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Physiological responses to fire that drive tree mortality

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A summer storm passes, flashing lightning but little rain and a fire starts to grow. Flames lick the bases of trees, charring stems and strong winds fan the fire at times, causing the flames to scorch foliage, as it burns through a forest. The fate of these burned trees after the flames are doused is one of intense interest. Will the forest become a carbon source? Will there be suitable wildlife habitat? Will enough trees survive to perpetuate and regenerate the forest? Are the trees now more vulnerable to bark beetle attacks or drought? To answer these questions, ecologists are reliant on accurate predictive models of fire-caused tree mortality. Yet, we still know remarkably little about the actual physiological impacts of fire on trees, limiting our ability to build mechanistic mortality models (Bär, Michaletz, & Mayr, 2019; Hood, Varner, van Mantgem, & Cansler, 2018).

Depending on the intensity and duration of heat that affects crown, stem and root tissues, some trees are killed immediately, others may die over the next several years, while others fully recover and survive future fires (Hood et al., 2018). Death of foliage and branch meristems in the crown during a high-intensity fire is the most well-described cause of tree death or top-kill in species capable of resprouting. There is far less research on the impact of lower intensity fires, where crown meristems are not as affected, but that cause injuries to the stem and ultimately tree death. Delayed mortality is inherently difficult to predict, as numerous factors, such as plant water stress, influence physiological responses that can increase post-fire tree mortality over time (Partelli-Feltrin et al., 2020; van Mantgem et al., 2013). Fire is thought to impair hydraulic function and cause tree mortality through two potential mechanisms: heat-induced embolism and deformation of xylem (Bär et al., 2019). The article by Partelli-Feltrin et al. in this issue of PCE tested these two proposed mechanisms of hydraulic dysfunction in explaining stem injury from fire that can cause both short- and long-term tree mortality. Heat-induced embolism may occur during fire when high temperatures and dry air result in extreme vapour pressure deficits that cause

embolisms in xylem conduits (i.e., air bubbles that break the continuous internal column of water within the tree), which if extensive enough would result in permanent reductions in water transport and conductivity (Kavanagh, Dickinson, & Bova, 2010). The second mechanism predicts that fire-caused heating of xylem tissue causes irreversible deformation of cell walls, thereby reducing hydraulic conductivity, that increases xylem tension and stomatal closure, eventually leading to tree death from a combination of depleted carbon stores and hydraulic failure (Michaletz, Johnson, & Tyree, 2012).

Partelli-Feltrin, Smith, Adams, Kolden, and Johnson (2020) examined immediate (1-day) and delayed (21-month) impacts of fire on tree hydraulics through a series of small-scale experimental fires using 1-year old *Pinus ponderosa* saplings. Importantly, the authors standardized the 'dose' of the fire using fire radiative energy (FRE), a measure of the intensity or radiative energy released from fuel during the fire, that each tree received to ensure that the treatments were applied consistently. Previous work by some of the authors has established the range of FRE dosages that are typically observed during surface fires in *Pinus ponderosa* forests (A. M. S. Smith et al., 2017) and corresponding mortality dose-response curves (Steady et al., 2019). They examined plant stem hydraulic responses to two fire intensity treatments: a high dose (1.4 MJ/m²) and a lower, sub-lethal dose (0.7 MJ/m²) in two independent experiments. Plants were well-watered both before and after the experiments.

The first experiment examined short-term impacts on plant hydraulics. One day after receiving a high dose of FRE, no differences were observed between the burned and unburned trees in terms of maximum xylem hydraulic conductivity (k_{max}), native percentage loss of conductivity (nPLC) or vulnerability to cavitation. These variables offer insight into a plant's ability to transport water and maintain hydraulic integrity. Hydraulic conductance is the efficiency of the xylem to transport water, where k_{max} is the maximum water flow rate of the xylem with no embolisms, and nPLC is the relative loss in

conductivity compared to $k_{\max}$. Xylem vulnerability to cavitation is a measure of nPLC at a given xylem pressure and is often displayed across a gradient of xylem pressures to show cavitation vulnerability under increasing water stress.

