

## Viewpoints

# Tree crown injury from wildland fires: causes, measurement and ecological and physiological consequences

### Summary

The dead foliage of scorched crowns is one of the most conspicuous signatures of wildland fires. Globally, crown scorch from fires in savannas, woodlands and forests causes tree stress and death across diverse taxa. The term crown scorch, however, is inconsistently and ambiguously defined in the literature, causing confusion and conflicting interpretation of results. Furthermore, the underlying mechanisms causing foliage death from fire are poorly understood. The consequences of crown scorch – alterations in physiological, biogeochemical and ecological processes and ecosystem recovery pathways – remain largely unexamined. Most research on the topic assumes the mechanism of leaf and bud death is exposure to lethal air temperatures, with few direct measurements of lethal heating thresholds. Notable information gaps include how energy transfer injures and kills leaves and buds, how nutrients, carbohydrates, and hormones respond, and what physiological consequences lead to mortality. We clarify definitions to encourage use of unified terminology for foliage and bud necrosis resulting from fire. We review the current understanding of the physical mechanisms driving foliar injury, discuss the physiological responses, and explore novel ecological consequences of crown injury from fire. From these elements, we propose research needs for the increasingly interdisciplinary study of fire effects.

### Introduction

Heat-damaged or killed foliage on woody plants is a common and obvious outcome of wildland fires (i.e. wildfires or prescribed fires) in savannas, shrublands, woodlands, and forests globally (Alexander *et al.*, 2019). Visible foliar discolouration or consumption of foliage are notable across taxa (Hood *et al.*, 2018; Fig. 1). Fire-caused injuries to tree crowns and forest canopies impact ecological processes and applications from the organism to whole ecosystems, such as ecosystem resilience, carbon and other nutrient dynamics, and hydrological cycles (Hood *et al.*, 2018; O'Brien *et al.*, 2018).

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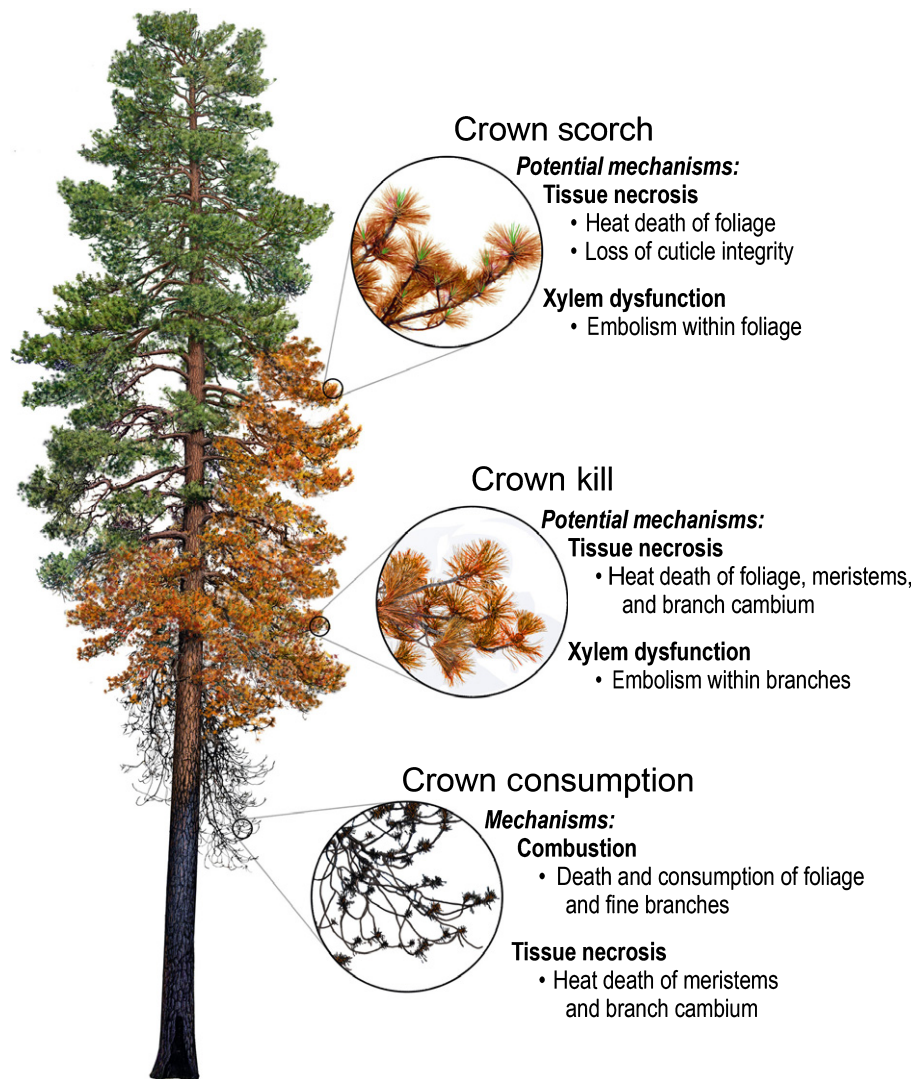
Crown scorch – the discoloured areas of foliage and buds after fire – is the most commonly referenced indicator of heat damage because it is an easy assessment of external injury and indicator of underlying physiological damage (Hood *et al.*, 2018). Importantly, crown scorch can be estimated from both ground and aerial methods, and can approximate fire intensity, making it valuable to researchers and fire practitioners (Alexander *et al.*, 2019). For example, crown scorch is an important tree-to-landscape-level indicator of the ecological consequences of fire, often termed fire severity (Eidenshink *et al.*, 2007; Catry *et al.*, 2013). Crown scorch is the primary predictor of post-fire tree mortality, especially for gymnosperms (Fernandes *et al.*, 2008; Cansler *et al.*, 2020). Beyond mortality, crown scorch is linked to both immediate and longer-term impairment of physiological activity (Aubrey *et al.*, 2012; Lodge *et al.*, 2018), which can impact tree growth (Valor *et al.*, 2018). Crown scorch is also used more broadly to assess burn severity through remote sensing techniques and to estimate changes in carbon pools with Earth system models (de Groot *et al.*, 2003).

While often the most visible indicator of fire effects, crown scorch is a loosely defined term based on ocular evidence, which may not include impacts to tree foliage, buds and branches. The lack of precise terminology causes assumptions about mechanisms and misunderstandings among disciplines, researchers and practitioners. Our aim here is to: (1) clarify the discrepancies in how crown injury terms are used in the literature; (2) review the physiological effects of fire on tree crowns; and (3) draw attention to potential ecological consequences. We also highlight priority research questions to further our understanding of the causes and effects of fire induced crown injury (Table 1).

