FINAL REPORT

Effects of different fire intensities on *Pinus ponderosa* sapling physiology and mortality.

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List of Abbreviations/Acronyms

CFDA - carboxyfluorescein diacetate
FOFEM – First Order Fire Effects Model
IFIRE – Idaho Fire Initiative for Research and Education
FLI – Fire Line Intensity
FRP – Fire Radiative Power
FRE – Fire Radiative Energy
LAOC – Western larch
PICO – Lodgepole pine
PIMO – Western white pine
PIPO – Ponderosa pine
PSME - Douglas fir
UIEF – University of Idaho Experimental Forest
USFS – United States Forest Service

Keywords

Fire intensity, fire severity, pryoecophysiology, fire-induced tree mortality

I. Abstract

Throughout the conifer forests of the western United States, wildfires are projected to become larger and more frequent under climate change. The use or prescribed fires is one pathway to mitigate these fires and reduce crown fire hazard. Regardless, whether more prescribed or wildfires, the result is that younger trees (<10 years old) are going to burn more often. A challenge of land managers tasked with making informed decisions is that very little data exists on how fire affects sapling mortality, physiology and recovery. An added challenge is that in some cases, certain tree species may be desirable (e.g., high merchantable value), while in other cases species may be considered weeds. As such knowledge of how much fire behavior kills some species, while protecting others, would be a powerful management tool. To meet this need, this GRIN proposal explored the effects of fire intensity on sapling morphology, physiology and mortality of different sapling size classes of ponderosa pine (*Pinus ponderosa*). We grew ponderosa pine from seed and conducted experimental burns in the laboratory and monitored the results of these experiments over a series of years. We also conducted prescribed fires and integrated our observations with prior studies we conducted on mature ponderosa pine. We also expanded the original scope of the GRIN to include a wider array of saplings from other important tree species and investigated the interactions of drought alongside fires. We demonstrated that 1.2 MJ/m^2 was a lethal fire intensity (as measured via fire radiative energy) threshold for 1-2-year-old saplings of 5 different conifer species (ponderosa pine, lodgepole pine, western larch, Douglas fir, and western white pine.). We further demonstrated that for each of lodgepole pine, western white pine, and ponderosa pine that 100% survival of 1-2-year-old saplings occurred when subjected to low intensity surface fires <0.4 MJ/m^2. We also presented conclusive evidence that deformation of xylem cells and loss of xylem hydraulic failure were not the primary mechanisms leading to mortality in ponderosa pine saplings. This result was counter to prevailing scientific knowledge of how fire causes fire-induced tree mortality and to confirm the results, we wholly repeated the experiment. Following 2^{nd} confirmation, we presented evidence to support the counterhypothesis that fire-induced tree mortality in ponderosa pine is due to localized carbon starvation due to lack of phloem transport of sugars and carbohydrates. Given saplings represent the worst-case scenario as trees generally become more fire resistant with age, the identification of a low fire intensity 100% survival threshold will be of considerable use to land managers seeking to use fire as a silvicultural tool. We are actively sharing this data with an international modeling team and developing a data synthesis paper with them. All the project data is being shared via the USFS Research and Development Data Archive. Future research should focus on a wider array of species and trees over a range of ages.

II. Objectives

The specific objectives of this project included:

1) Evaluate how fire behavior during prescribed fires leads to mortality of ponderosa pine saplings,
2) Describe the post-fire effects of the ponderosa pine saplings in terms of changes to the morphology and physiology, and
3) Improve predictions of sapling mortality and post-fire effects.

To meet these objectives, we seek to answer the following hypotheses:

H_{01}: Cambium necrosis and foliage damage increases with increasing fire intensity for all root collar diameter classes.

H_{02}: Net photosynthesis decreases with increasing fire intensity for all root collar diameter classes.

H_{03}: As ponderosa pine saplings increase in root collar diameters, greater fire intensities will be needed to cause mortality.

The products this project proposed to develop included (i) improved predictions of sapling mortality and fire effects that could be integrated with fire effects models such as FOFEM, (ii) and a look-up table where managers can readily infer sapling mortality from fire behavior.

III. Background

It is widely accepted that wildfire occurrence and severity is projected to increase in many western United States (US) ecosystems in response to climate change [Bowman *et al.* 2017; Fig 1A]. Across this region there is also a broad recognition of a ‘prescribed fire deficit’ [Kolden, 2019], which can only be addressed by increasing the number of prescribed fires [Voelker *et al.* 2019]. As fires become more frequent, younger cohorts of trees (<10 years old) will be more likely to experience fires. [Smith *et al.* 2017] We will also likely see a shift of fires to ecosystems where they have historically been less common (higher elevations, higher latitudes, wetter areas, etc.,). Recent US fire seasons, including 2021, have demonstrated the need to improve our understanding of how fires impact forested ecosystems to better predict and mitigate negative impacts on critical forest goods and services [Smith *et al.* 2014]. A current challenge on forecasting the impacts of fires on younger trees is that most research to date has focused on

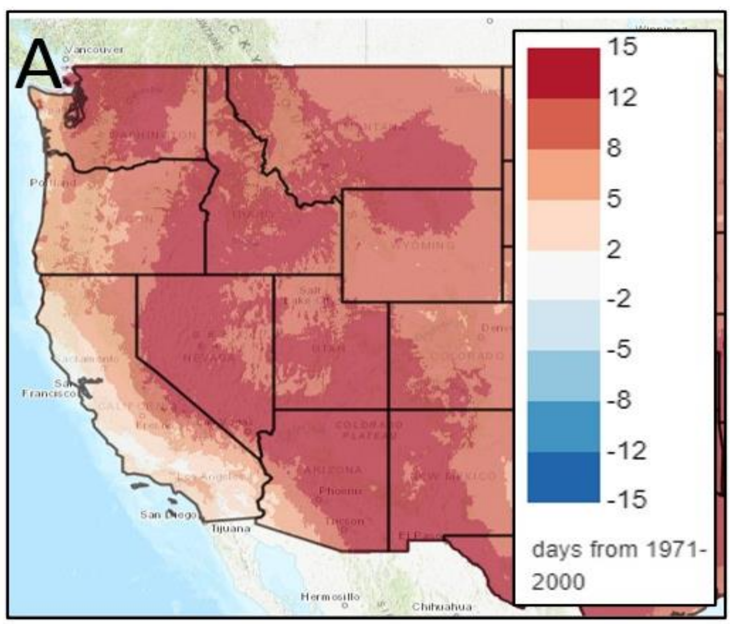

Fig 1. (A) Mean projected change in fire danger days for 2040-2069 versus 1971-2000 (J.T. Abatzoglou).