In the second experiment, plant hydraulics 21 months post fire were compared between unburned saplings and those receiving a low-dose FRE. The original design also included a high-dose treatment, but all of these saplings had died by the 21-month post-fire measurement. Just as in the short-term experiment, no differences in $k_{\max}$ or nPLC were found between burned and unburned saplings. Despite this, the burned saplings were more vulnerable to cavitation than the unburned ones. When the stem xylem tissue was examined, no deformation of the conduits was found in the xylem that had formed before the fire. In contrast, some stems had areas of cambium killed by fire and the stem xylem that formed adjacent to fire-killed cambium after the fire consisted of irregularly shaped tracheid and parenchyma cells. In addition, in the areas of these fire scars, resin was impregnating the pre-fire xylem. The authors attribute the increased vulnerability to water stress in the long term to the post-fire xylem wound tissue that formed and resin soaking and clogging pre-existing xylem.

The main finding of this work is the increased vulnerability to water stress that developed over the 21 months after the fire. Intriguingly, the findings support neither proposed mechanism of xylem dysfunction—the authors find little evidence of heat-induced embolism or deformation of pre-existing xylem conduits. Instead, the findings suggest it is deformation of xylem conduits formed after the fire that affect hydraulic function. Research on fire scar formation corroborates the finding of resin soaking into pre-existing xylem around the area killed by fire (K. T. Smith, Arbellay, Falk, & Sutherland, 2016). Mundo, González, Stoffel, Ballesteros-Cánovas, and Villalba (2019) found reduced xylem conductivity near fire scars and increased vulnerability to water stress, but there was a slow recovery in the years after the fire. Other field-based studies show mixed effects of fire-impacting hydraulic safety, with no effect observed in the main stems of *Pinus pinea* (Battipaglia et al., 2016) and increased vulnerability in the branches of *Pinus sylvestris* and *Fagus sylvatica* but not in *Picea abies* (Bär, Nardini, & Mayr, 2018).

The results of Partelli-Feltrin, Smith, et al. (2020) are consistent with experiments using water baths as a surrogate for fire-caused heating show increased vulnerability to water stress (Bär et al., 2018; Lodge, Dickinson, & Kavanagh, 2018; Michaletz et al., 2012; West, Nel, Bond, & Midgley, 2016). However, the finding that fire did not cause deformation of the pre-existing xylem conflicts with other research using water baths (Bär et al., 2018; Michaletz et al., 2012; West et al., 2016). This suggests that water baths may not be reliable substitutes to examine physiological effects of fire on plants. More research is needed to develop standardized protocols for pyroecophysiological studies. Differences in results may also be due to differences in tree sizes that range from the 1-year-old saplings to 40+ cm diameter trees.

The authors quantified the fire dose each sapling received using FRE, a measure of the radiative heat released during a fire. FRE has

the advantages of directly relating to the level of fuel consumed, it can be used to estimate the convective heat released, and it can be assessed with remote sensing techniques over large spatial scales (Kremens, Dickinson, & Bova, 2012; Smith et al., 2016). A limitation to FRE, however, is the inability to estimate conductive heat. While convective and radiant heat transfer are the primary mechanisms of energy release during flaming, conductive heat transfer is the main mechanism when strong temperature gradients persist for hours to days, such as during smouldering duff and peat fires (Varner et al., 2009). This is a fatal limitation of using FRE to measure physiological responses under conditions where conduction dominates because the heat transferred through thick bark and downwards into soil is unquantified. Advances in quantifying total heat flux from all heat transfer processes are needed to link the energy released during a fire to physiological and ecological effects (O'Brien et al., 2018).

During a fire, heat can affect both the stem and crown. The results of Partelli-Feltrin, Smith, et al. (2020) hint that some meristems were killed, and this may have contributed to mortality, but crown scorch and bud kill were not explicitly assessed. Carbon acquisition and hydraulic function are linked in ways still not fully understood, as evidenced by a study of experimental manual defoliation that caused an increased vulnerability to embolism (Hillabrand, Hacke, & Liefers, 2019). Fire may act in a similar way as defoliation to kill foliage, also causing changes to xylem anatomy. Quantifying impacts to foliage and meristems and tracking the time-to-death of saplings would have complemented the work, and future experiments should report both injuries to the crown and stem tissues if possible.

Fire is a natural ecological disturbance in many ecosystems around the world, and tree species have numerous adaptations to survive fire. Yet climate change is also increasing drought stress and driving changes in fire regimes that can alter tree susceptibility to fire. The discrepancies in existing studies on the physiological effects of fire suggest that responses are species dependent and driven by suites of 'pyrohydraulic traits' (West et al., 2016). Quantification of and accounting for traits known to affect tree responses to fire and drought are needed, such as has been documented for Mediterranean species (Paula et al., 2009). For example, bark thickness is perhaps the single most important trait protecting cambium from heating during fire (Pellegrini et al., 2017), but other traits such as meristem size and protection (Charles-Dominique, Beckett, Midgley, & Bond, 2015), xylem anatomy (West et al., 2016) and non-structural carbohydrate storage pools (Varner et al., 2009) almost certainly affect a species tolerance of fire.