### Crown injury defined

The literature is replete with different interpretations of crown scorch and injury. It is common for terms to be undefined or ambiguous, making results difficult to interpret or to compare among studies. We posit that part of the confusion around crown scorch emanates from the conflation of a spectrum of potential injuries (Figs 1, 2) that range from foliar damage (but not immediate mortality), foliar necrosis (acute injury to consumption), bud injury, and bud necrosis (acute injury to consumption). All of these conditions have been used to describe and quantify crown scorch. Most reports fail to distinguish injury across this spectrum, lumping them into a generic value referred to as ‘scorch.’ The ambiguity of the term is likely to be because numerous disciplines reference some metric of crown scorch, but little cross-disciplinary communication and the absence of formal standardised terminology creates wide discrepancies in meaning.

We propose that clearly defined terminology of visual symptoms of injury is needed to facilitate integrative research that facilitates comparisons across taxa and regions and links symptoms to



**Fig. 1** Post-fire crown injury in *Pinus ponderosa* (drawing by R. Van Pelt). Heat from fires causes diverse visual injuries to crown foliage, buds and branches. These injuries are linked to several potential mechanisms that result in stress, reductions in tree growth and branch and whole tree death.

physiological mechanisms. The definitions and terms are not new, but provide clarity:

- **Total crown injury:** portion of the crown (foliage, buds, branches) that is killed or injured by fire. Sum of scorch, kill, and consumption (has also been called total crown damage).
- **Crown scorch:** portion of the tree's foliage that is killed but not consumed during a fire. Foliage appears brown or red within days after fire.
- **Crown kill:** portion of a tree's buds (i.e. meristematic tissue that develops into branches, flowers, or foliage) and branches killed during fire.
- **Crown consumption:** portion of a tree's foliage, buds and fine branches that are either consumed during flaming combustion or is charred during a fire.

Importantly, these categories are not equivalent in their impact on overall tree injury. Crown scorch, crown kill, and crown consumption result from exposure to increasingly extreme thermal environments (Figs 1, 2). After fire, scorched leaves (i.e. killed

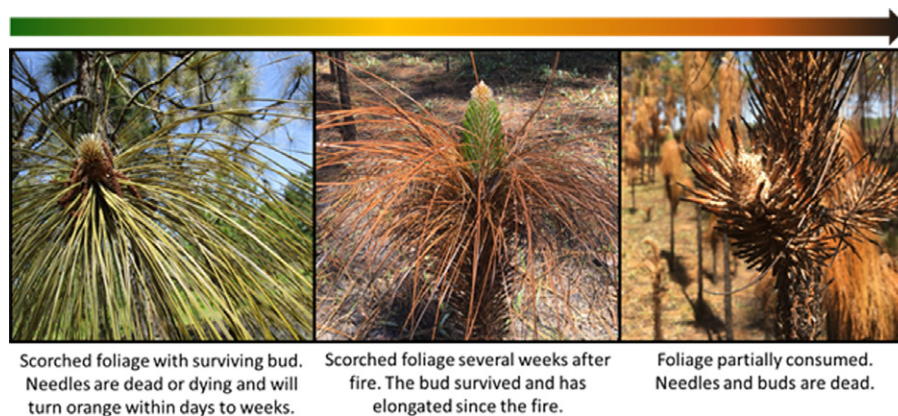
foliage, surviving meristems) senesce within weeks for some species and last months or longer for others (Wade & Johansen, 1986). Areas of crown kill are notable as they generate a partial marcescent crown (with leaves partially consumed, but remaining attached), lingering months to years following fire (Figs 2, 3). Crown kill via bud mortality is difficult to estimate until the growing season following fire, although this effect is often the most physiologically consequential to the tree. Crown consumption is the most immediately apparent condition with branches and buds that are either completely consumed or visibly charred.

### Physical processes of heat transfer in tree crowns

During low- and moderate-intensity surface fire, energy is transferred to the unburned local crown via buoyancy-driven convective gas movement and to a lesser extent by radiation (O'Brien *et al.*, 2018). The buoyant hot gases irregularly heat boundary layers within and surrounding the crown, including

**Table 1** Priority research questions to better understand fire-caused crown scorch.

Science discipline	Pressing questions
Fire behaviour	What are spatial and temporal patterns of convective and radiative heating around leaves and branches? How does tree stature and architecture (including lacunarity) affect heat transfer and flow? What are the horizontal heat fluxes within and around the canopy?
Leaf responses	How do leaf arrangement, density, moisture and other traits interact with heat transfer? How does heat injure and kill leaves? What is the capacity for nutrient resorption from scorched leaves? What is the physiological 'cost(s)' of lost photosynthesis? What are the costs of new leaf construction? What are the costs (or benefits) of reduce leaf area post-reflushing?
Fire-adapted traits	How do species compare in their susceptibility to and recovery from scorch? How do species differ in their ability to resorb nutrients from scorched foliage? Do juveniles within species differ in their responses?
Scorch measurement	How can we better differentiate scorch, bud survival and other forms of fire-caused crown injury? How can multispectral and hyperspectral remote sensing techniques be used to better characterise scorched leaves and bud injury? What are the shortcomings for experimental surrogates for fire (e.g. water baths, ovens, and radiative heaters) to simulate crown injury?
Modelling	What are the critical physical, chemical and thermal properties of buds, foliage and stems that influence their heat-transfer rates? How does radiative and convective heat transfer differ among species?

**Fig. 2** Foliar injury in *Pinus palustris*, illustrating immediate discolouration, scorched foliage and bud survival, and foliar consumption and bud necrosis. Arrow illustrates the continuum of foliar and bud injury.

stems, branches, leaves, and buds (Dickinson & Johnson, 2001). Once the temperature of the boundary layer rises, molecular contact at the gas–solid interface results in a rapid energy transfer to the exposed plant tissue. When buoyant hot gases are absent, near-ambient-temperature air is entrained and transfers energy away from the plant tissue (O'Brien *et al.*, 2018). A net accumulation of energy is needed (more warming than cooling) for plant tissue temperatures to rise. Assuming an active crown-fire is not present, the subcanopy heat power (rate at which energy is transferred (W)) affects the exposure time necessary for a lethal dose of heat flux ( $\text{W m}^{-2}$ ) to the individual parts of the crown. The amount or dose of energy delivered to the crown has been linked to reduced physiological function and possible mortality of the tree (Smith *et al.*, 2016). Foliage death may occur immediately, or it may be delayed, suggesting an important continuum of injury. At the extreme end of the dose spectrum, if the heat flux to the crown is sufficiently high, ignition and consumption of the foliage occurs, resulting in tree ignition (termed 'torching') and potentially tree-to-tree canopy spread.