older trees. Most logistic regressions used in fire effects modelling systems such as the First Order Fire Effects Model and the Forest Vegetation Simulator – Fire and Fuels Extension are only focused on mature trees [Rebain, 2015; Lutes, 2019]. Notably, in FOFEM, the only set of regressions focused on young saplings, was for *Pinus ponderosa* in the Black Hills of South Dakota [Battaglia *et al.* 2009]. Therefore, to enable land managers to make informed decisions on how to manage forests, research is needed to accurately predict how fires will affect sapling mortality, physiology and recovery across a variety of important tree species. An added challenge is that in some cases, certain tree species may be desirable (e.g., high merchantable value), while in other cases species may be effectively considered as weeds.
As such knowledge of how much fire on the ground it takes to kill some species, while protecting others would be a powerful management tool [Steady *et al.* 2019]. For land managers to plan prescribed fires more effectively to successfully predict post-fire sapling mortality, the effect of fire intensity on sapling tissue damage (e.g., cambium and foliage) is needed. Depending on the fire intensity, some small saplings can experience mortality, while other survive but grow at reduced rates [Smith *et al.* 2017]. Understanding the fire effects on sapling physiology can improve the predictions of mortality/recovery under different environmental conditions. To meet this need we in this GRIN proposed to extend an existing doctoral dissertation that was focused on improving the understanding of the effects of fire intensity on sapling morphology, physiology and mortality of different sapling size classes of ponderosa pine (*Pinus ponderosa)*. The project started in Fall 2019, at the start of the COVID-19 pandemic and faced considerable logistical and meteorological hurdles. Regardless, considerable research was performed that will help land managers use fire more effectively in the management of tree species.

IV. Materials and Methods

i. Overview

In this report, we describe five distinct sets of experiments:

A. The preliminary study on Ponderosa Pine saplings that was partially reported by Steady et al. (2019). As part of this final report, we report the additional analysis conducted after the start of this award that was not included in the publication of the preliminary work. The paper associated with the preliminary work that served as the basis of this GRIN project was co-led by Wade Steady and the GRIN student investigator Raquel Partelli-Feltrin.
B. A study exploring the impact of drought and different fire intensities on ponderosa pine saplings that was reported in Partelli-Feltrin et al. (2020).

Fig 2. Prescribed fire site showing locations of regular grid of 80 ponderosa pine saplings (shown by pink flags).

C. A study exploring whether xylem deformation or loss in hydraulic failure were the mechanisms responsible for why ponderosa pine saplings die in fire. This was reported in Partelli-Feltrin et al. (2021).
D. A study exploring whether localized starvation of carbohydrates in the phloem is the mechanisms responsible for why ponderosa pine saplings die in fire. At the time of this report, this is being prepared for publication.
E. A study exploring survival and mortality fire intensity thresholds for both Douglas fir and western white pine. At the time of this report, this is being prepared for publication. As part of this study, we conducted preliminary analysis of cambium death within the Douglas fir as a function of fire radiative energy as a potential pathway to assess Hypothesis H_{01}.

We further aggregated results from additional experiments on western larch and lodgepole pine saplings. Results from assessing the impacts on prescribed fires on ponderosa pine saplings are not shown as the prescribed fire in Fall 2020 caused 100% mortality, which the UI Experimental Forest staff attributed to excessive heat experienced prior to the fires. Pandemic restrictions throughout 2020 followed by an abnormally wet fall in 2021 limited the ability for additional prescribed fires on the University of Idaho Experimental Forest.

ii. Study Area and Experimental Overview

In the various experiments, all combustion laboratory experiments were conducted at the University of Idaho IFIRE Combustion Laboratory located at the Parker Farm in Moscow, Idaho. The prescribed fire studies were located on the University of Idaho Experimental Forest (UIEF) located approximately 20km north-east of Moscow Idaho. For each of the experiments with saplings, saplings were grown from seed and potted in 1-gallon pots, grown, and re-potted in 5-gallon pots with standard Sungro ® forestry mix number 3. Saplings were grown until 1.5-2 years old in a climate-controlled greenhouse at University of Idaho with maximum and minimum temperatures of 25 and 15°C, respectively. Saplings were watered every other day and fertilized once every month with 20:20:20 Technigro@ fertilizer. 80 1-year-old saplings used in prescribed fire experiments were planted at 1-year old in a regular grid.

A. Preliminary Study

In this study, 50 ponderosa pine saplings were used to explore FRE dose to plant morphology/physiology ‘response’ experiments, where the saplings were assessed over five treatment levels (L=5, n=10, N=50).

B. Drought and Fire Interaction Experiment

In this study, 60 ponderosa pine saplings were divided into two water treatment and three FRE groups: two levels of water stress defined by pre-dawn leaf water potential and three FRE treatment groups (n=10, N=60).

C. Testing Xylem Deformation and Loss of Hydraulic Conductivity

In this study, we experimentally evaluated fire effects on the xylem function of well-watered ponderosa pine saplings through combining two experiments that allowed us to assess both the short- and long-term impacts of fire. We assessed the short-term (1-day post-fire) impact of fire on hydraulic conductivity in plants exposed to a known lethal fire intensity. For the long-term evaluation (21-months post-fire), we only used saplings that were able to survive a lower intensity fire treatment. A total of 12 saplings were used in the short-term experiment and a future 54 in the long-term experiment. The hydraulic conductivity, knative and kmax, was measured in all species on excised stems using a degassed perfusion solution of 0.02M KCl and 0.012M HCl with a Sperry apparatus. Prior to measurements at each pressure, stem segments were submerged in the perfusion solution, and both ends recut to avoid cutting artifacts, following best practices [see Partelli-Feltrin *et al.* 2021 for details]. After native conductivity measurements, excised stems were placed under water and under vacuum until all emboli are removed, then remeasured for conductivity. Percent loss of conductivity (PLC) was calculated using PLC = 100*[1-(knative/kmax)]. Thin micro sections (30 μm width) were shaved from wet core blocks using a rotary microtome. The sections were then saturated with a staining agent: Safranin (red stain) and Astrablue (blue stain) applied as a 1:1 solution to produce a clear contrast between lignified and unlignified cell structures, respectively [see Partelli-Feltrin *et al.* 2021 for details].

D. Testing Localized Carbon Starvation in the Phloem

In this study, 100 ponderosa pine saplings were divided into multiple groups. 30 saplings were randomly divided in to two treatment groups – control and burned, and assessed 6-, 13-, and 27-days post-fire. A 3x3 factor design was used to evaluate the effects of fire on nonstructural carbohydrates. 50 saplings were randomly divided in three treatments: control, burned, and defoliated and assessed 7-, 14-, and 28-days post-fire. In addition, 5 saplings were measured for hydraulic conductivity and harvested for nonstructural carbohydrates one day before fire treatment to assess pre-fire physiological status. To indirectly evaluate phloem dysfunction, we measured nonstructural carbohydrate (NSC) concentrations in needles, stems, and roots. A buildup of NSC, or a stable concentration, in foliage, while NSC declines in stems and roots, as we observed in our preliminary data (**Fig 3E)** can be used to infer that phloem is unable to transport sugars from photosynthetic source tissues, to non-photosynthetic sink tissues. Samples werecollected, microwaved to halt metabolism, dried, ground, and stored following best practices. We used 80% ethanol for sugar extraction, alpha-amylase and amyloglucosidase for starch digestion, and the phenol-sulfuric acid method for quantification. This protocol produced repeatable measurements with <10% error among and between laboratories, addressing recent issues with NSC methods [Quentin *et al.* 2015; Landhäusser *et al.* 2020].

