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Post-fire Tree Mortality

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Synonyms

Delayed tree mortality; Fire-caused tree mortality; Fire-induced tree mortality

Definition

Tree death is caused either directly or indirectly by wildland fire.

Introduction

By killing trees, wildland fires influence ecosystems in many ways, including limiting ecosystem productivity, altering resource availability, and changing the structure and composition of vegetation (Bond and Keeley 2005). These changes can have both positive and negative impacts on carbon storage, biodiversity conservation, hydrologic processes, and economic and social services (Bowman et al. 2009). In fire-adapted and fire-dependent ecosystems, fire controls tree density and species dominance, creating habitat that supports diverse plant and animal species that cannot persist in the absence of fire. However, fire-adapted ecosystems may be vulnerable to climate-driven alterations to fire regimes that are an emerging threat in recent decades, with observations of increasing fire size, frequency, and severity (Flannigan et al. 2009; Pechony and Shindell 2010; Seidl et al. 2016). Climate-mediated increases in fire severity and frequency are projected to cause large decreases in carbon stocks through loss in forested area (Liang et al. 2017), and increased fire frequency is killing trees before maturity (Bowman et al. 2014). Such changes in fire regimes can shift forests to non-forested states (Fairman et al. 2016; Walker et al. 2018). These impacts make understanding fire-caused tree mortality essential to predicting fire effects from local to global scales.

Post-fire Tree Mortality Mechanisms

Post-fire tree mortality can be caused either directly from fire injury or from indirect effects. Tree death can be immediate or delayed over several years after a fire.

Direct Tree Mortality

Direct tree death from fire is due to cambium necrosis via heat transfer to the crown, stem, and root tissue (Fig. 1) (Bär et al. 2019; Hood et al. 2018). Tree death results from either com-

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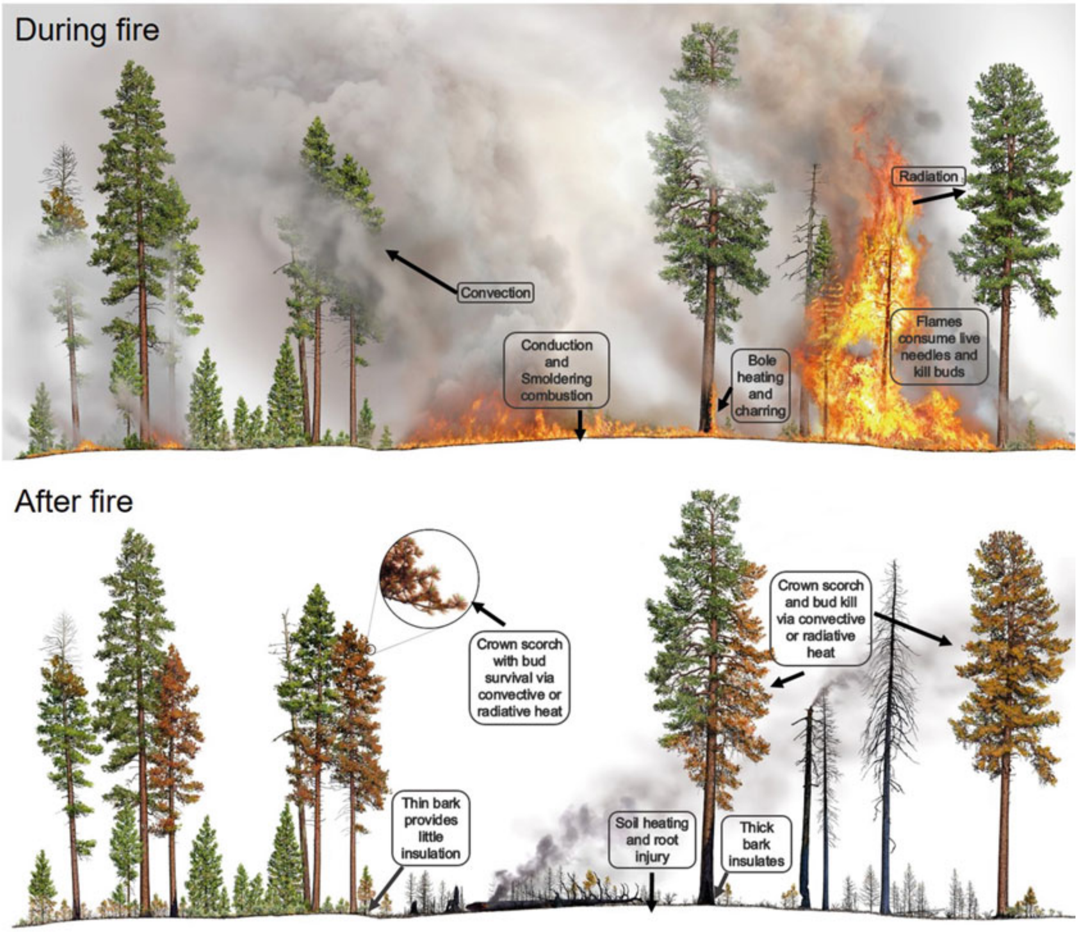