Multiple heat-transfer scenarios can lead to crown injury, however substantial questions arise over how the physiological integrity of leaves are impacted by fire and the subsequent potential consequences to ecosystem processes. While scorch estimation via temperature is common, thresholds have rarely been related to energy dose (Smith *et al.*, 2016; O'Brien *et al.*, 2018). Therefore, while these thresholds (such as  $60^{\circ}\text{C}$ ; *sensu* Wade & Johansen, 1986; Lodge *et al.*, 2018) are widely used in physical and empirical modelling, unanswered questions remain regarding exactly how heat from fire causes leaf death, what the physiological implications and ecological consequences are, and how trees recover (or die) from these periodic injuries (Table 1).

### The physiology of crown injury by fire

The physiological mechanisms of foliage, bud, and branch death by fire fall into two proposed pathways: tissue necrosis and xylem dysfunction. Death from the physical process of combustion may also occur. These injury pathways are not mutually exclusive

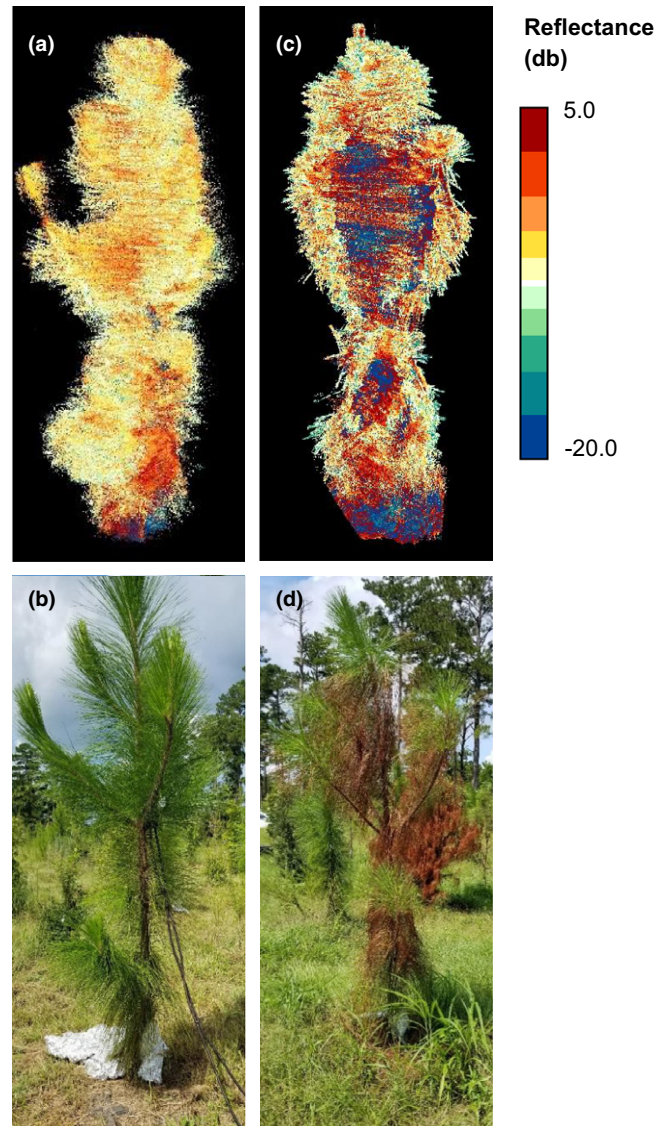


**Fig. 3** Heavy fire-caused scorch litterfall of *Pinus palustris* and *Quercus laevis* c. 30 d after a prescribed fire in northern Florida, USA. The implications of such substantial leaf senescence following fire has been overlooked by fire and ecosystem ecologists.

scenarios, but potential mechanisms that will interact to manifest crown injury (Fig. 1). Indeed, West *et al.* (2016) suggest that variation in heat-induced damage to plant hydraulic systems may be better characterised by a suite of pyrohydraulic traits based on xylem and foliage morphology and heat sensitivity rather than any single trait.

### Tissue necrosis

Tissue necrosis occurs as a result of lethal heat energy doses from fires (Smith *et al.*, 2016; Hood *et al.*, 2018). The standard estimate of threshold tissue temperatures that cause tissue death often does not incorporate time and is simply assumed to be c. 60°C (Wade & Johansen, 1986; Michaletz & Johnson, 2006a) or fluctuates widely from instantaneous (Wade & Johansen, 1986) to 1 min (Dickinson & Johnson, 2001). Conventional wisdom is that heating causes tissue necrosis via the temperature sensitivity of internal proteins (reviewed in Wade & Johansen, 1986). Leaves, meristems and distal, small diameter branches are sensitive to high temperatures via several internal pathways: damage to membranes; transformations of Rubisco and proteins; and desiccation (Kozłowski *et al.*, 1991). Hare (1961) stressed that a lethal tissue temperature is irrelevant without also quantifying exposure time, yet tissue impairment and death have rarely been related to energy dose or heat flux (Smith *et al.*, 2016; O'Brien *et al.*, 2018). Total heat energy is the integrated measure of a fire's heat flux to plant tissue and can allow more accurate estimation of lethal heating than simple thresholds. For example, cell viability decreased linearly after 1 min of experimental heating from 40 to 60°C in *Abies amabilis*, suggesting the 60°C threshold is not universal and is also not dependent on exposure time (Seymour *et al.*, 1983), likely to be due to a larger heat energy dose through exposure to lower heat fluxes over a longer time. In addition to the issues with temperature (e.g. air vs leaf tissue or surface vs interior membranes), studies based on thresholds often ignore the energy received before and



**Fig. 4** Potential exists for using short range infrared terrestrial laser scanning (TLS) to assess crown injury. A single experimentally scorched *Pinus palustris* sapling pre-scorch (1550 nm wavelength) (a), coincident pre-RGB (b), post-scorch scan (c), and coincident RGB (d). The post-scorch scan (c) shows a distinct decrease in TLS intensity (blue in image), corresponding to the true colour photograph of the same scorched sapling (d). This remote sensing approach may prove useful for more objectively characterising scorch and corresponding tree stress and mortality more rapidly and at larger scales.

after a threshold temperature is crossed. In other words, heat-transfer measures are ignored entirely in favour of a single temperature threshold. Recent work strongly suggests that tree growth is reduced even when 60°C is not reached (Smith *et al.*, 2017). Accounting for the total heat energy dose, information lost by focusing on temperature thresholds, is vital to understanding plant response (O'Brien *et al.*, 2018; Hood, 2021).