E. Lethal and Survival Thresholds in Western White Pine and Douglas Fir Saplings.

In this study, conducted in part as an add-on to offset the pandemic restrictions and subsequent challenges due to excessive rainfall that prevented a subsequent prescribed fire, we explored how a series of FRE levels impacted fire induced mortality in saplings of two additional tree species. In each case, 35 saplings were divided into 5 treatment groups. For a subset of unburned and fire-affected Douglas fir saplings we collaborated with Dr. Michael Knoblauch at Washington State University to assess the degree of cambium damage as a function of FRE. Our objective was to evaluate whether vital stains were a viable approach to assess hypothesis H_{01} and similar assessments of cambium damage in saplings experiencing fire. The direct assessment of cambium-phloem death was assessed using 5/6 carboxyfluorescein diacetate (CFDA, **Fig 3F**), which is a non-fluorescent, membrane permeant component that readily enters cells [Savage et al. 2017]. In the cytosol the component gets processed by cell integral esterases which are present in all known living cells. The diacetate is removed which releases negatively charged carboxyfluorescein (CF) that is not membrane permeant and is trapped inside the cell. As dead cells lack active esterases the component labels exclusively lining cells and has widely been used as cell viability stain.

iii. General Fire Behavior and Combustion Measurements

In all the experiments the fire intensity as described in terms of the fire radiative energy (FRE), which is related to the fire line intensity [Kremens et al. 2012]. In **Studies A and E**, the FRE doses were created from known fuel loads using the following relationship derived from calibration experiments: FRE (MJ) = 2.679 x pre-fire fuel load (kg of western white pine needles at 0% moisture content). **In Studies B-D**, a similar relationship was generated for Ponderosa pine needles as FRE (MJ) = 5.74 x fuel consumed (kg) and FRE (MJ) – 4.36 x fuel load (kg). FRE is the time integral of Fire Radiative Power (FRP) over the duration of the fire [Wooster et al. 2021]. Additional data not previously reported in the study by [Steady et al. 2019] in **Study A** included start and end times of the experiment and measurements of ambient air temperature and relative humidity both inside the combustion laboratory and outside. In **Study A** flame lengths were recorded using marked poles and videography.

In **Study A**, the FRE treatment levels were 0 (unburned), 0.2, 0.4, 0.6, 0.8 MJ/m^2.
In **Study B**, the FRE treatment levels were 0 (unburned), 0.7, 1.4 MJ/m^2.
In **Studies C and D**, the FRE treatment levels where 0 (unburned), 0.7, 1.4 MJ/m^2.
In **Study E**, the FRE treatment levels were 0 (unburned), 0.4, 0.6, 0.8, 1.0 MJ/m^2.

iv. Tree Morphology Metrics

In **Studies A and E** Diameter at root collar (DRC) measurements were taken pre-fire and once per week post-fire for up to four months or until winter dormancy occurred. In **Studies B-D**, DRC was measured at two locations and an average recorded, but only for each sapling in the water stressed group at the start of the experiment. In each of these studies, all saplings were marked on the bole at the root collar to allow for consistent height and stem measurements. All DRC measurements were conducted using digital calipers. In each study, heights were recorded from the soil surface to the tip of each sapling’s leader. In each study. all height measurements were conducted with measuring tapes.

v. Tree Physiology Metrics

In **In Study A,** data that were not originally presented in [Steady et al. 2019] included gas exchange data. Specifically, leaf water potential was measured at predawn (Ψpredawn) one day prior to the burn experiments and at 30 days post-fire using a Model 1505D Pressure Chamber (PMS Instruments Company, Albany, OR, USA). Three saplings from each dose group were randomly selected for measurement.

For each measurement, one needle fascicle in the upper third of the sapling canopy was used. Light-saturated (1500 µmol m-2 s-1 photosynthetic photon flux density) gas exchange measurements were performed on the same days as Ψpredawn using a LI-6400XT and 6400–05 LED light source and broadleaf chamber (LI-COR, Inc., Lincoln, NE) on five random-ly-selected plants in each dose group. Two, three-needle fascicles from each sapling were used per measurement. Needle area for each sample was measured with a LI-COR LI-3100C leaf area meter and used to calculate net photosynthesis and stomatal conductance on leaf area basis. In **Study B**, pre-dawn leaf water potential was measured 1 day pre-burn and 1, 14, 27, and 370-days post-fire using a Model 1505D Pressure chamber (PMS Instruments Co.). In **Study B**, measurements of photosynthesis were acquired at 1-day pre burn and at 1, 14, 27, and 370-days post-fire using light saturated (1400 µmol photons m-2 s-1 photosynthetic photon flux density) measurements with a LI-6400XT and 6400-05-LED light source and broadleaf chamber (LI-COR. Inc.).

V. Results and Discussion:

i. Survival and Mortality Thresholds

The relationship between FRE and sapling mortality for experiments that assessed sapling mortality at more than four doses of FRE generally exhibited a sigmoidal shape (**Fig 3A**). However, both western larch and western white pine exhibited a more linear relationship. Western white pine saplings also exhibited a 0.4 MJ/m^2 threshold below which survival was 100%, but 100% mortality occurred at 0.6 MJ/m^2, indicating a more binary response—although more FRE levels may be needed to tease out a response or the experiment repeated to confirm the results. In Douglas fir, we observed two clear states where fires < 0.6 MJ/m^2 led to ~60% survival and fires > 0.8 MJ/m^2 led to 100% mortality in 1–2-year-old saplings. Notably, 0.4 MJ/m^2, indicated zero mortality of lodgepole pine, ponderosa pine, and western white pine in doses below this threshold. This suggests a potential compensating mechanism that allows *Pinus* species subjected to low fire intensity dose fires to survive despite losing substantial foliage and other injuries, but clearly more *Pinus* species need to be assessed to evaluate whether this is a genus-based adaptation, associated with specific *Pinus* sub-groups, or just limited to these three species. As noted by [Steady et al. 2019], identification of 100% survival and 100% mortality thresholds on a species-by-species basis could help guide fire managers identify 'how much fire to put on the ground' to sustain selective species or kill species considered as weeds.

ii. Cambium Necrosis and Foliage Damage

As demonstrated by **Fig 3F**, we do observe increased degrees of cambium necrosis with increasing FRE in Douglas fir saplings. Notably, in the FRE treatments < 0.6 MJ/m^2. Evidence of living xylem, cambium, and phloem are apparent. This analysis was conducted 7 weeks post-fire. Clearly, although this preliminary data supports H_{01}, it by itself is not sufficient to be conclusive. However, it does serve as a valid proof-of-concept to conduct follow-up studies using vital stains as a methodology to explore how increasing fire intensity impacts phloem, cambium, and xylem damage in trees. The fire treatments in all the studies highlighted led to significant crown scorch and foliage damage in all dose groups, which could result in defoliation-like effects. **As shown in Fig 6, the observations clearly support H_{01} that foliage**