Increased vulnerability to cavitation makes trees more prone to death if a severe drought occurs within a few years of fire. As Partelli-Feltrin, Smith, et al. (2020) point out, how long this response persists is unknown. Studying a range of physiological responses to fire over time is required to ultimately integrate the responses into improved models of fire-induced tree mortality (Figure 1). For example, the authors' experiments caused an adverse effect over the 21-month time period (Figure 1a, right), but it is unknown which curve the saplings that were given the low dose of fire would have ultimately followed. Would they fully or partially grow out of the

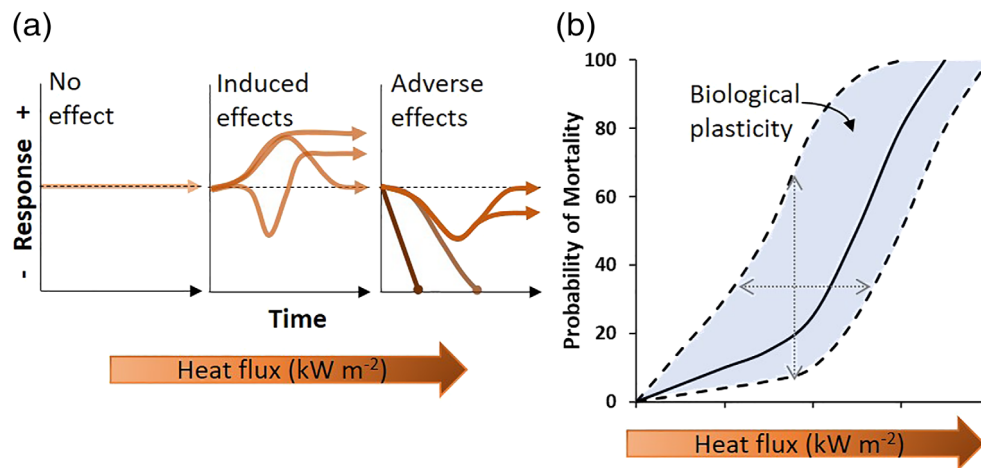


FIGURE 1 Delayed tree mortality from wildland fire is a function of the heat flux (time-integrated energy release) or 'dose' on numerous physiological responses. Heat flux includes the heat transfer processes of radiation, convection and conduction. (a) Potential non-linear physiological responses (orange lines) over time to a fire dose relative to baseline. Dots at end of orange lines indicate tree death, while arrows indicate survival. (b) Tree binary endpoint (mortality or survival) to a fire dose. The solid line is the average tree response, and dashed lines reflect the lower and upper bounds of responses based on species traits and environmental stress. The grey zone denotes the possible range of a species response or biological plasticity to fire; grey arrows provide examples of ranges of variation in mortality from the same heat flux or variation in heat flux that cause the same level of mortality

increased xylem vulnerability or would a drought interact to kill them during this phase? In contrast, studies have also documented induced effects of enhanced physiological activity after fire (Figure 1a, middle) to resin defenses (Hood, Sala, Heyerdahl, & Boutin, 2015) and increased stomatal conductance and photosynthesis (Gričar et al., 2020; Valor et al., 2018; Wallin, Kolb, Skov, & Wagner, 2003). These studies strongly suggest that several physiological responses are dependent on heat flux (i.e., dose). Research that examines how physiological responses interact with species traits (e.g., bark thickness, meristem size, xylem anatomy) and exogenous factors (e.g., bark beetles, climate, competition) will allow a better understanding of a species's range of biological plasticity and tolerance to fire to improve predictions of fire-induced tree mortality (Figure 1b).

