsuga menziesii*. All physiological (blue) and morphological (brown) variables were measured prior to fire. Higher values indicate variables that are more important to the classification. FMC, foliar moisture content; F_v/F_m, chlorophyll fluorescence; FRE, fire radiative energy; height, total sapling height; Ht to crown, height to live crown; # branches, number of live branches; DRC, diameter-at-root-collar.

studies underscores the need to repeat similar experiments in more species and size classes.

The most important mortality predictor variables were prefire FMC, F_v/F_m, and FRE dose, and the least important were morphological attributes. Our finding that prefire physiological status plays a dominant role in postfire survival is perhaps unsurprising given its observation in prior studies (e.g., Partelli-Feltrin et al. 2020; Sparks et al. 2018; Wilson et al. 2022); however, we demonstrate that measures of prefire physiological status coupled with fire intensity can increase the accuracy of postfire mortality prediction. FMC and chlorophyll fluorescence can be accurately estimated using airborne and satellite-based sensors (Yebra et al. 2013; Ač et al. 2015; Lad et al. 2023) and could potentially be used to predict tree mortality after fire across large spatial scales. This is in contrast to postfire characteristics used for mortality modeling, such as crown scorch and stem charring, which provide accurate mortality predictions but are difficult to collect at large scales as they need to be assessed on the ground (Varner et al. 2021). However, conifer foliage water content has been accurately quantified using multispectral terrestrial laser scanning systems (Junttila et al. 2015, 2018). A similar airborne sensor could potentially be used to infer the proportion of the tree crown that was scorched, as scorched foliage would likely have a lower FMC due to desiccation (Varner et al. 2021). Estimates of sapling FMC or F_v/F_m could be useful for informing prescribed fire practitioners of the sapling conditions and fire intensity needed to increase or reduce mortality in undesired or desired species, respectively (Smith et al. 2017; Steady et al. 2019). Beyond physiological condition and fire intensity, height was the most important morphological predictor variable. This finding is consistent with observed and theorized size-dependent fire-induced mortality where fire kills a higher proportion of smaller trees versus larger trees (McDowell et al. 2018; Stephens and Finney 2002). Generally, this mortality pattern occurs given fire-resistant traits such as thick bark, which protects sensitive cambium and phloem tissues, and high crowns, which protect sensitive foliage, are not fully developed in younger, smaller trees (Starker 1934; Vanderweide and Hartnett 2011). In our study, *P. monticola* that were alive at 10 weeks postfire had a higher average prefire height (83 cm) than those that died (80 cm). Likewise, living *P. menziesii* had a higher average prefire height (117 cm) than dead saplings (99 cm) at 10 weeks postfire. It is likely that shorter saplings had a higher proportion of crown scorch within a given FRE dose level given the relationship between fire intensity and crown scorch height (van Wagner 1973).

Although this study improves our understanding of compound disturbance effects on young conifers, several limitations should be explored in future research. This study watered saplings immediately after the fire treatments, which is unlikely to occur in natural ecosystems. Future research should examine the effects of pre- and postfire drought on tree injury and mortality to understand compounding effects more fully. Using potted saplings allows for highly controlled manipulation, including drought length and fire intensity; however, this approach does have limitations. Namely, potted saplings have limited rooting volume and likely have higher water stress than saplings in natural settings that have unrestricted rooting volume (Poorter et al. 2012). It is possible that the FRE-mortality relationships for saplings in natural settings would change given that their unrestricted root growth would allow for access to deeper water sources. Additionally, saplings and mature trees in natural settings may have improved resilience to and recovery from fire from local mycorrhizal symbioses (Atala and Molina-Montenegro 2023). This study used a random forest classification approach to predict mortality, which does have some limitations. In general, random forest approaches are less interpretable (i.e., "black box") than other modeling approaches when it comes to understanding why certain outcomes were produced (Cutler et al. 2007). However, in terms of modeling tree mortality, accurate prediction may be more important than interpretability for forest management applications (Shearman et al. 2019). The modeling also highlights that further research is needed to assess predictive mortality relationships that address coupled fire and drought interactions in other species with the goal to provide a critical update to fire effects modeling systems. Equally, future studies should consider incorporating additional dimensions of enquiry, such as how such shifts of the fire-intensity-to-mortality dose-response curves are affected by increases in tree age as well as other environmental, abiotic, and biotic factors such as nutrient availability, microclimatic conditions, topographic variables, among others.

Conclusions

The quantification of compound disturbance effects on trees is a forest management research need given projected increased frequency of drought and wildfire in the western United States. This study advances our understanding of drought and fire effects through the use of a controlled dose-response approach, where saplings were subjected to varying drought and fire intensities and physiological condition and mortality were measured for several months postfire. Results show that droughted *P. monticola* and *P. menziesii* saplings exhibit diminished recovery in terms of photosynthetic efficiency and greater mortality after low intensity surface fires. The higher postfire photosynthetic efficiency and lower mortality of *P. monticola* compared with *P. menziesii* demonstrates the higher fire resistance of *P. monticola* at this life stage. For both species, repeated observations of postfire chlorophyll fluorescence, an indicator of photosynthetic efficiency and stress, suggest that the trajectory of postfire fluorescence could be used as an early warning sign of impending tree death and a predictor variable in tree mortality modeling. Postfire mortality modeling using prefire physiological and morphological attributes and fire intensity provided accurate mortality predictions and highlights the importance of prefire tree physiological condition and fire intensity for mortality prediction. However, this analysis should be repeated for more species and size classes with a larger variation in morphological attributes. The results of this study and others lay a foundational knowledge base for natural resource managers seeking to understand which prefire tree condition and fire intensity decreases or increases mortality of desired and undesired species. Additionally, the amplified drought and fire sapling responses observed in this study and others highlights the need to incorporate these relationships into tree mortality models used by natural resource managers.

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability

The data underlying this article will be shared on reasonable request to the corresponding author.

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