<u>damage increases with increasing FRE</u>. These results were consistent with western larch and lodgepole pine and are observed in Douglas fir and western white pine (as shown in **Fig 8** below).

iii. Net Photosynthesis Changes

In the early studies by Smith et al. [2017], linear relationships between change in net photosynthesis and FRE doses were observed for both lodgepole pine and western larch and are shown in **Fig 4a.** As also shown in **Fig 4a**, the change in net photosynthesis for ponderosa pine is more complex. Ponderosa pine saplings in **Study A** exhibited increased photosynthesis in individuals subjected to higher FRE (up to ~0.6 MJ/m^2) (**Fig 4a**, **Fig 5**). Other studies have observed increasing net photosynthesis with increasing crown scorch in mature ponderosa pine, measured ~60 days post-burn [Wallin et al. 2003]. Likewise, in **Study A**, net photosynthesis increased with increasing dose and crown scorch (**Fig 4** and **5**), except at the highest dose where visibly damaged needles (i.e., discolored yellow-green needles) were used for the photo-synthesis measurement. Elevated levels of photosynthesis in undamaged foliage could allow saplings to compensate for lost foliage and ultimately survive. On the contrary, neither lodgepole pine nor western larch photosynthesis in [Smith et al. 2017] exhibited this increasing trend. It is possible that the slight differences in photosynthesis measurement between the different studies could account for this discrepancy. **<u>Overall, H_{02} is not supported for ponderosa pine, although it does hold for western larch and lodgepole pine.</u>**

iv. Effect of Diameter Size on Ponderosa Pine Mortality

As noted, the prescribed fire that occurred at the site of the planted saplings produced inconclusive data. The fire was originally planned for Fall 2019 and was operationally delayed due to restrictions imposed by the COVID-19 pandemic. The site was burned in Fall 2020 by the staff of the UI Experimental Forest without giving the project team any advance notice. As such, fire behavior was not recorded, and a post-fire census of the saplings revealed 100% mortality. Given the less-than-ideal outcome, we identified a site for an additional prescribed fire where a range of ponderosa pine saplings were present for a prescribed fire during Fall 2021. However, an exceptionally wet fall led to only a few acres being burned that did not include the planned site. **<u>As such, H_{03} was not tested.</u>** Given the inability to assess H_{03} in 2019 and given it was clear that uncertainty existed on whether the UI Experimental Forest could conduct a prescribed fire in 2020 and 2021 that would meet our expectations, we performed a series of '**added value**' experiments that extended the original objectives of the GRIN H_{01} and H_{02}.

v. Added Value 1: Impact of drought and fire treatments on ponderosa pine mortality.

As described in more detail in Partelli-Feltrin et al. (2020), this study demonstrated that regardless of whether ponderosa pine saplings were well-watered, or drought stressed, the 1.4 MJ/m^2 FRE value led to 100% mortality. More importantly, a lower FRE value of 0.7 MJ/m^2 demonstrated clear difference between well-watered and drought stressed saplings exposed to fire. Specifically, all drought stressed saplings exposed to a FRE of 0.7 MJ/m^2 died while 70% of the well-watered saplings recovered. In a further assessment of H_{02}, we observed that net change in photosynthesis declined regardless of the FRE or drought stress and that after a year following the fire the well-watered surviving saplings had similar photosynthesis levels to unburned saplings.

vi. **Added Value 2: Assessing whether deformations in xylem cell wall structure or loss of hydraulic conductivity cause fire-induced tree mortality in ponderosa pine.**

Although not described in Partelli-Feltrin et al. (2021), **we conducted this entire study twice to confirm the results as they ran counter to prevailing scientific opinion**. As shown in **Fig 3C**, in the first study we generated evidence that hydraulic conductivity was not significantly different between unburned saplings and saplings burned at a lethal FRE level for either of ponderosa pine or western white pine. As shown in **Fig 7**, we also in the first study did not observe any deformation of the xylem in either ponderosa pine or western white pine in saplings subjected to lethal (1.4 MJ/m^2) FRE levels. As presented in detail in Partelli-Feltrin et al. (2021), the repeated study conclusively demonstrated that hydraulic failure or xylem cell deformation is not the principal short-term driver of fire-induced mortality in ponderosa pine saplings. The second study did not repeat the experiment for western white pine due to a lack of available funds. As described by Partelli-Feltrin et al. (2021), an interesting result as that fires did cause the xylem to be less resistant to fire 21 months later, highlighting the challenges of managing for species where fire return intervals are short. Partelli-Feltrin et al. (2021) posited that this occurred due to the production to traumatic xylem.

vii. **Added Value 3: Assessing changes in nonstructural carbohydrates in ponderosa pine at different FRE levels.**

As shown in **Fig 3E**, significant differences are apparent between the unburned and burned whole plant nonstructural carbohydrates for ponderosa pine saplings burned at lethal FRE levels. We also observed that in the lethal FRE cases, cambium mortality was total. This data provides additional support for H_{01} that cambium necrosis and not hydraulic failure or xylem cell deformation is the principal mechanism of fire-induced tree mortality in ponderosa pine.

viii. **Added Value 4: Assessing impacts of FRE dose on western white pine and Douglas fir saplings.**

As shown in **Fig 8**, we were able to further support H_{01} in two additional species: western white pine and Douglas fir. As described in V.i we were also able to identify the FRE thresholds for 100% survival and 100% mortality in these species. The results from these extra studies are currently being prepared for publication.