The idea of fire having a dose-dependent effect on plant physiological responses is promising and needs much more research. Integrating the concept of 'hormesis', or non-linear responses and adaptative conditioning to the environment (Figure 1a hypothetical hormetic response curves, Agathokleous, Kitao, Harayama, & Calabrese, 2019), could provide a platform to develop additional hypotheses of plant responses to fire for future experiments. Droughts are becoming increasingly frequent and intense. Because fire-affected trees may be more vulnerable to water stress, the risk that a tree dies in the years after fire rises. The complex interactions of climate and fire on tree physiological responses and mortality underscore the importance of improving our understanding of how climate change and fire will impact terrestrial ecosystems. Advances in quantifying and predicting physiological effects of fire on trees will require a multi-disciplinary approach of plant ecophysiologicals, ecologists, physical scientists and modellers.

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CONFLICT OF INTEREST

The author has declared no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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REFERENCES

- Agathokleous, E., Kitao, M., Harayama, H., & Calabrese, E. J. (2019). Temperature-induced hormesis in plants. *Journal of Forestry Research*, 30(1), 13–20. <https://doi.org/10.1007/s11676-018-0790-7>
- Bär, A., Michaletz, S. T., & Mayr, S. (2019). Fire effects on tree physiology. *New Phytologist*, 223, 1728–1741. <https://doi.org/10.1111/nph.15871>
- Bär, A., Nardini, A., & Mayr, S. (2018). Post-fire effects in xylem hydraulics of *Picea abies*, *Pinus sylvestris* and *Fagus sylvatica*. *New Phytologist*, 217(4), 1484–1493. <https://doi.org/10.1111/nph.14916>
- Battipaglia, G., Savi, T., Ascoli, D., Castagneri, D., Esposito, A., Mayr, S., & Nardini, A. (2016). Effects of prescribed burning on ecophysiological, anatomical and stem hydraulic properties in *Pinus pinea* L. *Tree Physiology*, 36(8), 1019–1031.
- Charles-Dominique, T., Beckett, H., Midgley, G. F., & Bond, W. J. (2015). Bud protection: A key trait for species sorting in a forest-savanna mosaic. *New Phytologist*, 207(4), 1052–1060.