Post-fire Tree Mortality, Fig. 1 Heat is transferred to living tissues of trees during fire (top panel), resulting in injuries to different parts of trees after fire (bottom panel). Fire causes injuries to different parts of trees – buds, foliage, cambium in the stem, and roots – through three different heat transfer processes. *Combustion* directly consumes live needles and buds, small live branches, and small trees and causes tissue death. *Convection*, the movement of hot air, and *radiation*, heat traveling as energy waves, cause tissue death when temperatures are >60 °C for 1 s. *Bole heating*: Heat is conducted through the bark of trees, but because bark is a poor conductor, it insulates the live cambium underneath from heat. *Thick bark* insulates larger trees of some species, while *thin bark* provides little insulation on smaller trees and thin-barked species. *Soil and root heating* primarily occurs through *conduction during smoldering combustion* of duff and large logs. Graphics by R. Van Pelt. (From Hood et al. 2018)

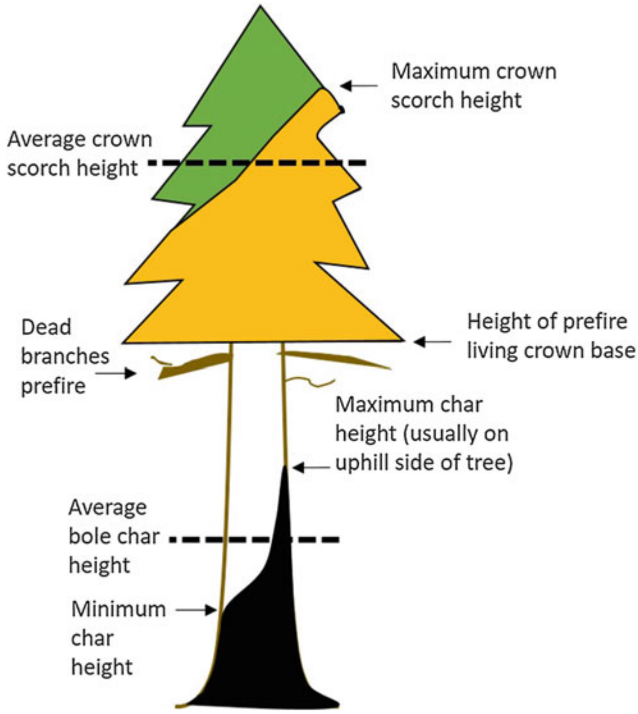
plete necrosis to any of these tissues or if partial injuries to multiple tissues are severe. Heat transfer occurs by convection, conduction, and radiation, and all three processes can cause tree injury and mortality (Fig. 1). If tissue temperatures rise above ≥60 °C, cambium necrosis (i.e., tissue death) occurs, although longer exposure at lower temperatures can also be lethal (Dickinson and Johnson 2001; Kelsey and Westlind 2017; Michaletz and Johnson 2007).