Tissue necrosis may also occur via loss of cuticle integrity. Plant water loss is limited by both stomata and cuticular conductance. Epicuticular waxes limit the diffusion of water from the foliage to the atmosphere and help leaves maintain turgor pressure. These waxes have very low volatilisation temperatures with midpoint

melting temperatures as low as 73°C for some species (Bueno *et al.*, 2019). Melting leaf surface waxes can expose plants to rapid post-fire desiccation through increased cuticular conductance, even if the foliage itself did not reach internal temperatures necessary to cause necrosis. Water potentials would rapidly decrease (become more negative), and continued water loss would be influenced by species differences in hydraulic segmentation whether low water potential would cause localised xylem cavitation in leaf petioles and small branch ends or more widespread cavitation further upstream in larger branches or the main stem (West *et al.*, 2016). Research on *Abies* spp. and *Picea sitchensis* reveal substantial cuticle temperature sensitivity, with temperatures and durations approximating the 60°C threshold causing melting and wax filling of stomata (Winner & Casadevall, 1983). Field and laboratory observations indicate that there are further threshold heat fluxes above 60°C that can dramatically change the physiological function of the leaf (Jolly *et al.*, 2012). For example, exposure to direct flames causes radiative and convective heat fluxes with gas temperatures well above common ignition temperatures (>320°C), causing the cuticle to mechanically fail via rupturing or combusting quickly to pyrolyse and form char (Yedinak *et al.*, 2019). In addition, high temperatures may lethally damage the guard cells that control stomatal aperture, contributing to plant water loss (Rogers *et al.*, 1981). Ultimately, damage from heat to either the cuticle or the stomatal guard cells could promote desiccation and create conditions commonly observed as post-fire crown scorch.

### Xylem dysfunction

Fire is thought to impair hydraulic function through two potential mechanisms: heat-induced embolism and deformation of xylem (Bär *et al.*, 2019). High temperatures and low relative humidity of buoyant fire plumes can lead to very high vapour pressure deficits at the leaf boundary layer, which increases transpiration and xylem tensions causing embolisms in xylem conduits and leading to cavitation in foliage and branches, which if extensive enough would result in reductions in water transport and conductivity (Kavanagh *et al.*, 2010). Well hydrated, intact branches exposed to temperatures near 250°C rapidly conduct water from stems to foliage in response to increasing vapour pressure deficits (Cohen *et al.*, 1990). Xylem dysfunction may also occur when fire-caused heating of xylem tissue causes irreversible deformation of cell walls, thereby reducing hydraulic conductivity that increases xylem tension and stomatal closure, which could eventually lead to foliage death from a combination of depleted carbon stores and hydraulic failure (Michaletz *et al.*, 2012). If sublethal temperatures are shown to cause extensive cavitation in foliage and small branches and/or xylem deformation in branches, these are mechanisms that may cause crown scorch as the foliage desiccates and visually discolours. Experiments using water baths as a surrogate for fire-caused heating have shown broad support for heat causing increased vulnerability to cavitation and loss in conductivity, although the underlying mechanisms vary, with some studies attributing responses to xylem deformation (Michaletz *et al.*, 2012; Bär *et al.*, 2018) and others to heat-induced embolism (West *et al.*, 2016; Lodge *et al.*, 2018). In contrast with water bath studies, field-based studies of trees exposed

to actual fire show mixed effects of fire impacting hydraulic safety, with no effect observed in the main stems of mature *Pinus pinea* (Battipaglia *et al.*, 2016) but increased vulnerability in the branches of *Pinus sylvestris* and *Fagus sylvatica* but not in *Picea abies* (Bär *et al.*, 2018) and main stems of 1 yr old *Pinus ponderosa* (Partelli-Feltrin *et al.*, 2020a). None of the studies with fire found decreased hydraulic conductivity and results suggest that increased hydraulic vulnerability, if found, was due to xylem deformation of pre-existing xylem (Bär *et al.*, 2018) or in xylem formed post-fire (Partelli-Feltrin *et al.*, 2020b). Further research is required to determine how well results from water bath experiments extend to conditions observed during wildland fire (Table 1). In addition, these studies have been focused on hydraulic integrity and tree mortality, and work is needed to directly test if xylem dysfunction causes crown injury. Research is also needed to integrate the effects of fire on carbon stores and hydraulic function. Carbon acquisition and hydraulic function are linked in ways still not fully understood, as evidenced by studies of experimental manual defoliation that caused an increased vulnerability to embolism (Hillbrand *et al.*, 2019) and depletion of nonstructural carbohydrates (NSC; Miranda *et al.*, 2020). NSC depletion impairs osmoregulation and turgor maintenance (Sapes *et al.*, 2021). Fire may act in a similar way as defoliation to kill foliage and impair or kill branch phloem, thereby causing changes to post-fire xylem anatomy and hydraulic integrity.

### Quantifying fire-caused crown injury from trees to landscapes

Crown injury is often quantified based on subjective ocular estimates of the percentage of the crown affected. Both crown volume (as a %) and length or height (as a value or %) are typical metrics (Alexander *et al.*, 2019). Crown volume estimates acknowledge that tree crown shapes are often irregular, making proportional volume estimation from measurements crude (Peterson, 1985; Hood *et al.*, 2010). Ocular estimates are relatively easy to make and can readily differentiate the range of crown conditions from scorched, to killed, to consumed. However, they are limited by requiring on-the-ground, individual tree assessments by trained staff after the fire occurs but before the killed foliage is shed as litter. Ocular estimates may also suffer from higher error in the intermediate injury values. For example, it is relatively easy to estimate the percentage of crown volume scorched on trees with little to no scorch and on trees with total (i.e. 100%) scorch; however, estimates of irregular crowns with intermediate scorch are more prone to error. Additionally, differences in crown condition can take days to months to become fully apparent to observers, requiring a time lag in quantifying the effects of fire. Furthermore, for species capable of quickly refoliating through multiple bud flushes and rapid leaf elongation (e.g. many southern US *Pinus*, subsection *Australes*), the window to observe crown injury is brief. Due to their small size, location on branches and typical height above the observer, bud injury is even more challenging to evaluate. Because of the coarse estimation of crown injury and confusion over the impairment mechanisms on physiological function, it may be that our metrics of scorch are simply correlative indicators of

above-ground heating, compromising our ability to mechanistically link cause and effect.

