Current Forestry Reports
https://doi.org/10.1007/s40725-018-0082-7

Advances in Mechanistic Approaches to Quantifying Biophysical Fire Effects

J. J. O'Brien[1] · J. K. Hiers[2] · J. M. Varner[3] · C. M. Hoffman[4] · M. B. Dickinson[5] · S. T. Michaletz[6] · E. L. Loudermilk[1] · B. W. Butler[7]

Abstract

Purpose of Review The search for causal mechanisms in fire ecology has been slow to progress for two main reasons. First, many fire ecology investigations often occur after fires, with no detailed information on fire behavior. These fire effects are then used to infer both fire behavior and the subsequent effects themselves. Second, that fire behavior is heterogeneous at many scales both spatially and temporally, and that heat transfer occurs in three dimensions is only now being appreciated. Spatially and temporally resolved measurement of heat and mass transport in fires is difficult; and even when fire is measured, it is often measured in ways that are not relevant to the effects of interest. General measurements like flame length, rate of spread, and consumption are only approximate descriptors of a complicated energy transfer environment and are of limited use when linking fires to their effects.

Recent Findings We review both progress in biophysical fire ecology and present recent advances in technology and analytical techniques used for measuring the fire environment. We discuss not only how models of fire-induced injury can be partitioned into belowground, stems, and crowns but also how understanding synergy among these injuries will be necessary to improve our understanding of fire effects. We also present how there are emerging opportunities to apply computational fluid dynamic models to address issues of scaling in biophysical fire effects.

Summary The conceptual linkage of fire energy release to mechanistic fire effects has value beyond simply understanding post-fire tree injury, function, and mortality. It can guide investigations that identify and isolate mechanisms driving other fire effects such as soil heating, organismal population dynamics, and biogeochemistry.

Keywords Fire behavior · Fire ecology · Fire effects · Tree mortality · Wildland fire

This article is part of the Topical Collection on *Fire Science and Management*

✉ J. K. Hiers
jkhiers@talltimbers.org

1 USDA Forest Service, Center for Forest Disturbance Science, Southern Research Station, Athens, GA 30602, USA

2 Tall Timbers Research Station, Tallahassee, FL 32312, USA

3 USDA Forest Service, Pacific Wildland Fire Sciences Lab, Pacific Northwest Research Station, Seattle, WA 98103, USA

4 Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, CO 80523, USA

5 USDA Forest Service, Forestry Sciences Laboratory, Northern Research Station, Delaware, OH 43015, USA

6 Department of Botany and Biodiversity Research Centre, University of British Columbia, Vancouver, BC V6T 1Z4, Canada

7 USDA Forest Service, Missoula Fire Sciences Laboratory, Rocky Mountain Research Station, Missoula, MT 59808, USA

Introduction

The energy released during combustion is the fundamental mechanism driving the ecological effects of wildland fire. While this might seem self-evident, for decades, many authors have pointed out that appropriate measurements of fire energy release are necessary to uncover the causal links driving the physical, biological, and ecological impacts of fire [1–8]. These recommendations from pioneers in the field have largely gone unheeded. Again, nearly two decades after Johnson and Miyanishi [9] reiterated that the slow pace of discovery was driven by a lack of appreciation of fire as a *biophysical process*, the field of fire ecology still struggles to link energy transfer to plant response. The Michaletz and Johnson [10, 11] reviews of biophysical processes on fire-induced plant mortality emphasized that while the body of knowledge connecting fire behavior to fire effects was growing, they noted that progress remained sluggish (see also [12, 13]). Current

Published online: 15 September 2018

methods for predicting fire-induced plant mortality are still largely empirical. These methods do not exhibit a wide range of applicability and are not readily linked to duff burning, soil heating, and surface fire behavior models [13–16]. Defining fire as a biophysical process means understanding fire's impact on organisms and the environment as a function of the transfer of heat, mass, and momentum, all processes rarely measured by fire ecologists. Furthermore, the transfer of energy from fire to organisms and the environment is heterogeneous in both space and time [17–19], which makes its quantification difficult at spatial resolutions relevant to fire effects on individual organisms. While this criticism remains relevant today, there have been many advances in both mensuration and modeling that allow spatially resolved fire energy to be mechanistically linked to ecological fire effects [20–24, 25•, 26•, 27•, 28••, 29]. Still, the field lacks a comprehensive review of these advances and their applicability towards building mechanistic models of biophysical fire effects, especially in a spatially explicit manner.