Tree crowns consist of foliage, buds, and branches. Convection is the dominant heat transfer process causing necrosis to crown tissue (Dickinson and Johnson 2001; Michaletz and Johnson 2007; Van Wagner 1973). Heated air in the fire plume or direct flame contact can kill foliage and vascular tissue in buds and branches

Post-fire Tree Mortality, Fig. 2 Upper photo: complete crown scorch caused from convection of the heated air to foliage during a surface fire. Lower photo, foreground: complete crown consumption caused from direct flame contact during a crown fire

(Fig. 2). Fire-caused necrosis to the crown is often lumped into one estimate of injury termed crown scorch that includes scorched and killed foliage, consumed foliage, and killed buds (Figs. 1 and 3) (Hood et al. 2018), but the difference between the amount of foliage versus buds killed can be sizable for some species with thick branches and large buds, such as *Pinus ponderosa* and *Pinus palustris* (Figs. 1 and 4). Partial crown scorch reduces photosynthetic capacity, causes remobilization of stored nonstructural carbohydrates (NSC) to rebuild foliage, and is an indicator of heating to the surrounding branches and stem (Hood et al. 2018). Fires causing 100% bud necrosis (i.e., bud kill via heated air or direct consumption), which also implies 100% foliage necrosis, are immediately killed if the tree is not a resprouting species. Although values differ slightly by species, trees can typically survive up to 70% crown scorch (Fowler et al. 2010;

Post-fire Tree Mortality, Fig. 3 Schematic of a tree with crown scorch and bark char showing the common ways crown and stem injuries are assessed



Grayson et al. 2017). Crown scorch values of 100% are survivable if few buds are killed (Fig. 5) (Dieterich 1979). Trees with crown scorch values between 70% and 100% often die within a few years after the fire.

Heat transfer to the tree bole or stem occurs through conduction, radiation, and convection (Fig. 1) (Dickinson and Johnson 2001; Michaletz and Johnson 2007). Damage to the conductive tissues in the stem is often the primary cause of mortality in small and thin-barked species compared to crown scorch (Lawes et al. 2011a, b; Michaletz and Johnson 2008). Heating to the stem can damage the phloem and xylem and thus impair translocation of photosynthates to roots and water and nutrients to the crown, leading to acute and chronic stresses that can result in eventual death regardless of the level of crown scorch (Midgley et al. 2011). Bark thickness is an important determinant of tree resistance to fire (Brando et al. 2012; Pausas 2015; Pellegrini et al. 2017). Thick bark protects the underlying vascular cambium and epicormic buds from fire and is the primary bark trait influencing heat transfer to the cambium (Bova and Dickinson 2005). The presence of bark char is indicative of heating to the stem. If a tree has thin bark, any area with char most likely has dead cambium underneath; however, bark char on trees with thick bark is not a sign of injury to the underlying cambium (Hood et al. 2008).

Long-term smoldering combustion can conduct heat through soil, leading to lethal heat levels that injure and kill roots and mycorrhizae. This impact decreases water transport and nutrient acquisition in the short-term and results in nonstructural carbohydrate drains to rebuild lost roots over longer periods (O'Brien et al. 2010; Taudière et al. 2017; Varner et al. 2009). Fire-caused tree mortality from root death alone is uncommon, as mineral soil is a poor conductor of heat and forest floor organic soils insulate underlying mineral soil and roots from flames (Hartford and Frandsen 1992). Long-term heating required to kill roots often also impacts the tree stem, making resulting tree death a combination of injuries to the roots and stem. Delayed tree mortality is a concern when reintroducing fire into long-unburned areas where deep accumulations of duff at the bases of trees can smolder and cause

Post-fire Tree Mortality, Fig. 4 *Pinus palustris* sapling several months after a wildfire that scorched all needles (i.e. 100% crown scorch). However, the meristematic buds survived (i.e., 0% bud kill) and are reflushing to replace needles killed by the fire