Remote sensing techniques offer promise for better estimation of crown injury (Eidenshink *et al.*, 2007). Remote sensing is commonly used to assess burn severity as a function of the forest canopy change from fire through both passive and active systems light detection and ranging (LiDAR). The appropriate scale of remote sensing platforms is dependent on the expected extent of crown injury. Laboratory-based experiments on individual trees tested gradients of thermal dosing on individual trees using an array of spectral indices (Sparks *et al.*, 2016). Spectral indices, such as the differenced normalised burn ratio (dNBR) or the differenced normalised vegetation index (dNDVI), are now common in predicting either average crown injury and post-fire tree survival at coarse scales (Lentile *et al.*, 2009; Furniss *et al.*, 2020). At the coarsest scales of satellite remote sensing (375 m to 1000 m), LiDAR fuel consumption estimates were related to fire radiative energy from level 2 MODIS active fire products (McCarley *et al.*, 2020). Coarse scale satellite imagery requires a large spatial extent that is more broad than individual scorched trees or patches. Active fire detection systems such as Visible Infrared Imaging Radiometer Suite (VIIRS) may hold promise for relating fire radiative power to scorch, as the spatial resolution of this system is potentially proximal in scale with scorch events. It is not yet clear how well these methods can differentiate between the various components of crown injury. For example, dNBR was a better predictor of crown consumption than crown scorch immediately and 1-yr post-fire (Lentile *et al.*, 2009).

LiDAR at a similar gradient of scales (tree to stand level) may explain more variability in crown injury than traditional passive remote sensing methods. LiDAR can differentiate between living and dead foliage, whether aerial or ground-based terrestrial scanning (Fig. 4). The diversity of remotely sensed methods offers promise to differentiate between leaf injury, bud kill and crown consumption. Combining two or more methods that detect change of crowns have been demonstrated via LiDAR for measuring equivalent water thickness (Junttila *et al.*, 2015), which can be used to assess changes in foliar moisture that result from drought, disease, live and dead proportion, and potentially scorch (Fig. 4), airborne LiDAR systems integrated with multispectral imagery to assess canopy foliar chemical traits (Asner *et al.*, 2015) and canopy height distributions with hyperspectral data to assess burn severity and post-fire recovery rate (Meng *et al.*, 2018). Characterisation of moisture loss or degradation of physical structure offer promise for detecting relevant foliar changes on individual trees at large fire scales (Table 1).

## Modelling applications: linking fire behaviour to crown injury

### Intrinsic and extrinsic factors influencing crown injury

Most fire effects models define scorch height as the maximum vertical height at which lethal heating (i.e. reaches 60°C) occurs during fire (Alexander *et al.*, 2019). The basic equation predicts scorch height based on calculated fireline intensity, with additional

options for accounting for ambient air temperature and wind speed. Scorch height is then used to estimate total crown injury assuming that all crown tissue (foliage, buds, branches) within the scorch height zone is dead (Van Wagner, 1973). However, determination of vertical profiles of actual tissue temperature as it relates to fire injury is challenging (O'Brien *et al.*, 2018). To reduce error and simplify estimation, the 60°C threshold has been widely used in physical and empirical modelling rather than energy dose, limiting the ability to accurately model crown injury and plant death. Thermal tolerance is species specific and dependent on numerous traits (West *et al.*, 2016). Tree architecture and forest structure also alter convective heat transfer, such that heat flux around crowns of individual trees or shrubs can contrast sharply with behaviour in open patches away from neighbouring trees (Parsons *et al.*, 2011). Crown, branch, and foliage architecture further influence heat transfer, and therefore overall resistance to injury during fire (Michaletz & Johnson, 2006b; Fernandes *et al.*, 2008).

Important species-specific differences in foliage traits, such as bud surface area-to-volume ratios or specific leaf area, could improve tree injury models. As a first step to improving empirical fire effects prediction systems, it would be possible to group species by crown morphology and architectural traits to apply different crown injury equations. Michaletz & Johnson (2007) developed a crown injury model that allows for differential tissue necrosis due to species morphological differences. The Van Wagner (1973) scorch height model similarly could be used in the simplest scenario for species with similar foliage and bud necrosis zones. For species known to have large potential differences between foliage and meristem necrosis, the Michaletz & Johnson (2007) equation could be overlaid with the Van Wagner model to predict total crown damage, as well as the difference zones of crown scorch and kill. Next steps should include incorporating crown and canopy heterogeneity at scales beyond individual trees. Measuring fire and its relevant interactions with the architecture of leaves and crown branches as well as at the leaf surface *in situ* is a challenge, but clearly needed for understanding mechanistic fire effects (O'Brien *et al.*, 2018).

Fire's noted role in the evolution of land plants is tied to its lethality and the differential mortality across life forms (He *et al.*, 2012). As with other species traits (e.g. serotinous cones, heat and smoke-triggered reproduction, thick bark, flammable litter, lower branch self-pruning; Stevens *et al.*, 2020), it is reasonable to postulate that differential tolerance to heat or partitioning of crown injury is a fire-adapted trait. Leaf arrangement, as in the 'shielding' of large angiosperm leaves or dense bundles of leaves, such as those found in many conifers (Michaletz & Johnson, 2006a,b; Bär *et al.*, 2019), may be emergent patterns in fire-prone plant communities. Evidence of differential scorch and kill sensitivity in tree mortality datasets (e.g. Fowler *et al.*, 2010) suggests that adaptations such as large buds, thick terminal branches, and high specific leaf area, increase tree survival in frequent, low-severity fire regimes. For tree species incapable of resprouting, juvenile tolerance to scorching may provide additional security in fire-prone environments. More studies focusing on the potential fire-adapted traits that enable species to withstand or avoid crown injury are needed (Table 1).

## Ecological consequences of crown scorch

Beyond the fire-caused death of leaves there remain several important unknowns regarding the consequences of scorched foliage. First, since scorch is a broad category of injury, tissue death results from many mechanisms (or combinations detailed above) dependent on the nature of the heat dose. The reductions in leaf area and the vertical pattern of crown scorch are somewhat analogous to clipping, or perhaps pruning, as both processes are concentrated on the lowest branches. Because leaves, even in evergreen gymnosperms and angiosperms, have phenological variation (with flushing, hardening, photosynthetic, and senescence stages), there are seasonal differences in responses to heating. For example, Harrington (1993) reported that tree mortality was 2.5 times higher in spring and summer fires compared with autumn fires for trees with similar levels of crown scorch in ponderosa pine. In their study on defoliation via pruning, Weise *et al.* (2016) found that mortality in loblolly and slash pine only occurred in trees defoliated in October, whereas all trees defoliated in January, April and July survived, although no mechanisms were tested. The disparate research on diverse species without mechanistic tests lacks synthesis and nuance, pointing to the need for experimentation that incorporates taxonomic diversity and field-scale fire experimentation of mechanisms.