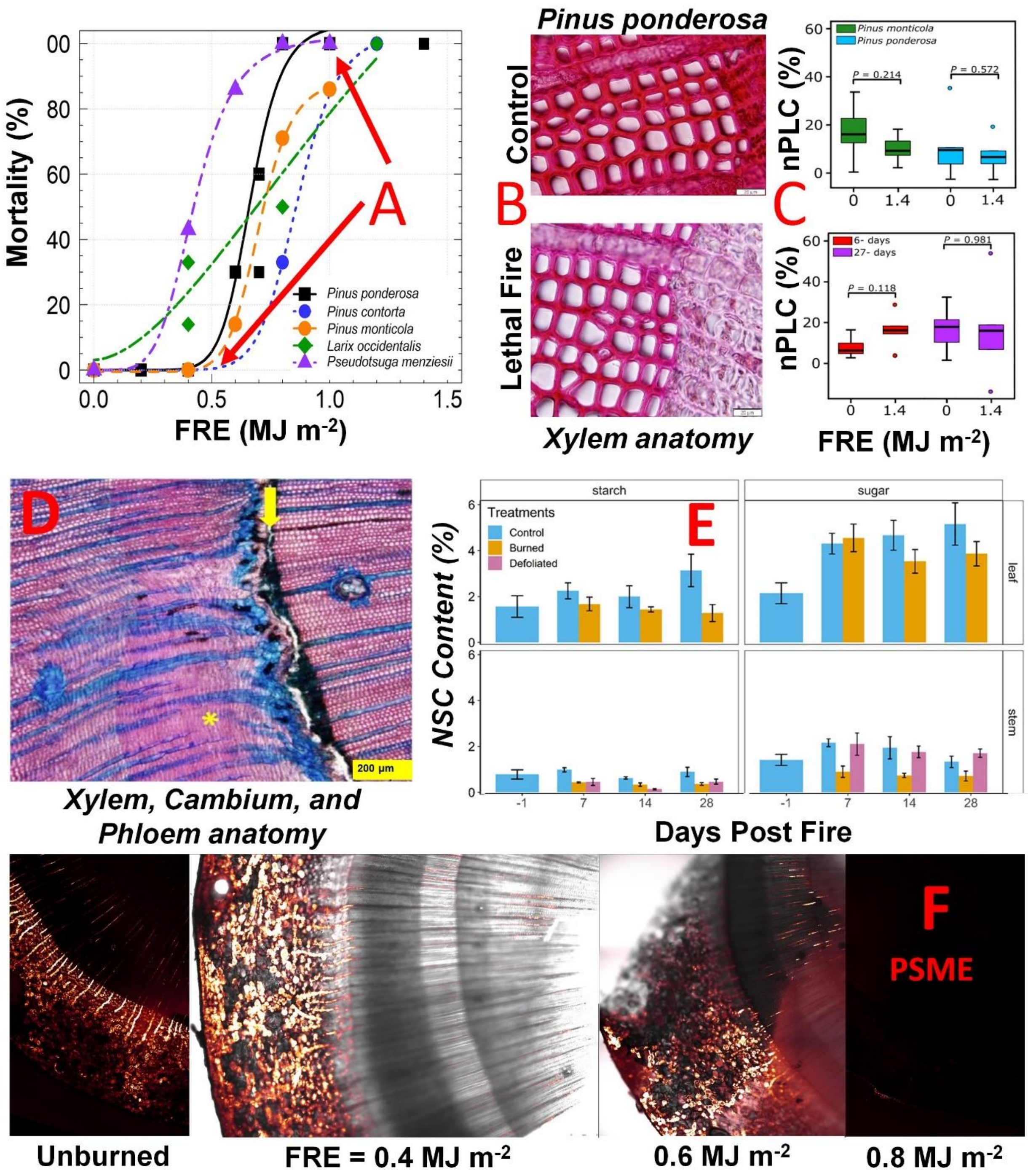

Fig 3. Selection of study results. (A) Survival and lethal thresholds, (B) Lack of xylem deformation in ponderosa pine experiencing no fire or lethal levels of fire. (C) No evidence of loss of hydraulic conductivity in ponderosa pine experiencing lethal levels of fire. (D) Evidence of new cambium and xylem growth following fires. (E) Evidence of significant differences in sugars and starches in burned, defoliated, and control ponderosa pine. (F) Evidence of phloem, cambium, and xylem vitality (alive = red) as a function of FRE in Douglas fir saplings at 7-weeks post-fire.

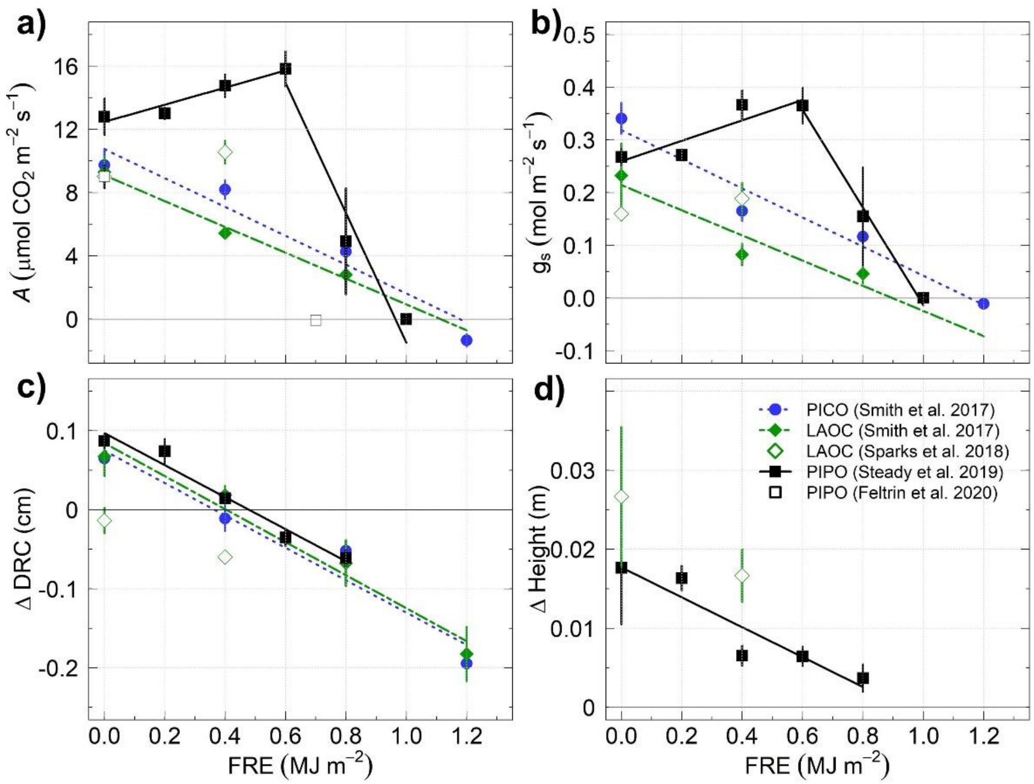

Fig 4. The relationship between sapling physiology and growth metrics and Fire Radiative Energy (FRE), approximately 30 days post-fire. Sub-plots are as follows: a) A (net photosynthesis) vs FRE, b) gs (stomatal conductance) vs FRE, c) post-pre change in Diameter at Root Collar (DRC) vs FRE, d) Post-pre change in height vs FRE. All plots show mean (±SE) and lines represent the linear regression line of best fit. Species codes are as follows: LAOC = Larix occidentalis, PICO = Pinus contorta, PIPO = Pinus ponderosa.

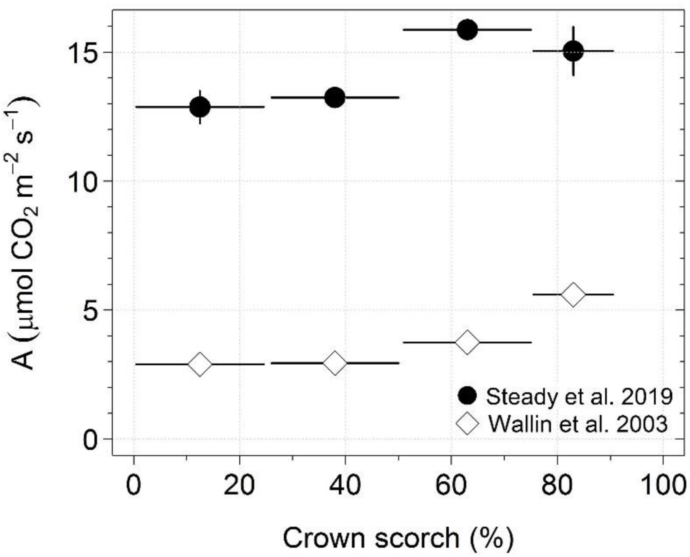

Fig 5. Unpublished data from [Steady et al. 2019]. Net photosynthesis (mean ± SE) in the remaining live needles generally increased with increasing crown scorch. Horizontal bands show sapling crown scorch classes (0-25%, 26-50%, 51-75%, 75-90%) and are the same as Wallin et al. [2003] for comparison purposes.