The field of fire ecology is a relatively new discipline with few guiding principles [30, 31]. The discipline has often focused on correlations between metrics of fire behavior and effects [4] or using fire effects to infer both fire behavior and the effects of fire behavior, e.g., stem char height and crown scorch height as both an index of intensity and a predictor of mortality (e.g., [32–34]). Often, a failure to detect an impact of surface fire behavior on fire effects is because the surface fire metric used—such as flame length, rate of spread, fuel consumption—cannot capture the relevant or interacting sources of energy transfer [22, 35, 36]. Furthermore, commonly employed measurement devices like temperature-sensitive paints and thermocouples are often used without an understanding of how they relate to fire behavior and energy transfer [22, 37]. Though fire effects are driven by energy released through combustion, ecologists and foresters are generally not trained in combustion science. Conversely, physicists and engineers interested in combustion are unfamiliar with plant ecology, despite vegetation being the source of fuels in wildland fires. This divide also extends to laboratory versus field studies of fire and was described as the "two solitudes of fire research" by Van Wagner [38]. Bridging the two solitudes will be critical for meaningful advances in fire ecology as was reviewed by Johnson and Miyanishi [9]. This will require an appreciation of concepts and terminology unique to both camps and an appreciation in the important sources of variation in heat transfer as was reviewed in Michaletz and Johnson [11]. In our review, we also argue progress is further hindered by the fact that the importance of spatial and temporal variation and complex interactions among multiple mechanisms are underappreciated. Our aims in this paper are to (1) discuss why spatially explicit and temporally resolved wildland fire heat transfer is critical to measure, (2) present advances in linking these measurements to relevant biophysical mechanisms, and (3) present a framework for fire ecology to move this mechanistic approach into a more *spatially and temporally explicit* context. Our conceptual model for understanding biophysical fire effects inherently embraces variation in the fire environment as a critical source of fire effects (Fig. 1). This variability is a critical element defining how fires affect organisms and must be considered at the relevant scale. We argue that like much of ecology in general, fire ecology is characterized by pattern detection and scale mismatch that hinders identification of underlying mechanisms [39]. Building on the basic framework of Michaletz and Johnson [11], we re-examine fire effects from the ground up, from soils, to plant stems, to crowns, and finally to landscapes, that we believe will advance fire ecology by exploiting both temporally and spatially explicit models. We also present how multi-dimensionality of measurements (in both space and time) and in heat transfer itself matters for understanding mechanisms driving fire effects. A discussion follows on how adding appropriate spatial and temporal dimensions to fire behavior can be used to more effectively understand the mechanisms governing injuries in plant roots, boles, and crowns and how these interact to influence post-fire plant function, growth, and mortality. We also posit that to answer questions critical for improving fire management, the field must (1) consider fire-atmosphere interactions and (2) structure sampling to capture relevant fire and fuels metrics in three dimensions. For example, prescribed fire practitioners can manipulate the ignition pattern of a fire in myriad ways so understanding the impacts of various ignition patterns on fire behavior is critical for achieving the desired objectives of the burn (e.g., minimizing crown scorch, maximizing shrub mortality, and maintaining rare species populations). These objectives also must be achieved simultaneously. Furthermore, ignition pattern drives smoke production and transport, a critical concern for fire managers. How fire ecology can inform these decisions depends on a mechanistic understanding of complex phenomena such as fire-atmosphere feedbacks, heat transfer, spatial patterns of mortality, and how these drive post-fire ecological responses. Likewise, the wildfire environment can be as or more complex than prescribed fires. Fire energy release varies over orders of magnitude in wildfires and assigning ecological impacts to fire requires knowledge of the patterns of fire intensity that are rarely measured.

Moving from describing to explaining

Fire behavior and effects have been shown to be spatially correlated with vegetation structure and pattern at relatively fine scales (e.g., < 0.25 m^2 [17, 18] and < 0.01 m^2 [28]). Previous studies have suggested that this relationship is due to several possible cross-scale interacting mechanisms including variations in the ignition and combustion characteristics of

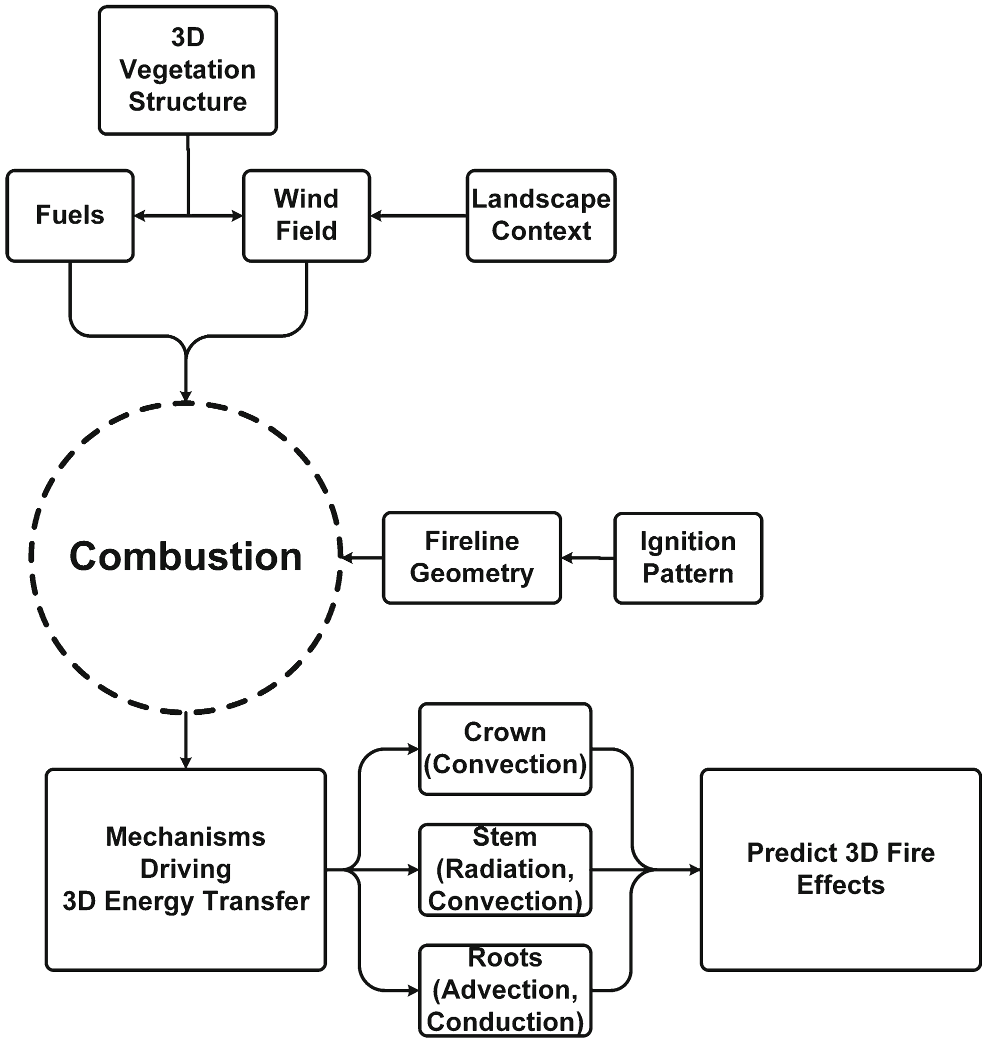

Fig. 1 Conceptual diagram of mechanisms governing fire behavior and related biophysical fire effects that can be explored using empirical and modeling approaches of time resolved three-dimensional energy transfer. Combustion, the central connection among processes is encircled by a dashed line to indicate the combined influence of multiple factors acting simultaneously to drive subsequent energy release and effects. Although there can be interactions and indirect effects among fireline geometry, wind, and fuels, we chose to isolate fireline geometry as it, along with fuels, are the main aspects driving fire behavior that can be controlled by a fire manager