Surviving crown injury, however, is not without consequences. Weise *et al.* (2016) found that surviving trees in their defoliation experiment had significant reductions in radial growth in the years following treatment. Other studies have documented similar reductions in radial growth in pines that survived fire-caused crown injuries (Johansen & Wade, 1987; Valor *et al.*, 2018). The links to reduced tree growth and carbon acquisition in surviving trees hints at multiple lines of research on the resilience of trees and forests to fire.

Important questions remain over whether heat-damaged leaves are capable of retranslocation or resorption of labile nutrients, stored carbohydrates, and hormones (Table 1). If scorched leaves are incapable of retranslocation, scorching represents a substantial loss to the tree and potentially substantial nutrient pulses to the ecosystem (Fig. 3). The degree to which scorched foliage can mobilise products from scorched foliage to living branches has important implications for trees' nutrient budgets and post-fire recovery (Hare, 1961). Observations of a continuum of scorching suggests that resorption occurs, but also that leaves may survive partial injury and either compartmentalise the dead portions or have reduced function over time until eventual senescence. In many fire-prone ecosystems, tree crowns can be fire-injured as often as several times per decade. With this high frequency of leaf loss, and if retranslocation is not possible, there might be substantial losses of internal leaf compounds that could cascade to stand or ecosystem level biogeochemical fluxes. This novel path for investigation is clearly warranted.

After leaf senescence and before reflushing, there are several other processes that are poorly documented. The most obvious is the immediate reduction of photosynthetic capacity and potential depletion of stored carbohydrates and nutrients as buds break and construct new leaves. Species such as *P. palustris* and *Liquidambar*

*styraciflua* have sufficient carbohydrate reserves to allow for reflushing foliage (Ruswick *et al.*, 2021), but relatively little information is known regarding nutrient reserves and reflushing capacity (Sayer *et al.*, 2018). The costs of reconstruction of new post-fire leaves in terms of N, other macronutrients and micronutrients, and the loss of stored nonstructural carbohydrates for refoliation deserves attention. Beyond leaf damage, the role of fungal endophytes (Huang *et al.*, 2016) and mycorrhizas (Sapes *et al.*, 2021) to potentially modulate the impact of crown injury and post-fire survival is intriguing.

Following leaf flushing, the physiological functioning of post-fire leaves and the tree's defences have received greater attention. Intrinsic water use efficiency can increase in uninjured foliage after fire (Wallin *et al.*, 2003; Battipaglia *et al.*, 2014), but not always (Thompson *et al.*, 2017). Induced resin production initially declines before then rising to above pre-fire levels in numerous *Pinus* species (Cannac *et al.*, 2009), but this is likely to be a nonlinear response as resin flow decreased in trees with crown volume scorch >50% (Wallin *et al.*, 2003; crown kill not quantified). Additionally, there is evidence that the age and level of drought stress play a part in the overall response of the trees (Partelli-Feltrin *et al.*, 2020b). Whether the stress caused by the initial scorching similarly affects stored carbohydrates, hormonal dynamics, or other processes is less well understood (Aubrey *et al.*, 2012). It is possible that scorch of lower crown foliage – which replaces old foliage with young foliage that has increased photosynthetic rates and higher water use efficiency – could benefit trees by reducing short-term post-fire water demand (Bär *et al.*, 2019). These potential outcomes represent critical nuance in our understanding of the ecological consequences of scorch.

As with scorch, crown consumption may have similar effects on trees as pruning, as it kills buds (and perhaps branch vascular tissues) on the lowest branches. A vital difference in crown consumption compared with pruning is that the proximal nonconsumed foliage is typically scorched. Temperatures associated with foliage consumption (presumably *c.* 250°C or more to ignite; Xanthopoulos & Wakimoto, 1993) suggests that nearby branches and perhaps the cambial tissues on the primary stem were subjected to similar heating and likely injury. Indeed, many species that can tolerate entire crown scorching are sensitive to minimal levels of crown consumption (Varner *et al.*, 2007; Fowler *et al.*, 2010). Injury or death of buds is often conflated with crown consumption and scorch as noted above, evidence that bud death is tightly linked to elevated tree mortality across taxa (Hood *et al.*, 2018).

Virtually unknown are the long-term physiological and genetic effects of sublethal fire on tree tolerance to subsequent fires. This topic is particularly relevant in forests and savanna ecosystems that burn frequently, with the same trees scorched repeatedly over time. Heat stress from high ambient air temperatures causes numerous cellular and metabolic responses that affect plant survival, including synthesis of heat shock proteins and stress and defence-related hormones such as abscisic acid, salicylic acid, and ethylene (Wahid *et al.*, 2007; Bitá & Gerats, 2013), but it is unknown how these responses extrapolate to heating that occurs during wildland fires.

## Conclusions

Major questions remain to improve our understanding of fire-caused crown injury and its relationship to ecological effects. To understand how fire affects leaves and crowns as well as what the physiological, biogeochemical and ecological outcomes are for fire-prone ecosystems, we propose segregating the crown scorch phenomenon into observations and measurements before, during, and after fire. Linking the characteristics of fires to their physiological and ecological outcomes is at the frontier of fire ecology; this Viewpoint identifies where some of those linkages are missing. There are several apparent oversights and assumptions of past research on crown injury that complicate interpretation. We hope that this Viewpoint stimulates physiologists, ecologists and fire scientists working to mechanistically understand how fire influences trees in savannas, woodlands, and forests and encourages relevant discoveries to overcome how little we know about such a common outcome of wildland fires.







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JMV, SMH and DPA conceptualised the paper. All authors contributed ideas, wrote and edited the manuscript.