Fig 6. Example variation in canopy defoliation in ponderosa pine as a function of FRE dose.

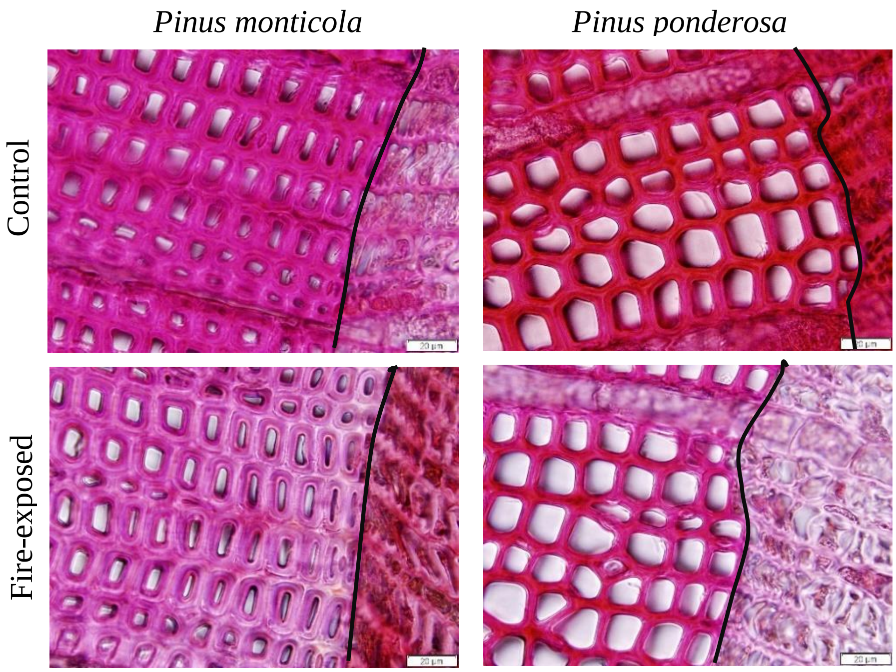

Fig. 7. Xylem conduits structure in control (FRE = 0) and fire-exposed (FRE = 1.4 MJ m^{-2}) of *Pinus monticola* and *Pinus ponderosa.* The black lines separate the phloem (right) and xylem tissue (left). Photographs are from control segment stems from control and fire-exposed plants used to measure xylem water conductivity. Stem cross-sections were made approximately at the highest bark temperature measured just after the plants were subjected to fire. Bar scale in the photographs are 20µm.

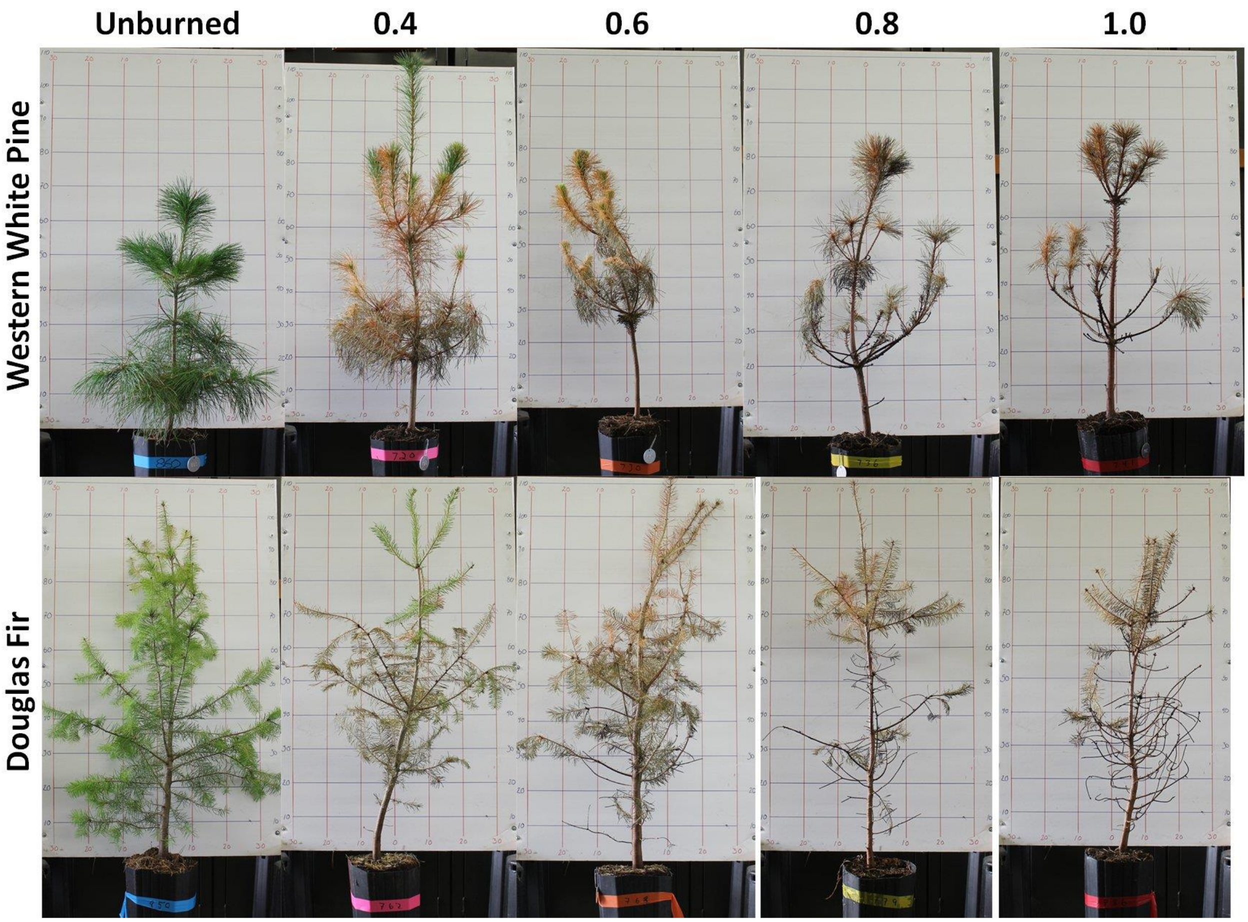

Fig 8. Variation in canopy defoliation as a function of FRE dose for western white pine and Douglas fir saplings. The numbers represent FRE in MJ/m^2, where photographs were taken 1 week after the fires.

ix. Science Delivery

The research performed as part of this GRIN has to-date resulted in three peer-reviewed publications, with two with Raquel Partelli-Feltrin as the first author, and several additional publications that are in various stages of production (see Appendix B). We also delivered the results of this GRIN project through different stakeholder meetings and scientific conferences (see Appendix B).