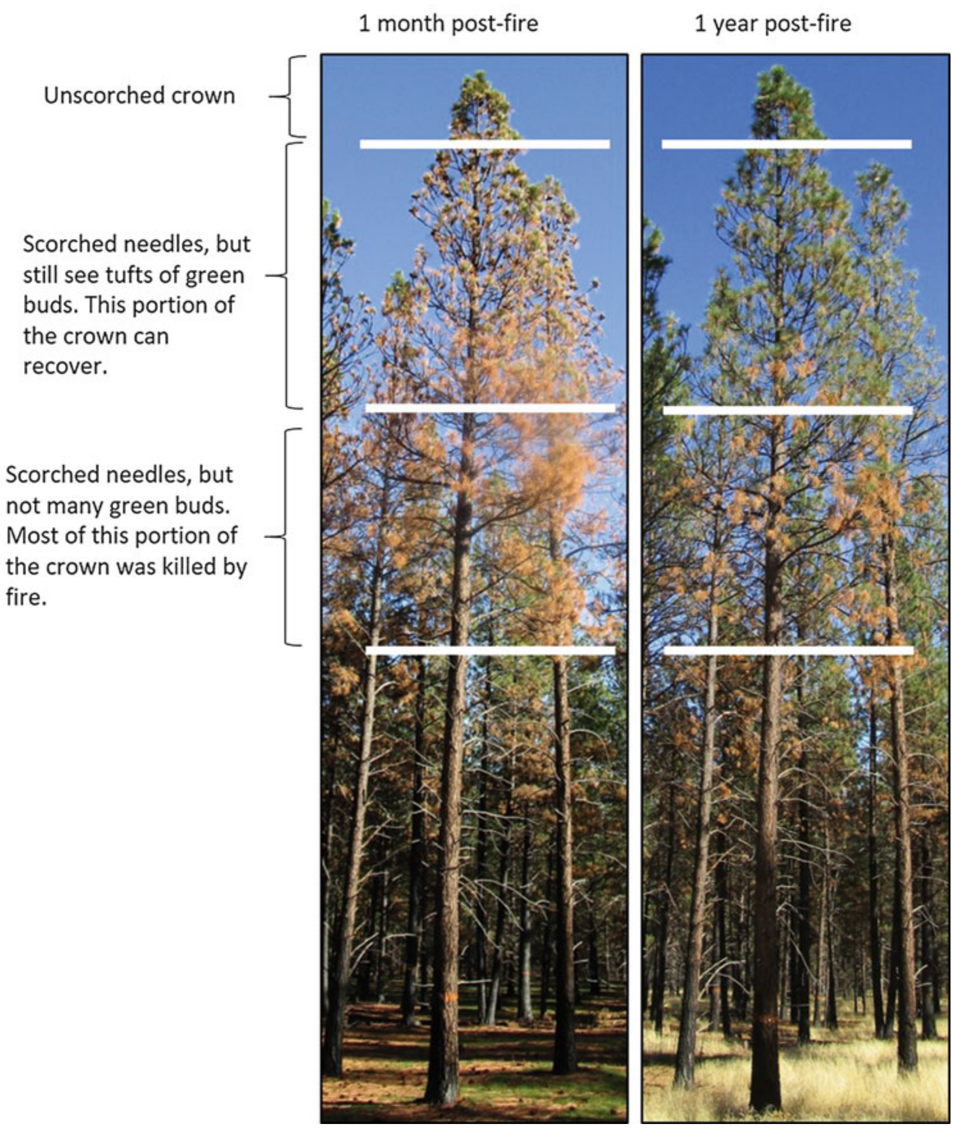
injuries to the stem and roots (Hood 2010; Varner et al. 2007).

Indirect Tree Mortality

Indirect mortality that occurs over several years after fire may be influenced by pre-fire stress from competition, drought, and disease, or by post-fire conditions such as elevated bark beetle populations (Hood et al. 2018; Kane et al. 2017b). Drought can increase the likelihood of tree death following fire, even after accounting for fire injuries (van Mantgem et al. 2013, 2018). Forest density can influence fire-induced tree mortality through two primary ways: by affecting local fire behavior and through competition with neighboring trees. Forest structure influences fuel arrangement, local moisture, and fire-atmosphere interactions, thereby also influencing fire behavior that causes direct injury to trees (Agee and Skinner 2005). Indirectly, competition can influence fire-induced tree mortality, by limiting aboveground and belowground resources, thereby increasing stress. Increased fire-induced mortality from competition has been documented (Platt et al. 1988; van Mantgem et al. 2018; Yu et al. 2009), with slower-growing trees more likely to die given the same level of fire-caused injury than faster-growing trees (Nesmith et al. 2015; van Mantgem et al. 2003). Alternatively, decreases in tree density and competition after fire can increase resource availability, potentially compensating for the short-term impacts of injury to release surviving trees (Alfaro-Sánchez et al. 2016). Insects and pathogens can increase stress before fire by decreasing growth, NSC reserves, and impairing hydraulic conductivity, as well as causing additional mortality in trees that otherwise would have survived fire injuries (Bär et al. 2019; Hood et al. 2018; Kane et al. 2017b; Parker et al. 2006). Because bark beetles require living trees with healthy phloem to reproduce, trees killed immediately by fire are not suitable hosts. Host suitability and attraction after fire vary by tree and bark beetle species, but in general, bark beetles attack and kill trees with intermediate levels of both crown scorch and cambium injury or higher levels of either crown scorch or cambium kill (Jenkins et al. 2014). Bark beetle activity after fire can cause a short-term pulse in mortality, but generally do not result in outbreaks or sustained levels of beetle-caused tree mortality (Davis et al. 2012).

