Physiological responses to fire that drive tree mortality

Sharon Hood[1]

[1]US Forest Service

October 21, 2020

Abstract

This article comments on: 'Short- and long-term effects of fire on stem hydraulics in Pinus ponderosa saplings' by Partelli-Feltrin et al. (2020), https://doi.org/10.1111/pce.13881.

Title: Physiological responses to fire that drive tree mortality

Author: Sharon M. Hood

Contact information:

sharon.hood@usda.gov

ORCID 0000-0002-9544-8208

US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, 5775 Highway 10 W, Missoula, MT, 59808

Running head: Tree physiological fire effects

Abstract

This article comments on: '*Short- and long-term effects of fire on stem hydraulics in Pinus ponderosa saplings* ' by *Partelli-Feltrin*et al. (*2020*), https://doi.org/10.1111/pce.13881.

Keywords: hydraulics, hormesis, fire effects, drought, disturbance interactions

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, causing injuries to the stem and ultimately tree death. Delayed mortality is inherently difficult to predict, as numerous factors influence physiological responses, such as plant water stress, that can increase post-fire tree mortality over time (Partelli-Feltrin, Johnson, et al., 2020; van Mantgem et al., 2013). The article by Partelli et al. (2020) tested the two leading hypotheses explaining stem injury from fire that can cause both immediate and delayed tree mortality, cambium necrosis and xylem dysfunction (Bär et al., 2019). The cambium necrosis hypothesis predicts that when fire kills stem phloem and cambium tissue it severs the connection between foliage and roots. Over time, without photosynthates to replenish carbon reserves, roots die, increasing xylem tension until tree mortality occurs due to hydraulic failure. The xylem dysfunction hypothesis predicts that fire-caused heating of xylem tissue causes irreversible deformation of cell walls, 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.

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 MJm^{-2}) and a lower, sub-lethal dose (0.7 MJm^{-2}) through two 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 in maximum xylem hydraulic conductivity (k_{max}), native percentage loss of conductivity (nPLC), or vulnerability to cavitation between the burned and unburned trees.

The second experiment examined plant hydraulics 21 months post-fire between unburned saplings and those receiving a low dose FRE. The original design also included a high dose treatment, but all saplings receiving this treatment died by the 21-month postfire measurement. As in the short-term experiment, no differences k_{max} or nPLC were found between burned and unburned saplings. Despite this, the burned saplings were more vulnerable to cavitation than the unburned saplings. When the stem xylem tissue was examined, no deformation of the conduits was found in the xylem that had formed before the fire. However, several of the burned saplings had traumatic xylem tissue forming post-fire in response to the fire killing cambium and phloem tissue. 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 wound tissue that formed and resin soaking and clogging preexisting xylem.

The main finding of this work is the increased vulnerability to water stress that developed over the 21 months after the fire. 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 afterwards. Results are also consistent with experiments using water baths as a surrogate for fire-caused heating showing increased vulnerability to water stress (Bär, Nardini, & Mayr, 2018; Lodge, Dickinson, & Kavanagh, 2018; Michaletz, Johnson, & Tyree, 2012; West, Nel, Bond, & Midgley, 2016). Field-based studies of burned tree branches showed mixed support of fire impacting hydraulic safety (Bär et al., 2018; Battipaglia et al., 2016).

The finding that fire did not cause xylem deformation conflicts with other research (Michaletz et al., 2012; West et al., 2016). These studies used water baths as a surrogate for fire, suggesting that water baths are not reliable substitutes for examining physiological effects of fire on plants. More research is needed to develop standardized protocols for pyro-ecophysiological studies. Differences in results may also be due to differences in tree sizes that range from the one-year old saplings to 40+ cm diameter trees.

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 nonstructural carbohydrate storage pools (Varner et al., 2009) almost certainly affect a species tolerance of fire.

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 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, & Lieffers, 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.

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, can be used to estimate the convective heat released, and can be assessed with remote sensing techniques over large spatial scales (Kremens, Dickinson, & Bova, 2012; A. M. Smith et al., 2016). A limitation, however, is the inability to estimate conductive heat. In fires where long-term smoldering occurs (Varner et al., 2009), this is a fatal limitation of using FRE to measure physiological responses. 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).

Increased vulnerability to embolism 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, Partelli's experiments caused an adverse effect, as shown in Figure 1a, over the 21-month time period, but it is unknown which curve the saplings given the low dose of fire would have ultimately followed. Would they fully or partially grow out of the increased xylem vulnerability or would a drought interact to kill them during this phase of increased vulnerability? Other studies have documented induced effects of enhanced physiological activity after fire 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). How physiological responses interact with species traits and exogenous factors will determine long-term, fire-induced tree mortality (Figure 1B) and allow a better understanding of the full range of a species's biological plasticity and tolerance to fire (Figure 1C).