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## References

- Alexander ME, Cruz MG, Taylor SW. 2019. Crown scorch height. In: Manzello SL, ed. *Encyclopedia of wildfires and wildland-urban interface (WUI) fires*. Berlin, Germany: Springer. doi: 10.1007/978-3-319-51727-8\_72-1.
- Asner GP, Martin RE, Anderson CB, Knapp DE. 2015. Quantifying forest canopy traits: imaging spectroscopy versus field survey. *Remote Sensing of Environment* 158: 15–27.
- Aubrey DP, Mortazavi B, O'Brien JJ, McGee JD, Hendricks JJ, Kuehn KA, Teskey RO, Mitchell RJ. 2012. Influence of repeated canopy scorching on soil CO<sub>2</sub> efflux. *Forest Ecology and Management* 282: 142–148.
- Bär A, Michaletz ST, Mayr S. 2019. Fire effects on tree physiology. *New Phytologist* 223: 1728–1741.
- Bär A, Nardini A, Mayr S. 2018. Post-fire effects in xylem hydraulics of *Picea abies*, *Pinus sylvestris* and *Fagus sylvatica*. *New Phytologist* 217: 1484–1493.
- Battipaglia G, De Micco V, Fournier T, Aronne G, Carcaillet C. 2014. Isotopic and anatomical signals for interpreting fire-related responses in *Pinus halepensis*. *Trees* 28: 1095–1104.
- 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: 1019–1031.
- Bitá C, Gerats T. 2013. Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat stress-tolerant crops. *Frontiers in Plant Science* 4: 273.
- Bueno A, Alfarhan A, Arand K, Burghardt M, Deininger A-C, Hedrich R, Leide J, Seufert P, Staiger S, Riederer M. 2019. Effects of temperature on the cuticular transpiration barrier of two desert plants with water-spender and water-saver strategies. *Journal of Experimental Botany* 70: 1613–1625.
- Cannac M, Barboni T, Ferrat L, Bighelli A, Castola V, Castola J, Costa J, Trecul D, Morandini F, Pasqualini V. 2009. Oleoresin flow and chemical composition of Corsican pine (*Pinus nigra* subsp. *laricio*) in response to prescribed burnings. *Forest Ecology and Management* 257: 1247–1254.
- Cansler CA, Hood SM, van Mantgem P, Varner JM. 2020. A large database supports the use of simple models of post-fire tree mortality for thick-barked conifers, with less support for other species. *Fire Ecology* 16: art 25.
- Catry FX, Pausas JG, Moreira F, Fernandes PM, Rego F. 2013. Post-fire response variability in Mediterranean Basin tree species in Portugal. *International Journal of Wildland Fire* 22: 919–932.
- Cohen WB, Omi PM, Kaufmann MR. 1990. Heating-related water transport to intact lodgepole pine branches. *Forest Science* 36: 246–254.
- Dickinson MB, Johnson EA. 2001. Fire effects on trees. In: Johnson EA, Miyanishi K, eds. *Forest fires: behavior and ecological effects*. San Diego, CA, USA: Academic Press, 477–525.
- Eidenshink J, Schwind B, Brewer K, Zhu Z, Quayle B, Howard S. 2007. A project for monitoring trends in burn severity. *Fire Ecology* 3: 3–21.
- Fernandes PM, Vega JA, Jiménez E, Rigolot E. 2008. Fire resistance of European pines. *Forest Ecology and Management* 256: 246–255.
- Fowler JF, Sieg CH, McMillin J, Allen KK, Negrón JF, Wadleigh LL, Anhold JA, Gibson KE. 2010. Development of post-fire crown damage mortality thresholds in ponderosa pine. *International Journal of Wildland Fire* 19: 583–588.
- Furniss TJ, Kane VR, Larson AJ, Lutz JA. 2020. Detecting tree mortality with Landsat-derived spectral indices: Improving ecological accuracy by examining uncertainty. *Remote Sensing of Environment* 237: 111497.