Resprouting Versus Top-Kill

Fires can cause complete death of the tree or only top-kill. Top-kill occurs when fires kill meristematic tissue above ground, but the tree resprouts from epicormic buds or belowground bud banks (Pausas et al. 2018) (Fig. 6). Burning during dormant seasons or periods when active growth has ceased can reduce bud kill and subsequent tree mortality (Harrington 1987; Valor et al. 2017). Indeterminate growth species can sustain higher levels of crown loss if burning occurs at the beginning of the growing season compared to later in the season (Weise et al. 1987), and species that can resprout from epicormic buds can survive higher levels of crown injury (Bond and Midgley



Post-fire Tree Mortality, Fig. 5 *Pinus ponderosa* with crown scorch and bud kill 1 month after a wildfire (left photo) and 1 year later (right photo)

2001). In ecosystems where resprouting following top-kill is common (e.g., savannas, temperate deciduous forests), ramets may still follow standard patterns of mortality (e.g., bark thickness confers fire resistance), but successional patterns and recovery times are faster than ecosystems dominated by non-sprouting species (Pausas and Keeley 2017).

Predicting Post-fire Tree Mortality

Accurate predictions of fire-induced tree mortality with quantified uncertainty are needed for models used in planning, post-fire management, predicting future landscape dynamics, and feedback to the global carbon cycle. Most post-fire mortality models use empirically based, logistic regression equations to predict which trees will die based on species, the level of crown scorch, and tree size (Woolley et al. 2012). Model

Post-fire Tree Mortality, Fig. 6 *Quercus gambelii* resprouting after a wildfire top-killed the main stem

applications vary from individual tree to global scales (Hood et al. 2018). The First Order Fire Effects Models (FOFEM), BehavePlus, and Fire and Fuels Extension to the Forest Vegetation Simulator (FFE-FVS) are free software packages that predict post-fire tree mortality. Individual tree death predictions are used for post-fire salvage. Stand-level mortality predictions are used for developing prescribed fire burn prescriptions and predicting post-fire forest structure and composition, while landscape-level predictions provide insight into vegetation type and carbon stocks with changing fire regimes.

Although current logistic models can accurately predict mortality for some species (Furniss et al. 2019; Ganio and Progar 2017; Grayson et al. 2017; Hood and Lutes 2017; Kane et al. 2017a), they are far removed from the actual physiological and ecological processes that cause immediate and delayed post-fire mortality. Development of process models to predict post-fire tree death is an active area of research (Bär et al. 2019; Hood et al. 2018; O'Brien et al. 2018). Independent, tissue-specific models exist to predict circumference and height of cambium kill (Chatziefstratiou et al. 2013) and differences in crown scorch and bud kill heights (Michaletz and Johnson 2006). A whole-tree coupled physical-physiological model is necessary to predict physical heat transfer and resulting fire effects based on living plant physiological traits and thus the prediction of fire-induced tree mortality and growth. However, such a model would still have a host of limitations and uncertainties (Adams et al. 2013) and is not yet available. The wide-ranging applications associated with fire-induced tree mortality does not lend itself to a one-size-fits-all approach, and it seems unlikely that empirical models will be replaced due to the need to balance model complexity with model application. Instead, empirical models need to be refined for use in land management applications in the near-term, while heating and physiological process models should be developed and linked to create a hybrid-based approach to improve mechanistic understanding to predict mortality under novel scenarios (Hood et al. 2018).

Cross-References

▶ Conduction
▶ Convection
▶ Crown Fire
▶ Crown Scorch Height
▶ Direct Flame Contact
▶ Fire Severity

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▶ First- and Second-Order Fire Effects
▶ First-Order Fire Effects Model (FOFEM)
▶ Radiant Heat
▶ Smoldering Combustion

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