contrasting vegetation types and alterations to the ambient and fire induced air flow [40–43, 44•]. For example, the interaction among fire lines results in complex patterns of strong buoyant updrafts which can also result in localized variability in fire behavior and heat transfer from the fire to plant tissues [45, 46]. Unfortunately, such fire-atmospheric interactions have traditionally been ignored, assessed in isolation, or studied at the wrong scales required to advance our understanding of the extent to which of various factors control fine-scale variability in fire behavior and effects. Furthermore, the current suite of fire behavior prediction tools does not explicitly incorporate fire-atmosphere interactions and resulting spatial variation in heat transfer. For example, most managers and researchers rely on modeling tools (e.g., BehavePlus, FFE-FVS, FCCS) that are based on simplified non-spatial representations of forest structure and fuels [47]. Although this approach can be useful in the context of large-scale wildfires, it ignores the inherent spatial complexity of fuels and fire atmospheric feedbacks that have been shown to drive surface fire behavior and effects. To clearly understand mechanisms of heat transfer relevant to ecological effects, it is critical to identify the significance of the "fuel" and "atmospheric" roles independently then carefully examine their interactions, which are often nonlinear. For example, in a dense pine stand, the vegetation plays competing roles as it offers an abundance of combustible material but simultaneously blocks the wind and can even serve as a heat sink.

Recent developments in wildland fire behavior models based upon fluid dynamics, such as HIGRAD/FIRETEC [48] and the Wildland Urban Interface Fire Dynamics Simulator (WFDS) [49], have provided new opportunities to explicitly represent and understand the underlying mechanisms and interactions driving fire behavior over both space and time. For example, recent studies have utilized these models to gain new insight into the dominant controls of fire spread [41, 50], three-dimensional canopy-mediated flow [46], and spatial patterns of fuel consumption [44•, 51, 52•]. These models are also beginning to be used to predict fire effects such as seed survival [24], plant crown heating and cavitation [15, 53•], and plant growth and mortality [25•].

Notwithstanding some concerns regarding model validation [54], the advantages of three-dimensional physics-based models over empirical or semi-empirical models are that they can: (1) represent the three-dimensional structure of the entire fuels complex; (2) capture nonlinear dynamics arising from interactions among the fire, atmosphere, and fuels complex; (3) provide predictions of fire behavior metrics that directly relate to biophysical fire effects (e.g., heat fluxes, temperatures, gas velocities); and (4) can be extended to novel fuel and environmental conditions.

Although advances in fire behavior modeling and new measurement techniques have been useful for enhancing our understanding of fine-scale spatial patterns of fire behavior, our ability to adequately connect the modeled fire environment to post-fire effects still has several critical shortcomings. Previous studies have shown that heat from fires can injure plants in many ways [55], including necrosis of tissues and organs or cavitation and deformation of xylem [10, 15, 20, 53•, 56, 57, 58••]. In addition, the loss of non-structural carbohydrate reserves [59] and the characteristics of the immediate post-fire environment may lead to further stress or the inability to defend against secondary mortality agents such as bark beetles [57, 60, 61•]. Taken together, fire-caused injuries are complex as are the ways that plants respond. Further complicating the picture are species-specific adaptations to avoid or recover from fire injury that cloud generalizations on the impact of tissue damage. For example, long-needled pines of SE North America regularly survive 100% crown scorch after surface fires [62], and can recover crown function in less than a month [63]. Variation in bark texture and thickness can determine a species' susceptibility to stem mortality due in part to complex boundary layer dynamics that result in uneven heating around the stem circumference, yet this cannot be adequately characterized by most stem heating models that are driven by one-dimensional conduction estimates (Fig. 2). No formal synthesis of these mechanisms has been undertaken, nor have any experiments evaluated the potential interactions of these injuries on post-fire plant growth, stress, or mortality. Clearly, only a mechanistic approach examining multiple hypotheses is up to the challenge.

Given the lack of experimental research, most hypothetical models of heat transfer and the vast bulk of published research oversimplifies the thermal environment that plant tissues are exposed to and the underlying plant physiological responses to injury. For example, most models relate the thermal environment as measured by the spatially averaged fireline intensity or flame length to an observable measure of injury, such as bark char height or crown scorch [64, 65]. However, the lack of spatial resolution and mechanistic basis of fire behavior limits their applicability across regions, species, and the highly heterogeneous fuel and environmental conditions that comprise many fire-prone areas. This pattern within the discipline likely represents an inability to measure or describe fire events