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 (Agathokleous, Kitao, Harayama, & Calabrese, 2019), could provide a platform to develop additional hypotheses of plant responses to fire for future experiments. As droughts become increasingly frequent and intense, fire-affected trees may be more vulnerable to water stress, thereby increasing the chance a tree dies in the years after fire. The complex interactions of climate and fire on tree physiological responses and mortality underscores 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 ecophysiologists, ecologists, physical scientists, and modelers.

Conflict of Interest statement

The author has declared no conflict of interest.

Acknowledgments

The author thanks the feedback of Morgan Varner and Charlotte Reed on an earlier version of this manuscript. This work was supported by the USDA Forest Service, Rocky Mountain Research Station, Fire, Fuel, and Smoke Program.

References

Agathokleous, E., Kitao, M., Harayama, H., & Calabrese, E. J. (2019). Temperature-induced hormesis in plants. *Journal of Forestry Research, 30* (1), 13-20. doi:10.1007/s11676-018-0790-7

Bär, A., Michaletz, S. T., & Mayr, S. (2019). Fire effects on tree physiology. *New Phytologist, 223* (0), 1728-1741. doi: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. doi: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., Eler, K., & Vodnik, D. (2020). Post-fire effects on development of leaves and secondary vascular tissues in Quercus pubescens. *Tree Physiology, 40* (6), 796-809. doi:10.1093/treephys/tpaa030

Hillabrand, R. M., Hacke, U. G., & Lieffers, V. J. (2019). Defoliation constrains xylem and phloem functionality. *Tree Physiology, 39* (7), 1099-1108. doi: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.

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. doi: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. doi: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. doi: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. doi:10.1002/ajb2.1395

O'Brien, J. J., Hiers, J. K., Varner, J. M., Hoffman, C. M., Dickinson, M. B., Michaletz, S. T., Loudermilk, E. L., & Butler, B. W. (2018). Advances in Mechanistic Approaches to Quantifying Biophysical Fire Effects. *Current Forestry Reports, 4* (4), 161-177. doi: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 & Environment* . doi:10.1111/pce.13881

Paula, S., Arianoutsou, M., Kazanis, D., Tavsanoglu, Ç., Lloret, F., Buhk, C., Ojeda, F., Luna, B., Moreno, J. M., Rodrigo, A., Espelta, J. M., Palacio, S., Fernández-Santos, B., Fernandes, P. M., & Pausas, J. G. (2009). Fire-related traits for plant species of the Mediterranean Basin. *Ecology, 90* (5), 1420-1420. doi:doi: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., Sheil, D., Franco, A. C., & 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. doi:10.1111/ele.12725

Smith, A. M., Sparks, A. M., Kolden, C. A., Abatzoglou, J. T., Talhelm, A. F., Johnson, D. M., Boschetti, L., Lutz, J. A., Apostol, K. G., & 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., Apostol, K. G., Tinkham, W. T., Abatzoglou, J. T., Lutz, J. A., Davis, A. S., Pregitzer, K. S., Adams, H. D., & 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. doi: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., Lutz, J. A., Boschetti, L., Hudak, A. T., Nelson, A. S., & 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 δ13C and δ18O isotopes. *Forest Ecology and Management, 424* , 276-287. doi: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. doi: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. doi:10.1111/nph.13979

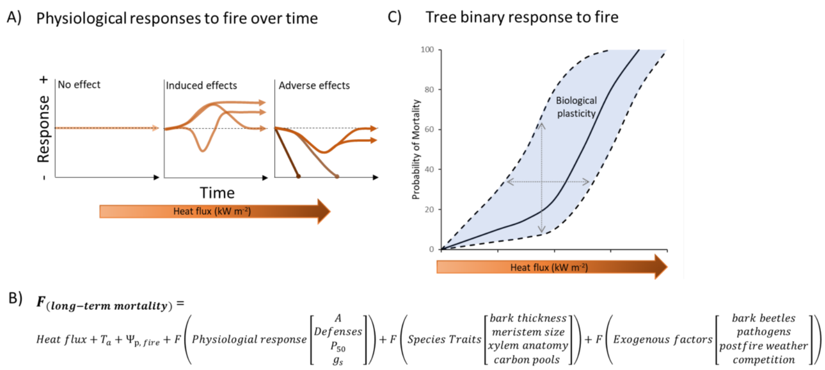

Figure 1. Delayed tree mortality from wildland fire is a function the heat flux (time-integrated energy release) or "dose" on numerous physiological responses. Heat flux includes the heat transfer processes of radiation, convection and conduction. A) Potential physiological responses (oranges lines) over time to a fire dose relative to baseline. Dots at end of orange lines indicate tree death, while arrows indicate survival. Responses potentially affected by fire include, but are not limited to, photosynthetic rate (A), defense traits, predawn water potential causing 50% loss of stem conductivity (P_{50}), and stomatal conductance (g_s). B) Long-term, tree mortality from fire is a function of the total heat flux , plant water stress (Ψ_p) and ambient air temperature (T_a) at the time of fire, physiological responses, species traits, and exogenous factors. C) 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 response based on species traits and environmental stress. The grey zone denotes 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 causes the same level of mortality.