- Gričar, J., Hafner, P., Lavrič, M., Ferlan, M., Ogrinc, N., Krajnc, B., ... Vodnik, D. (2020). Post-fire effects on development of leaves and secondary vascular tissues in *Quercus pubescens*. *Tree Physiology*, 40(6), 796–809. <https://doi.org/10.1093/treephys/tpaa030>
- Hillabrand, R. M., Hacke, U. G., & Liefers, V. J. (2019). Defoliation constrains xylem and phloem functionality. *Tree Physiology*, 39(7), 1099–1108. <https://doi.org/10.1093/treephys/tpz029>
- Hood, S., Sala, A., Heyerdahl, E. K., & Boutin, M. (2015). Low-severity fire increases tree defense against bark beetle attacks. *Ecology*, 96, 1846–1855.
- Hood, S., Varner, M., van Mantgem, P., & Cansler, C. A. (2018). Fire and tree death: Understanding and improving modeling of fire-induced tree mortality. *Environmental Research Letters*, 13, 113004.
- Kavanagh, K. L., Dickinson, M. B., & Bova, A. S. (2010). A way forward for fire-caused tree mortality prediction: Modeling a physiological consequence of fire. *Fire Ecology*, 6(1), 80–94.
- Kremens, R. L., Dickinson, M. B., & Bova, A. S. (2012). Radiant flux density, energy density and fuel consumption in mixed-oak forest surface fires. *International Journal of Wildland Fire*, 21(6), 722–730. <https://doi.org/10.1071/WF10143>
- Lodge, A. G., Dickinson, M. B., & Kavanagh, K. L. (2018). Xylem heating increases vulnerability to cavitation in longleaf pine. *Environmental Research Letters*, 13(5), 055007. <https://doi.org/10.1088/1748-9326/aabbe5>
- Michaletz, S. T., Johnson, E. A., & Tyree, M. T. (2012). Moving beyond the cambium necrosis hypothesis of post-fire tree mortality: Cavitation and deformation of xylem in forest fires. *New Phytologist*, 194(1), 254–263. <https://doi.org/10.1111/j.1469-8137.2011.04021.x>
- Mundo, I. A., González, C. V., Stoffel, M., Ballesteros-Cánovas, J. A., & Villalba, R. (2019). Fire damage to cambium affects localized xylem anatomy and hydraulics: The case of *Nothofagus pumilio* in Patagonia. *American Journal of Botany*, 106(12), 1536–1544. <https://doi.org/10.1002/ajb2.1395>
- O'Brien, J. J., Hiers, J. K., Varner, J. M., Hoffman, C. M., Dickinson, M. B., Michaletz, S. T., ... Butler, B. W. (2018). Advances in mechanistic approaches to quantifying biophysical fire effects. *Current Forestry Reports*, 4(4), 161–177. <https://doi.org/10.1007/s40725-018-0082-7>
- Partelli-Feltrin, R., Johnson, D. M., Sparks, A. M., Adams, H. D., Kolden, C. A., Nelson, A. S., & Smith, A. M. S. (2020). Drought increases vulnerability of *Pinus ponderosa* saplings to fire-induced mortality. *Fire*, 3(4), 56.
- Partelli-Feltrin, R., Smith, A. M. S., Adams, H. D., Kolden, C. A., & Johnson, D. M. (2020). Short- and long-term effects of fire on stem hydraulics in *Pinus ponderosa* saplings. *Plant, Cell Environ*, 44, 696–705. <https://doi.org/10.1111/pce.13881>
- Paula, S., Arianoutsou, M., Kazanis, D., Tavsanoglu, Ç., Lloret, F., Buhk, C., ... Pausas, J. G. (2009). Fire-related traits for plant species of the Mediterranean Basin. *Ecology*, 90(5), 1420–1420. <https://doi.org/10.1890/08-1309.1>
- Pellegrini, A. F. A., Anderegg, W. R. L., Paine, C. E. T., Hoffmann, W. A., Kartzinel, T., Rabin, S. S., ... Pacala, S. W. (2017). Convergence of bark investment according to fire and climate structures ecosystem vulnerability to future change. *Ecology Letters*, 20(3), 307–316. <https://doi.org/10.1111/ele.12725>
- Smith, A. M., Sparks, A. M., Kolden, C. A., Abatzoglou, J. T., Talhelm, A. F., Johnson, D. M., ... Yedinak, K. M. (2016). Towards a new paradigm in fire severity research using dose–response experiments. *International Journal of Wildland Fire*, 25(2), 158–166.
- Smith, A. M. S., Talhelm, A. F., Johnson, D. M., Sparks, A. M., Kolden, C. A., Yedinak, K. M., ... Kremens, R. L. (2017). Effects of fire radiative energy density dose on *Pinus contorta* and *Larix occidentalis* seedling physiology and mortality. *International Journal of Wildland Fire*, 26(1), 82–94. <https://doi.org/10.1071/WF16077>
- Smith, K. T., Arbellay, E., Falk, D. A., & Sutherland, E. K. (2016). Macroanatomy and compartmentalization of recent fire scars in three North American conifers. *Canadian Journal of Forest Research*, 46(4), 535–542.
- Steady, W. D., Partelli Feltrin, R., Johnson, D. M., Sparks, A. M., Kolden, C. A., Talhelm, A. F., ... Smith, A. M. S. (2019). The survival of *Pinus ponderosa* saplings subjected to increasing levels of fire behavior and impacts on post-fire growth. *Fire*, 2(2), 23.
- Valor, T., Casals, P., Altieri, S., González-Olabarria, J. R., Piqué, M., & Battipaglia, G. (2018). Disentangling the effects of crown scorch and competition release on the physiological and growth response of *Pinus halepensis* Mill. using $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotopes. *Forest Ecology and Management*, 424, 276–287. <https://doi.org/10.1016/j.foreco.2018.04.056>
- van Mantgem, P., Nesmith, J. C. B., Keifer, M., Knapp, E. E., Flint, A., & Flint, L. (2013). Climatic stress increases forest fire severity across the western United States. *Ecology Letters*, 16(9), 1151–1156. <https://doi.org/10.1111/ele.12151>
- Varner, J. M., Putz, F. E., O'Brien, J. J., Hiers, J. K., Mitchell, R. J., & Gordon, D. R. (2009). Post-fire tree stress and growth following smoldering duff fires. *Forest Ecology and Management*, 258(11), 2467–2474.
- Wallin, K. F., Kolb, T. E., Skov, K. R., & Wagner, M. R. (2003). Effects of crown scorch on ponderosa pine resistance to bark beetles in northern Arizona. *Environmental Entomology*, 32, 652–661.
- West, A. G., Nel, J. A., Bond, W. J., & Midgley, J. J. (2016). Experimental evidence for heat plume-induced cavitation and xylem deformation as a mechanism of rapid post-fire tree mortality. *New Phytologist*, 211(3), 828–838. <https://doi.org/10.1111/nph.13979>