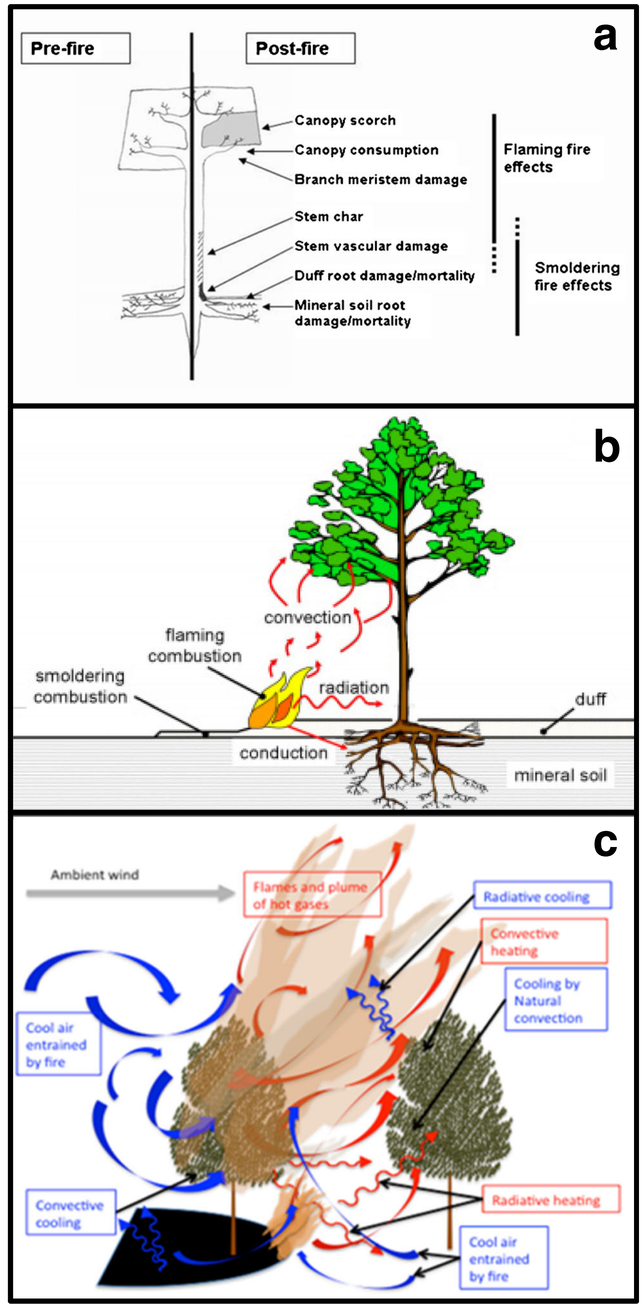

Fig. 2 Conceptual models for understanding biophysical fire effects have evolved to show complexity. These conceptualizations of simple 1-D or 2-D models (Varner et al. 2005) or whole tree models [11] of heat transfer, now include an understanding of vegetation as an active driver of spatially resolved fluxes to vegetation from fire-atmospheric feedbacks, such as convective cooling [43]

that drive fire effects. These shortcomings ultimately constrain the ability to predict local heterogeneity in plant injury and responses observed. Furthermore, the ability of these tools may be further limited when complicated fire-atmosphere dynamics significantly alter local heat exposures. Recent research suggests that treating heat as a "dosage" provides a way forward to understand how heat affects plants [66••, 67••]. In this sense, heat can be characterized as a quantifiable dose and used to predict plant responses either at the tissue or whole organism level. We argue next-generation approaches where the heat dose is mechanistically linked to the response through some relevant heat transfer mode (e.g., conduction into a plant stem) offer the greatest promise to link local fire behavior to the three-dimensional thermal environment and, in turn, to specific tissue injury. For instance, Jones et al. [14] and Chatziefstratiou et al. [23] use stem-surface heat flux to model stem heating and injury while others [13, 56] use a plume model that uses fire behavior variables to provide canopy exposures that are then used to model needle and branch heating. New insights derived from a consideration of mechanisms will ultimately address why and how plants are affected by fire.

We argue that a model with a mechanistic foundation is required to predict fire dynamics under changing conditions. While a model's predictive ability is often touted as the critical measure of success, there is a critical difference between *prediction* and *manipulation* [68]. *Predictive* empirical models use knowledge of starting and ending conditions to forecast a response without knowledge of how the system works; manipulation requires knowledge of both how a system starts and an understanding of how a system works to forecast responses. While there is undeniable utility in empirical models, these can be challenged not only by uncertainties generated by climate change, altered land-use patterns, and novel species assemblages but also by local patterns not exploited in the model development. While many of the major physical mechanisms driving combustion are well understood, often, the implications of these mechanisms are not fully explored, especially in the context of the complex wildland fire environment. For example, fire behavior and variation in energy transferred is structured through convection dominated processes, including draft dynamics of buoyant plumes [48, 69], but most fire behavior and effects models are simple, non-spatial and, more importantly, are correlative. These approaches fail to adequately characterize the complexity of the physical world or the phenomena being investigated.

Moving Forward: New Tools Used to Capture Relevant Heat Transfer and Fire Relevant Forest Characteristics

Relatively recent technological advances have generated opportunities to capture two- and three-dimensional characteristics of both the fuels and the combustion environment. For example, LiDAR and photogrammetry allow the three-dimensional characterization of both the forest structure and fuels from the millimeter to kilometer scales [70, 71•, 72–74]. Infrared thermal imagery has also allowed the ability to capture radiant heat transfer and temperatures of fire-heated tissues across a range of spatial and temporal scales [26•, 27•]. Novel techniques such as background-oriented Schlieren photography [75] and optical flow image analysis [76] show promise in enumerating convective heat fluxes in three dimensions. Even well-established technology such as thermocouples can also be employed in new ways with the widespread availability of relatively inexpensive microprocessors [77, 78]. These same microprocessors promise to allow the deployment of extensive radiometric measurements as well, using small infrared thermal imager chips currently available commercially.

Soil

Belowground fire effects have remained understudied, despite the acknowledged role of soil heating or consumption on plant stress and mortality [35, 57, 59, 79]. When considered, belowground fire effects research has relied on coarse measurements and relatively simple one- or two-dimensional approaches [80]. More recently, Massman et al. [81, 82] have modeled extreme advective transfer into soils during fire, and Smits et al. [83] studied the effects of a pile burn and a wildfire on soil thermal properties, effects that may translate to intense wildfires and long-term soil heating below burning duff. Improving our understanding of smoldering surface fires may be critical for understanding mechanisms of tree mortality in boreal ecosystems that are dominated by fire regimes where organic soil horizons are commonly consumed. For example, about 80% of the boreal forest in Russia is thought to burn in surface fires often with much duff consumption [84–87]. In frequently burned surface fire regimes, fuels capable of heating more than the top few millimeters of soil are sparse and unevenly distributed in space and time (Fig. 3). For example, woody fuels are more frequent beneath crowns and cones in species such as longleaf pine are produced in large quantities only intermittently over decades. This variability in energy density has recently been shown to drive both understory plant community dynamics and diversity [28••, 88••]. Prior to these studies, energy transfer was not generally considered as a direct effect on the relationship between fire and diversity, but rather as an indirect effect by moderating competition among plants [89].