- de Groot W, Bothwell P, Carlsson D, Logan K. 2003. Simulating the effects of future fire regimes on western Canadian boreal forests. *Journal of Vegetation Science* 14: 355–364.
- Hare RC. 1961. *Heat effects on living plants. Occasional paper 183*. Asheville, NC, USA: USDA Forest Service. Southern Forest Experiment Station.
- Harrington MG. 1993. Predicting *Pinus ponderosa* mortality from dormant season and growing-season fire injury. *International Journal of Wildland Fire* 3: 65–72.
- He T, Pausas JG, Belcher CM, Schwillk DW, Lamont BB. 2012. Fire-adapted traits of *Pinus* arose in the fiery Cretaceous. *New Phytologist* 194: 751–759.
- Hillabrand RM, Hacke UG, Lieffers VJ. 2019. Defoliation constrains xylem and phloem functionality. *Tree Physiology* 39: 1099–1108.
- Hood SM. 2021. Physiological responses to fire that drive tree mortality. *Plant, Cell & Environment* 44: 692–695.
- Hood SM, Smith S, Cluck D. 2010. Predicting tree mortality for five California conifers following wildfire. *Forest Ecology and Management* 260: 750–762.
- Hood SM, Varner JM, van Mantgem P, Cansler CA. 2018. Fire and tree death: understanding and improving modeling of fire-induced tree mortality. *Environmental Research Letters* 13: 113004.
- Huang YL, Devan MN, U'Ren JM, Furr SH, Arnold AE. 2016. Pervasive effects of wildfire on foliar endophyte communities in montane forest trees. *Microbial Ecology* 71: 452–468.
- Johansen RW, Wade DD. 1987. Effects of crown scorch on survival and diameter growth of slash pines. *Southern Journal of Applied Forestry* 11: 180–184.
- Jolly WM, Parsons RA, Hadlow AM, Cohn GM, McAllister SS, Popp JB, Hubbard RM, Negrón JF. 2012. Relationships between moisture, chemistry, and ignition of *Pinus contorta* needles during the early stages of mountain pine beetle attack. *Forest Ecology and Management* 269: 52–59.
- Junttila S, Kaasalainen S, Vastaranta M, Hakala T, Nevalainen O, Holopainen M. 2015. Investigating bi-temporal hyperspectral LiDAR measurements from declined trees—experiences from laboratory test. *Remote Sensing* 7: 13863–13877.
- Kavanagh KL, Dickinson MB, Bova AS. 2010. A way forward for fire-caused tree mortality prediction: modeling a physiological consequence of fire. *Fire Ecology* 6: 80–94.
- Kozłowski TT, Kramer PJ, Pallardy SG. 1991. *The physiological ecology of woody plants*. San Diego, CA, USA: Academic Press.
- Lentile LB, Smith AMS, Hudak AT, Morgan P, Bobbit MJ, Lewis SA, Robichaud PR. 2009. Remote sensing for prediction of 1-year post-fire ecosystem condition. *International Journal of Wildland Fire* 18: 594–608.
- Lodge AG, Dickinson MB, Kavanagh KL. 2018. Xylem heating increases vulnerability to cavitation in longleaf pine. *Environmental Research Letters* 13: 055007.
- McCarley TR, Hudak AT, Sparks AM, Vaillant NM, Meddens AJ, Trader L, Mauro F, Kreitler J, Boschetti L. 2020. Estimating wildfire fuel consumption with multitemporal airborne laser scanning data and demonstrating linkage with MODIS-derived fire radiative energy. *Remote Sensing of Environment* 251: 112114.
- Meng R, Wu J, Zhao F, Cook BD, Hanavan RP, Serbin SP. 2018. Measuring short-term post-fire forest recovery across a burn severity gradient in a mixed pine-oak forest using multi-sensor remote sensing techniques. *Remote Sensing of Environment* 210: 282–296.
- Michaletz ST, Johnson EA. 2006a. A heat transfer model of crown scorch in forest fires. *Canadian Journal of Forest Research* 36: 2839–2851.
- Michaletz ST, Johnson EA. 2006b. Foliage influences forced convection heat transfer in conifer branches and buds. *New Phytologist* 170: 87–98.
- Michaletz ST, Johnson EA. 2007. How forest fires kill trees: a review of the fundamental biophysical processes. *Scandinavian Journal of Forest Research* 22: 500–515.
- Michaletz ST, Johnson EA, Tyree MT. 2012. Moving beyond the cambium necrosis hypothesis of post-fire tree mortality: cavitation and deformation of xylem in forest fires. *New Phytologist* 194: 254–263.
- Miranda JC, Rodríguez-Calcerrada J, Pita P, Saurer M, Oleksyn J, Gil L. 2020. Carbohydrate dynamics in a resprouting species after severe aboveground perturbations. *European Journal of Forest Research* 139: 841–852.
- O'Brien JJ, Hiers JK, Varner JM, Hoffman C, Dickinson MB, Michaletz S, Loudermilk EL, Butler BW. 2018. Advances in mechanistic approaches to quantifying biophysical fire effects. *Current Forestry Reports* 4: 161–177.
- Parsons RA, Mell WE, McCauley P. 2011. Linking 3D spatial models of fuels and fire: effects of spatial heterogeneity on fire behavior. *Ecological Modelling* 222: 679–691.
- Partelli-Feltrin R, Johnson DM, Sparks AM, Adams HD, Kolden CA, Nelson AS, Smith AMS. 2020a. Drought increases vulnerability of *Pinus ponderosa* saplings to fire-induced mortality. *Fire* 3: 56.
- Partelli-Feltrin R, Smith AM, Adams HD, Kolden CA, Johnson DM. 2020b. Short-and long-term effects of fire on stem hydraulics in *Pinus ponderosa* saplings. *Plant, Cell, & Environment* 44: 696–705.
- Peterson DK. 1985. Crown scorch volume and scorch height: estimates of postfire tree condition. *Canadian Journal of Forest Research* 15: 596–598.
- Rogers C, Sharpe PJH, Powell RD, Pence RD. 1981. High-temperature disruption of guard cells of *Vicia faba*. *Plant Physiology* 67: 193–196.
- Ruswick S, O'Brien JJ, Aubrey DP. 2021. Carbon starvation is absent regardless of season of burn in *Liquidambar styraciflua* L. *Forest Ecology and Management* 479: art118588.
- Sapes G, Demaree P, Lekberg Y, Sala A. 2021. Plant carbohydrate depletion impairs water relations and spreads via ectomycorrhizal networks. *New Phytologist* 229: 3172–3183.
- Sayer MAS, Tyree MC, Dillaway DN, Rudd BM. 2018. Foliage re-establishment of *Pinus palustris* Mill. saplings after spring or fall prescribed fire. *New Forests* 49: 851–869.
- Seymour VA, Hinckley TM, Morikawa Y, Franklin JF. 1983. Foliage damage in coniferous trees following volcanic ashfall from Mt. St. Helens. *Oecologia* 59: 339–343.
- Smith AMS, Sparks AM, Kolden CA, Abatzoglou JT, Talhelm AF, Johnson DM, Boschetti L, Lutz JA, Apostol KG, Yedinak KM *et al.* 2016. Towards a new paradigm in fire severity research using dose–response experiments. *International Journal of Wildland Fire* 25: 158–166.
- Smith AMS, Talhelm AF, Johnson DM, Sparks AM, Kolden CA, Yedinak KM, Apostol KG, Tinkham WT, Abatzoglou JT, Lutz JA *et al.* 2017. Effects of fire radiative energy density dose on *Pinus contorta* and *Larix occidentalis* seedling physiology and mortality. *International Journal of Wildland Fire* 26: 82–94.
- Sparks AM, Kolden CA, Talhelm AF, Smith A, Apostol KG, Johnson DM, Boschetti L. 2016. Spectral indices accurately quantify changes in seedling physiology following fire: towards mechanistic assessments of post-fire carbon cycling. *Remote Sensing* 8: 572.
- Stevens J, Kling M, Schwillk D, Varner JM, Kane JM. 2020. Biogeography of fire regimes in western US conifer forests: a trait-based approach. *Global Ecology & Biogeography* 29: 944–955.
- Thompson MT, Koyama A, Kavanagh KL. 2017. Wildfire effects on physiological properties in conifers of central Idaho forests, USA. *Trees* 31: 545–555.
- Valor T, Casals P, Altieri S, González-Olabarria JR, 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.
- Van Wagner CE. 1973. Height of crown scorch in forest fires. *Canadian Journal of Forest Research* 3: 373–378.
- Varner JM, Hiers JK, Ottmar RD, Gordon DR, Putz FE, Wade DD. 2007. Tree mortality resulting from re-introducing fire to long-unburned longleaf pine ecosystems: the importance of duff moisture. *Canadian Journal of Forest Research* 37: 1349–1358.
- Wade DD, Johansen RW. 1986. *Effects of fire on southern pine: observations and recommendations*. USDA Forest Service General Technical Report SE-41. Asheville, NC, USA: Southeastern Forest Experiment Station.
- Wahid A, Gelani S, Ashraf M, Foolad MR. 2007. Heat tolerance in plants: an overview. *Environmental and Experimental Botany* 61: 199–223.
- Wallin KF, Kolb TE, Skov KR, Wagner MR. 2003. Effects of crown scorch on ponderosa pine resistance to bark beetles in northern Arizona. *Environmental Entomology* 32: 652–661.
- Weise DR, Wade DD, Johansen RW, Preisler HK, Combs DC, Ach EE. 2016. *Defoliation effects on growth and mortality of three young southern pine species*. Albany, CA, USA: USDA Forest Service Pacific Southwest Research Station PSW-RP-267.

West AG, Nel JA, Bond WJ, Midgley JJ. 2016. Experimental evidence for heat plume-induced cavitation and xylem deformation as a mechanism of rapid post-fire tree mortality. *New Phytologist* 211: 828–838.

Winner WE, Casadevall TJ. 1983. The effects of the Mount St. Helens eruption cloud on fir (*Abies* sp.) needle cuticles: analysis with scanning electron microscopy. *American Journal of Botany* 70: 80–87.

Xanthopoulos G, Wakimoto RH. 1993. A time to ignition–temperature–moisture relationship for branches of three western conifers. *Canadian Journal of Forest Research* 23: 253–258.

Yedinak KM, Nemens DG, Anderson MJ, Peltrin RP. 2019. Leaf ruptures: acoustic impulse events in wildland fires. *The Journal of the Acoustical Society of America* 146: 2784–2785.

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