We have taken several steps to directly meet the science delivery objective of improving predictions of sapling mortality and fire effects that could be integrated with fire effects models such as FOFEM. Specifically, we reached out to several Earth-system and fire effects modeling groups to realize substantial improvements of existing models that determine how fire severity and intensity impacts tree survival and recovery across landscapes. The data and relationships have been openly shared with developers of the First Order Fire Effects Model (FOFEM), BioEarth, and the Spread and InTensity of FIRE (SPITFIRE) model that is included within the Community Land Model (CLM) version 5.0 and the Max Planck Institute's Earth System Model (MPI-ESM) version 1.2. Notably, results from this project with included in a recent synthesis of active fire remote sensing by Wooster et al. (2021) published in Remote Sensing of Environment. We are also directly working with these model developers to develop and submit a data paper to the international journal, Fire. This paper will include links to all the data created as part of the GRIN and the prior 6 years of related FRE to tree physiology 'dose-response' experiments.

Although an expanded set of data and relationships are including in the data paper, we present highlights below. The equations presented here represent data from trees of different species, variable ages, and mortality assessed at between 29- and 140-days post-fire. In each case these data are denoted by the subscripts "species 4 letter code", "[age range]year", and "[days post-fire]d" respectively.

Equations for fire-induced tree mortality (M) as a function of Fire Radiative Energy dosage level are given by sigmoidal Emax functions of the form:

$$\mathbf{M}_{\mathbf{PIPO,\ 1\text{-}2yr,28d}} = -0.004 + 106.139\frac{FRE^{10}}{0.666^{10} + FRE^{10}} \quad (1)$$

$$\mathbf{M}_{\mathbf{PICO,\ 1\text{-}2yr,28d}} = -0.024 + 103.738\frac{FRE^{10}}{0.863^{10} + FRE^{10}} \quad (2)$$

$$\mathbf{M}_{\mathbf{LAOC,\ 1\text{-}2yr,28d}} = 3.104 + 228.911\frac{FRE^{1.743}}{1.5^{10} + FRE^{1.743}} \quad (3)$$

Importantly, it is yet unknown how these relationships change with increasing tree age and associated increases in diameter and height. As such, it is critical that landscape fire experiments are conducted to evaluate if and how these relationships vary with tree age. Net photosynthesis, A, for each 1–2-year-old sapling 28 days following burning is expressed by the following relations:

$$\mathbf{A}_{\mathrm{PIPO},1-2\mathrm{yr},28\mathrm{d}} = \begin{cases} -\mathbf{41.08}\,[\boldsymbol{FRE}] + \mathbf{39.58}\ \boldsymbol{for\ FRE} > \mathbf{0.6} \\ \mathbf{5.41}\,[\boldsymbol{FRE})] + \mathbf{12.48}\ \boldsymbol{for\ FRE} < \mathbf{0.6} \end{cases} \quad (4)$$

$$\mathbf{A}_{\boldsymbol{PICO},\mathbf{1-2yr,28d}} = -\mathbf{9.12}[\boldsymbol{FRE}] + \mathbf{10.74} \quad (5)$$

$$\mathbf{A}_{\boldsymbol{LAOC},\mathbf{1-2yr,28d}} = -\mathbf{8.17}[\boldsymbol{FRE}] + \mathbf{9.09} \quad (6)$$

Given studies have observed relationships between maximum instantaneous fire radiative power (FRP, W m^{-2}) and fire line intensity (FLI, kW m^{-1} s^{-1}) [Kremens et al. 2012] and other studies have visually demonstrated increases in flame length (an indicator of fire line intensity) correlate with FRE [Steady et al. 2019]; future research could focus on further developing such crosswalk relationships between FRE and FLI:

$$\mathbf{FRP}_{\boldsymbol{peak}} = \mathbf{0.0311} * \mathbf{FLI} \quad (7)$$

Height change (ΔHeight). In each case these data are denoted by the subscripts "species 4 letter code", "[age range]year", and "[days post-fire]d" respectively.

$$\boldsymbol{\Delta Height}_{\boldsymbol{PIPO},\mathbf{1-2yr,28d}} = -\mathbf{0.019}[\boldsymbol{FRE}] + \mathbf{0.018} \quad (8)$$

Diameter at Root Collar change (ΔDRC). In each case these data are denoted by the subscripts "species 4 letter code", "[age range]year", and "[days post-fire]d" respectively.

$$\boldsymbol{\Delta DRC}_{\boldsymbol{PIPO},\mathbf{1-2yr,28d}} = -\mathbf{0.203}[\boldsymbol{FRE}] + \mathbf{0.097} \quad (9)$$

$$\boldsymbol{\Delta DRC}_{\boldsymbol{PICO},\mathbf{1-2yr,28d}} = -\mathbf{0.205}[\boldsymbol{FRE}] + \mathbf{0.075} \quad (10)$$

$$\boldsymbol{\Delta DRC}_{\boldsymbol{LAOC},\mathbf{1-2yr,28d}} = -\mathbf{0.209}[\boldsymbol{FRE}] + \mathbf{0.084} \quad (11)$$

In Sparks *et al.* (2017) relationships between maximum instantaneous FRP during the fire and long-term changes in stem radial growth for mature *Pinus ponderosa* trees were determined. Relative change in stem radial growth (%) was calculated as [($Growth_{postfire}$ – $Growth_{prefire}$)/$Growth_{prefire}$]. In this case the data are denoted by the subscripts "species 4 letter code", "[age range]year", and "[years post-fire]yr" respectively.

$$\boldsymbol{Relative\ growth}_{\boldsymbol{PIPO},\mathbf{30-40yr,2yr}} = -\mathbf{3.55} * \boldsymbol{FRP_{peak}} + \mathbf{12.58} \quad (12)$$

VI. Conclusions and Implications for Management/Policy and Future Research

The first major finding of this GRIN project is that for the saplings of five different tree species, clear 100% survival and 100% mortality fire behavior (FRE) thresholds exist. Of particular note, is the common 100% survival threshold of 0.4 MJ/m^2 that was shared by three different *Pinus* species: lodgepole pine, ponderosa pine, and western white pine. This is important information that informs land manager seeking to retain these species that such low intensity surface fires can be used without causing death in these species, as it is very unlikely that older trees would exhibit lower resistance to fire than these saplings experienced. Although we were unable to explore this in this GRIN project, prior work by our research team on prescribed fires on mature ponderosa pine trees (JFSP: 13-1-05-7) demonstrated that FRE values more than 12 MJ/m^2 was insufficient to cause death in 30–40-year-old ponderosa pine trees.