Organic and mineral soils are structurally complex and their dynamic moisture relationships have implications for heat transfer and subsequent impacts to plant roots [90]. Where duff ignites and combustion is sustained is often key for understanding patterns of shrub and herb mortality [91]. The opacity of soil restricts our ability to observe heat transfer and measurements often disrupt the physical integrity of intact soil. While the physical structure of the soil is critical in advective heat transfer, making useful measurements is extremely difficult. In fact, soils have been referred to as a black box for these reasons [92]. Aboveground fuels, whether fine or

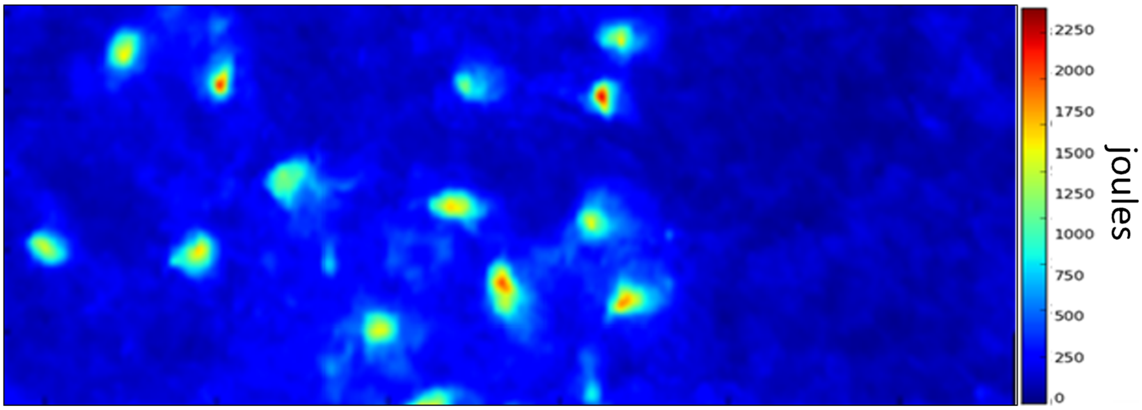

Fig. 3 Cumulative fire radiative energy release (total joules per pixel) of fine and woody fuels in 18 months of fuel accumulation within a 1 × 3 m thermal image of fire in a longleaf pine stand in Florida. The fire energy was integrated for total time when pixel temperature exceeded 300 °C. Cones released more than 10 times more energy than fine fuels, a sufficient quantity of energy into the soil to cause mortality in normally fire-resilient resprouting plants

woody, transfer surface fire energy to mineral soils either directly or through combustion of overlying organic horizons [72, 76]. The thermal conductivity of soil varies widely depending on both coarse and fine-scale properties and can be affected by heating in single fires or by repeated burning [81]. Moisture variability over time further complicates the heat transfer properties. Because soil heating is perceived as minimal in most surface fire regimes, the focus of the bulk of fire effects research has ignored or overlooked below-ground effects [93, 94]. Where it is considered, it is usually in the context of high-intensity fires altering soil properties such as water infiltration, nutrient dynamics, or erosion potential [95]. Soil heating in fires is driven primarily by conduction and advection and can lag aboveground flame passage and be slow to cool [93]. The duration of heating can be substantial (hours to days) despite the relatively low temperatures measured below-ground (typically less than 200 °C). This long-duration heating causes fine and coarse root death, root carbohydrate drain, reduced sap flux, diminished resin defenses, and ultimately, tree death [57, 59, 61•]. Considerably less attention has been paid to heating effects on soil microbes [96] and biota more broadly, though clearly, fire impacts more than just plant roots. The duration and effects of individual heating events over longer time scales is of relevance in ecosystems where repeated burning has taken place for millennia, a critical temporal effect often overlooked in studies of fire effects.

Stems

Plant stem heating models have received considerable attention over the decades, evolving from statistical and analytical to numerical, with the latest incorporating the key physical processes including heat flux boundary conditions that vary around a tree's circumference, conduction heat transfer, desiccation, devolatilization, bark swelling, and tissue necrosis [14, 20, 23]. Key gaps include a need for model parameters for a range of species, which are often seasonally variable, like bark and sapwood moisture content and the current state of modeling cannot be used to explore the potential for water transport during fires to reduce stem heating, a phenomenon that may explain the relative resistance to long-term basal heating observed in some trees [97]. Bark combustion (smoldering and flaming) complicates the bark surface heat budget, increasing heat transfer into the stem of a fibrous-barked Australian eucalyptus species [98]. Also, the role of fine-scale three-dimensional fluid dynamics at the fire-bark surface interface has remained unexplored though heat flux boundary condition provides a means for linking the stem heating model to fire behavior models [13]. Required to complete the link are data (e.g., [56]) and models of convective and radiative heat transport and deposition, including the complex fluid dynamics that govern the formation of leeward vortices and standing leeward flames that cause uneven tree stem heating [99]. The uneven heating of a cylindrical bole in a cross-flow [81] has little relevance where trees are heavily buttressed, a common feature of tropical trees, and where, as in Amazonian first-entry fires, intensities may generally be low [100]. Pinard and Huffman [101] suggest that buttresses may protect trees, perhaps because of the effect on fire dynamics. Bark roughness varies at a range of scales (e.g., from fissuring at centimeter scales to unevenness at millimeter scales) presenting challenges to predicting incident heat fluxes needed by stem heating models. Measurements of incident convective and radiant heat fluxes to tree stems using Schmidt-Boelter (copper plug) dual sensors positioned flush with the bark surface are problematic in that the copper plug has surface properties different from tree bark relative to convection [20, 56]. An inverse method based on embedded thermocouple measurements [68] provides only net surface total heat flux (convective and radiative flux combined). Thermal imagery can capture the combined influence of radiative and convective heating at the relevant spatial scales (Fig. 4a). Furthermore, digital surface models can capture the bark topography at fine scales (Fig. 4b). Deconvoluting the magnitude of radiative and convective heating using infrared thermography combined with targets of known emissivity could be a productive method.

There are two main hypotheses for how stem heating can influence post-fire plant mortality: the cambium necrosis hypothesis and the xylem dysfunction hypothesis [7, 10, 102, 103]. According to the cambium necrosis hypothesis, phloem and cambium necrosis limits carbon translocation to roots, so that root growth must rely upon stored carbon reserves. When these reserves are depleted, fine root production ceases and plant mortality occurs because of hydraulic failure [104]. According to the xylem dysfunction hypothesis, heating reduces the hydraulic conductivity of the xylem, which increases xylem water tensions, increases periods of stomatal closure, and limits carbon assimilation and growth. Plant mortality may then result from hydraulic failure or carbon starvation [104, 105]. Plant mortality in fires has typically been thought to result from cambium necrosis. The traditional methodology for defining mortality due to fire-induced heating of plant stems has been to define a temperature of 60 °C as the lethal temperature limit above which tissue necrosis occurs instantaneously [99]. While the lethal temperature concept may give a useful estimate for predicting plant mortality, the shortcomings of such an approach have been long recognized. Dickinson and Johnson [12] showed that this approach is not intuitively sound from a biological perspective, particularly when long-duration heating at temperatures below 60 °C occurs and causes mortality in roots in soils below combusting duff. The process of thermally induced cell and tissue impairment in plants is rate-dependent, governed both by the temperature magnitude and duration of exposure [12, 106]. Here again, a dose-dependent approach might prove useful.

There is evidence that the hydraulics-based view for fire effects on plants can be important [107••]. Stem heating experiments have shown that heat impairs plant hydraulic function. For example, stem heating caused reductions in sap flux density, stomatal conductance, and net photosynthesis [55]. While these results are consistent with the xylem dysfunction hypothesis, they are not conclusive since the experiments also caused phloem and cambium necrosis. Thus, it is unclear whether the results reflect limitation of fine root growth by phloem necrosis, limitation of xylem growth by cambium necrosis, heat-induced xylem dysfunction or some completely unexplored phenomenon. In another study, stem heating reduced the cross-sectional area of functional xylem, which reduces the hydraulic conductivity of the stem [102]. These reductions were semi-permanent following leaf flush to remove air embolisms, suggesting that heating reduced the xylem conductivity by one or more mechanisms that were not fully consistent with air seed cavitation alone.

Building on this work, Michaletz et al. [10] used laboratory air injection experiments to demonstrate that heating reduces the hydraulic conductivity of xylem via at least two mechanisms: (1) air seed cavitation resulting from temperature-dependent changes in sap surface tension and (2) conduit wall deformation resulting from thermal softening of viscoelastic cell wall polymers (lignin, hemicelluloses, and cellulose). Both mechanisms were subsequently observed to reduce xylem conductivity in laboratory heat plume experiments [58••]. While air seed cavitation can be repaired, conduit wall deformation is permanent once the xylem cools and viscoelastic polymers return to a glassy state. Thus, conduit wall deformation is especially injurious. While heat-induced cavitation and deformation of xylem have been demonstrated in the laboratory, it has been unclear how common they are in wildfires. Several studies provide indirect evidence for xylem dysfunction in wildfires. For example, heat transfer simulations forced with wildfire temperature data predicted substantial reductions in the cross-sectional area of functional xylem in tree stems [10]. Consistent with these predictions, anatomical analyses of fire-injured tree stems have revealed large areas of discolored, nonfunctional xylem [108, 109]. Wildfires also reduced stomatal conductance and predawn water potential [110••], and caused higher mortality rates compared with stems that had their phloem and cambium removed [103]. Post-fire mortality rates also vary inversely with wood density [111], which likely reflects the role of wood density in prevention of heat-induced cavitation and conduit wall deformation [10]. Bär et al. [112] provided the first quantitative evidence for xylem dysfunction following wildfire. They showed that fires can permanently reduce xylem conductivity via conduit wall deformation, which had previously only been observed in laboratory experiments [10, 58••]. They also showed for the first time that wildfires can permanently alter xylem vulnerability to cavitation, rendering plants more susceptible to future disturbances such as fire [113] and drought [114]. This had not been observed in previous studies that tested for it [10, 115]. Interestingly, reduced xylem conductivity following fires has been observed in angiosperms but not gymnosperms, and these results were associated with differences in the severity of conduit wall deformation between angiosperms and gymnosperms [112]. This suggests that angiosperms and gymnosperms may differ in the kinetics of conduit wall polymer softening, or that softened vessels and tracheids may differ in their responses to stresses imposed by tensile sap water [107••]. Further work is needed to identify how variation in xylem traits operates via these mechanisms to drive variation in fire effects and how the temperatures at which xylem deformation occur interact with tissue damage and potential

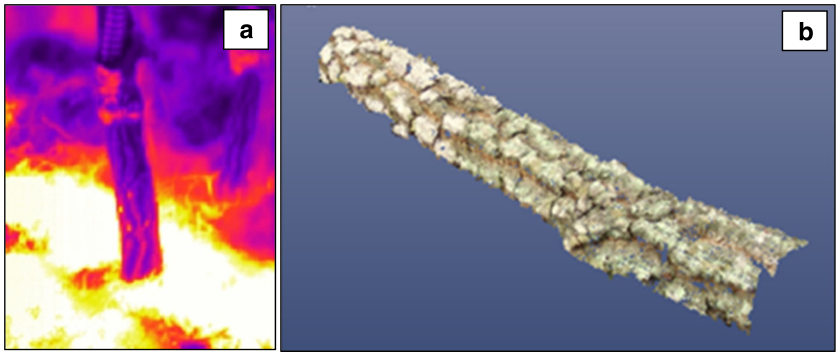

Fig. 4 **a** Thermal image of a *Quercus laevis* (Walter) stem approximately 4 cm in diameter on fire in Florida. Temperatures are shown by color; white ~ 700 °C and black being ambient (35 °C). The furrows in the bark reached 180 °C with the ridges achieving a maximum temperature of 250 °C. Bark roughness mediated the variable heating through boundary layer dynamics and the increased area over which incident radiation is spread. **b** Photogrammetric digital surface model of the *Q. laevis* stem at a resolution of 1 mm. Despite observing less heating in fissures, damage to the cambium can sometimes be localized behind the thinner bark of the fissures, indicating a complex dynamic between bark characteristics, energy transfer and tissue injury

recovery. The glass transition of lignin is thought to occur between 60 and 90 °C [116], temperatures above the mortality threshold for meristematic tissue. The glass transition kinetics and how these interact with tensile xylem water tension to cause xylem conduit deformation is just beginning to be examined [10].