This common 100% survival threshold also raises compelling questions of whether the *Pinus* genus exhibits a potential genomic compensating mechanism that allows these species under low fire intensity conditions to survive fire. We acknowledge that more *Pinus* species need to be assessed to evaluate whether this is a genus-based adaptation, associated with specific Pinus sub-groups, or just limited to these three species. Also of note are that for these five different tree species, 1.2 MJ/m^2 is a common level at which 100% mortality is certain. We acknowledge that as species age, they will develop greater morphological protections to fire (thicker bark, growth out of flame zone, etc.,) and that higher FRE levels will be required to produce the similar effects. As noted by [Steady et al. 2019], identification of 100% survival and 100% mortality thresholds on a species-by-species basis could help guide fire managers identify 'how much fire to put on the ground' to sustain selective species or kill species considered as weeds. In addition, given trees that survive grow at reduced growth rates, managers may wish to decide whether it is cost effective to retain surviving saplings growing at reduced rates for 1-2 years following a fire, or simply replant a new crop.

The second major finding of this GRIN project is that we presented conclusive evidence that deformation of xylem cells and xylem hydraulic failure are not the primary mechanisms leading to mortality in ponderosa pine saplings. We however presented compelling evidence that fire-induced tree mortality in ponderosa pine is due to cambium and phloem dysfunction. This is an important result as it runs contrary to the current scientific understanding of fire-induced tree mortality, but it does provide reassurance to current representation of fire-

Fire Radiative Energy

FRE	0	0.2	0.4	0.6	0.8	1.0	1.2
PIPO	0	0	0	30	60	100	100
LAOC	0	20	33	40	50	75	100
PICO	0	0	0	15	33	70	100
PSME	0	25	57	57	100	100	100
PIMO	0	0	0	100	100	100	100

Probability of Sapling Death

induced tree mortality in Earth system and fire effects models, which rely on predictions of the duration of cambium heating to predict tree mortality.

Through aggregating the results from all five sapling species, we created this easy-to-use lookup table of how increasing FRE values will result in probability of death in saplings. Clearly, before such tables can be widely adopted to help guide land managers, research is needed to create a crosswalk between the more common fire line intensity and flame length metrics of fire behavior and FRE.

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Appendix B List of Completed/Planned Scientific/Technical Publications/Science Delivery Products

Published Peer-Reviewed Publications

- Partelli-Feltrin R, Johnson DM. Sparks AM, Adams HD Kolden CA, Nelson AS, Smith AMS. 2020. Drought increases vulnerability of Pinus ponderosa saplings to fire-induced mortality, Fire, 3, 56. doi: 10.3390/fire3040056
- Partelli-Feltrin R, Smith AMS, Adams HD, Kolden CA, Johnson DM. 2021. Short- and long-term effects of fire on stem hydraulics in Pinus ponderosa saplings, *Plant, Cell, and Environment*, 44, 3, 696-705. doi: 10.1111/pce.13881
- Wooster MJ, Roberts GJ, Giglio L, Roy DP, Freeborn P, Boschetti L, Justice CO, Ichoku CM, Schroeder W, Davies DK, Smith AMS, Setzer A Csiszar I, Strydom T, Frost P, Zhang T, Xu W, De Jong M, Johnson JM, Ellison L, Vardrevu KP. Sparks AM, Nguyen H, McCarty JL. Tanpipat V, Schmidt C, San-Miguel-Ayanz J. 2021. Satellite Remote Sensing of Active Fires: History and Current Status, Applications and Future Requirements, Remote Sensing of Environment, 267, 112694. doi: 10.1016/j.rse.2021.112694
- Partelli-Feltrin R, Smith AMS, Adams HD, Kolden CA, Johnson DM. 2021. Cover Image, Plant, Cell, and Environment, 44, 3, 1.

In addition, we are currently preparing several publications that will are in various stages of production:

- Partelli-Feltrin R, Smith AMS, Adams HD, Thompson RA, Kolden CA, Yedinak KM, Johnson DM. Ponderosa pine hydraulic conductivity and non-structural carbohydrate response to a lethal fire intensity, Plant, Cell, and Environment, in preparation.
- Smith AMS, et al. Pyroecophysiology data for Pinus contorta var. latifolia, Larix occidentalis, and Pinus Ponderosa: Connections to Fire Effects and Earth System Models, and Future Directions, *Fire*, in preparation.
- Blanco A, Wilson D, Sparks A, Smith AMS, Adams HD, Funke H, Hardman D. The Survival of Pinus Monticola Saplings Subjected to Increasing Levels of Fire Behavior and Impacts on Post-Fire Growth, *Fire*, in preparation.
- Wilson D, Blanco A, Sparks A, Smith AMS, Adams HD, Funke H, Hardman D. The Survival of Pseudotsuga menziesii Saplings Subjected to Increasing Levels of Fire Behavior and Impacts on Post-Fire Growth, *Fire*, in preparation.

. Presentations included:

- Partelli-Feltrin R, Seminar: The fire effects on Pinus ponderosa physiology, Missoula Fire Sciences Laboratory 2019-2020 seminar series. November 21, 2019.
- Partelli-Feltrin R, Johnson DM Adams HD, Smith AMS. Effects of fire on tree hydraulic and carbon processes. AFE Fire Congress, December 1, 2019

Appendix C. Metadata and Data Availability

We are currently in the process of finalizing a data paper for the journal Fire. This data paper summaries the data collection methods and the main plant physiology and morphology measurements. The data paper also presents logistic regressions that can be directly inputted into FOFEM and other fire effects and earth-system models. We are directly working with the developers of multiple models.

A Metadata Document was submitted on December 20th, 2021, to the USFS Research and Development Data Archive. We will upload the final version to the JFSP reporting system once it is approved. Alongside the Metadata Document, three excel Data Descriptors were also submitted. The citations of published and in preparation articles associated with this data are:

1) Partelli-Feltrin R, Johnson DM. Sparks AM, Adams HD Kolden CA, Nelson AS, Smith AMS. 2020. Drought increases vulnerability of Pinus ponderosa saplings to fire-induced mortality, Fire, 3, 56. https://doi.org/10.3390/fire3040056;
2) Partelli-Feltrin R, Smith AMS, Adams HD, Kolden CA, Johnson DM. 2021. Short- and long-term effects of fire on stem hydraulics in Pinus ponderosa saplings, Plant, Cell, and Environment, 44, 3, 696-705. https://doi.org/10.1111/pce.13881;
3) Blanco A, Wilson D, Sparks A, Smith AMS, Adams HD, Funke H, Hardman D. The Survival of Pinus Monticola Saplings Subjected to Increasing Levels of Fire Behavior and Impacts on Post-Fire Growth, Fire, in preparation.;
4) Wilson D, Blanco A, Sparks A, Smith AMS, Adams HD, Funke H, Hardman D. The Survival of Pseudotsuga menziesii Saplings Subjected to Increasing Levels of Fire Behavior and Impacts on Post-Fire Growth, Fire, in preparation

Data from 1) and 2) are freely available for use. Data from 3) and 4) will be freely available for use following publication. Articles 1), 3), and 4) are published in an open access article distribution format under the terms and conditions of the Creative Commons Attribution (CC BY) license.