Crowns

Crown damage research has long identified the interactions of fire intensity, ambient temperature, and wind speed for convective cooling as critical variables driving canopy tissue mortality [3]. This has also led to a focus on quantifying the impact of crown scorch and consumption on tree mortality [117, 118]. While some evidence finds close correlation of mean scorch height to fire intensity [3], simple extrapolations using flame length or fireline intensity are often inadequate in predicting patterns of crown scorch [119], as variation is tremendous [3]. However, connecting crown scorch to the relevant fire energy transfer mechanism of convection is challenged by the difficulty in scaling the impacts of energy flux on individual leaves up to whole crowns [65, 117]. For example, the heating of an individual pine needle in a tree crown is a complex balance between convective and radiative heating and cooling rates influenced by ambient and fire-induced flows and the geometric properties of individual needles and their distribution within the tree crown [120–122]. This turbulent fluid flow can be organized across scales and create complex patterns of crown scorch and consumption, from an individual branch to landscapes (Fig. 5). Tree crowns or individual branches can alter turbulence and patterns of convective heat transfer [25•, 43] and thus drive localized patterns of crown scorch. Fortunately, detailed characterizations of both the canopy structure and the fire-atmosphere dynamics within the crown can be resolved in three dimensions with new technology including LiDAR [73, 124] and spectral imaging [125]. An unresolved challenge remains in discriminating between leaf-only damage (scorch) and complete crown tissue destruction including meristematic tissue when entire crowns are damaged.

Further exacerbating the challenge of defining scorch impacts is the taxon-specific sensitivity to crown damage implying underlying mechanisms that remain elusive. Like stems, fire effects on crowns have traditionally been viewed through the lens of tissue and meristem necrosis [3, 122]. Others hypothesize hydraulic failure during fire-induced convective plumes as the mechanism explaining post-fire mortality [10, 15, 58••, 103]. While some taxa suffer high mortality at relatively low scorch thresholds and altered hydraulic properties [107••, 112], others can experience chronic crown scorch and show remarkable resilience to repetitive and extensive crown damage with little or no mortality [62]. Hydraulic failure in these taxa either does not often occur, can be rapidly repaired, or either hydraulics or cavitation vulnerability is segmented [58••]. For example, in longleaf pine, xylem sap flux returns to pre-scorch rates as soon as new needles have fully elongated [63] and scorch did not predict mortality after a wildfire [57].

Most of the physiological studies relating fire to canopy response at the leaf or within-crown scale are based on lab experiments, though more recent work [10, 15, 53•, 58••] draw conclusions based on the combined use of laboratory measurements and physical models, while Bär et al. [112] present data from a wildfire. Kavanagh et al. [15] modeled plume vapor pressure deficit (VPD) by mixing ambient with combustion-generated water vapor in an integral, 2D plume model [126]. A sharp increase in VPD associated with plume passage observed in data [127] should be further evaluated as

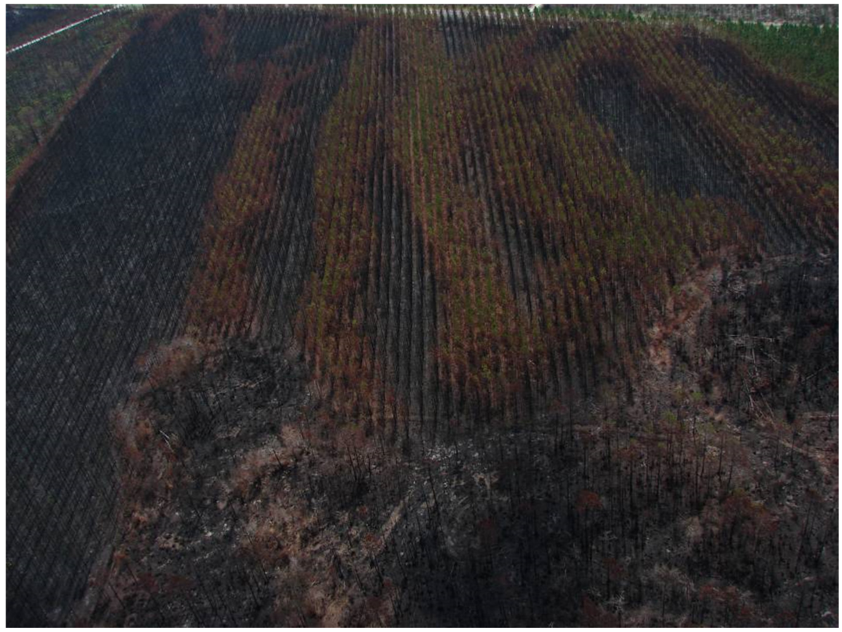

Fig. 5 Crown streets (sensu Haines [123]) seen on the 2007 Georgia-Florida Bay Complex in the Okefenokee National Wildlife Refuge (USA) illustrate the critical role of convective cooling through fresh air entrainment in fast moving crown fires (Photo by J. K. Hiers)

to how, when, and if the high evaporative demand leads to hydraulic failure. While heat-induced hydraulic failure has been proposed as the mechanism in how convection drives canopy leaf death, there is conflicting evidence that it is responsible for tree stress and mortality [10, 58••, 107••, 112].

Further clouding the mechanisms of how energy transfer damages tissue are the methods used. For example, historical approaches have relied on water baths to determine temperature thresholds of plant tissue death [58••]. Lethal temperature thresholds are often used in biophysical fire effects studies with poor understanding of the implications of how a tissue is heated. For example, many important proteins and membrane constituents denature at 60 °C as plant organs heat but the dynamics of heating is a complex balance of heat transfer, heat sinks, and cooling that belies a simple temperature threshold. The duration of heating and the interactions of leaf and crown boundary layers complicate a simple binary threshold concept for foliar death and likely other tree and shrub tissues as discussed above. Clearly, there exists a further opportunity to apply a dose-response approach in the canopy as well. The degree of crown heating occurs across a wide range from undetectable during low-intensity surface fires to complete crown consumption. Energy transport in wildland fires varies greatly in time and space [128] and the past decade has seen many emerging technologies that will continue to provide insight into the three-dimensional time resolved fire energy transfer to canopies. Plant physiological function would likely also show a wide range of both thresholds and responses across this spectrum of heating and in situ advanced spatially explicit measurements of fire heat fluxes are necessary to understand these mechanisms.

Linking Plant Tissue Injuries to Whole-Plant Function

One of the primary fire effects relevant to fire managers is predicting patterns of post-fire tree mortality. Numerous studies have focused on how fire injures and kills trees, but the clear majority do not relate direct heat flux to the patterns of mortality. Statistical models continue to constrain our understanding and prediction of fire effects. Recently, many have begun to critique statistical approaches and present frameworks for more processed based models that incorporate heat transfer, tissue necrosis, and physiological effects and integrate effects of injury to different parts of the plant [98, 129, 130].

Despite our growing knowledge of how plant physiology responds to fire and other disturbances such as drought and insect outbreaks, we still have a limited understanding of how the responses interact to control whole-plant function and mortality, especially over longer time periods [11, 131, 132]. A better understanding of cumulative injury from tissue damage to plant mortality is needed. Plants are integrated networks of organs that exchange resources to maintain physiological function, thus damage to any organ can cause mortality, but damage to multiple components may act synergistically or in nonlinear ways. Most frequently, plant mortality in response to fire is assumed to result largely from thermal damage to tissues, such as foliar scorching, bud death or cambial necrosis in stems or branches, or heat-induced embolism in stems or branches [11, 14, 15, 20, 53•]. These different injuries influence tree physiology in multiple ways. For example, scorched foliage imposes a carbon deficit that requires repayment from stored reserves, but also represents a cost of lost assimilation during the period between leaf death and foliage replacement and a loss of nutrients bound in dead leaves. Damage to the cambium and buds that results in necrosis can impact the transport of photosynthate throughout the plant, limit uptake, and can be irreparable. Heat-induced embolisms can impact water transport and thus rates of assimilation, potentially leading to hydraulic failure or carbon starvation. Even the carbon starvation and hydraulic failure hypotheses central to the mechanisms of fire injury described above might not be universal or might only partly explain plant mortality [133]. Besides unexplored aspects of fire impacts on plant function such as nutrient availability for tissue repair, the search for a single causal mechanism might be futile due to interactions and cascades of indirect effects of damage. For example, the lack of sufficient carbohydrates to maintain osmoregulation led to hydraulic failure in pinyon pine [105]. There remain many possible avenues of interacting fire driven impacts on plant function that remain to be explored. Any single one of these mechanisms, or a combination of them, could lead to mortality. Despite how common fire is across the landscape, we still have a relatively poor understanding of how these different types of damage interact to cause mortality. Needed are models that mechanistically link fire injuries to whole-plant carbon, nutrient, and water budgets [10] perhaps using a dose-response approach. Such a framework can be used for plant responses to multiple disturbance stressors such as drought and insects and is a next step towards incorporating cumulative disturbance impacts into climate–vegetation models [114].

Fire Measurement and Modeling across Scales

Recent theory shows how post-fire mortality of individuals scales up via community size-frequency distributions to determine post-fire ecosystem stocks and fluxes such as total standing biomass, productivity, and stand transpiration [104]. However, a better characterization of landscape scale fire behavior is still needed. While conceptualizing plant damage and mortality as a dose-dependent function is a clear advancement over logistic regression models common in fire effects, a clearer understanding of variation in the fire environment is needed to advance such concepts to landscape scale predictions of mortality. Mortality of trees is also complicated by landscape factors that challenge the scaling of biophysical effects. As integrated organisms with functional redundancy to fire-related damage [57], spatial patterning of fire effects can control cumulative impacts of tissue damage responsible for patterns of mortality. This scaling up of biophysical effects is also complicated by difficulty in the characterization of convective energy flux (particularly in crowns) and the influence of non-fire related sources of stress such as drought and insect outbreaks that can influence mortality [113, 114, 131, 134]. Patterns of damage, e.g., aggregated versus disaggregated, can interact with beetle population dynamics and other classical second-order fire effects to drive mortality [134]. While such landscape variation may challenge scaling of biophysical fire effects, there is opportunity in linking effects of fluid dynamics approaches to energy transfer in complex fire environments at broad scales. Currently, the only measurements of fire energy transport that can conceivably be made across multiple spatial scales at high temporal resolution are remotely sensed fire radiation [22, 27•, 135] (Fig. 6). Even so, fire radiation measurements are complicated by a lack of confidence in accuracy and precision especially at large spatial scales [26•] and by challenges associated with temporal under-sampling [71•]. Examples of fire radiation mapping at relatively fine spatial scales in the literature are derived from overhead (nadir) spaceborne and airborne imagers [26], as well as terrestrial imagers on tripods, towers, and oblique platforms [27•]. Once spatiotemporal fire radiation data are in hand, the challenge becomes inferring the magnitude of other kinds of heat transfer, especially convective energy which can account for a large proportion of the energy dissipating from the combustion zone [128, 136].

Fire and plume models can also provide inputs to fire effects models in high spatial and temporal resolution. Relatively simple plume models (e.g., [126]) could be driven by remotely sensed fire radiation measurements. Coupled fire-atmosphere models are even better suited to providing ecologists with highly resolved inputs to effects models. Examples of the application of coupled fire-atmosphere models to ecological problems include the use of WFDS to provide information on gas mixing into tree cavities during fires as a means of assessing cavity-nesting bird vulnerability to smoke [137], as well as to predict cone heating and seed survival in high-intensity forest fires [24]. The convective environment of wildland fires creates dramatic temporal variation in fluxes [50]. While we have reviewed above the recent advances in the physiological linkages of convective heat to plant injuries, understanding variation in these fluxes is critical in overcoming thermal inertia, creating variation in evaporative demand, and mixing local boundary layers. Within the context of wildland fires, however, the balance between convective *cooling* and heating appears to be the dominant heat transfer mechanism [30, 41, 43, 52•, 128]. The convective fluxes of wildland fires can vary at frequencies greater than 100 Hz and can significantly exceed radiant heating magnitudes [128]. The rate of change in these convective fluxes are contextual and dependent on the intricacy of fireline interactions, fire-atmospheric feedbacks, crown position, and canopy roughness. Thus, scaling results to predict biophysical fire effects still requires an even greater understanding of variability in fire behavior that challenges simple characterizations of dose-

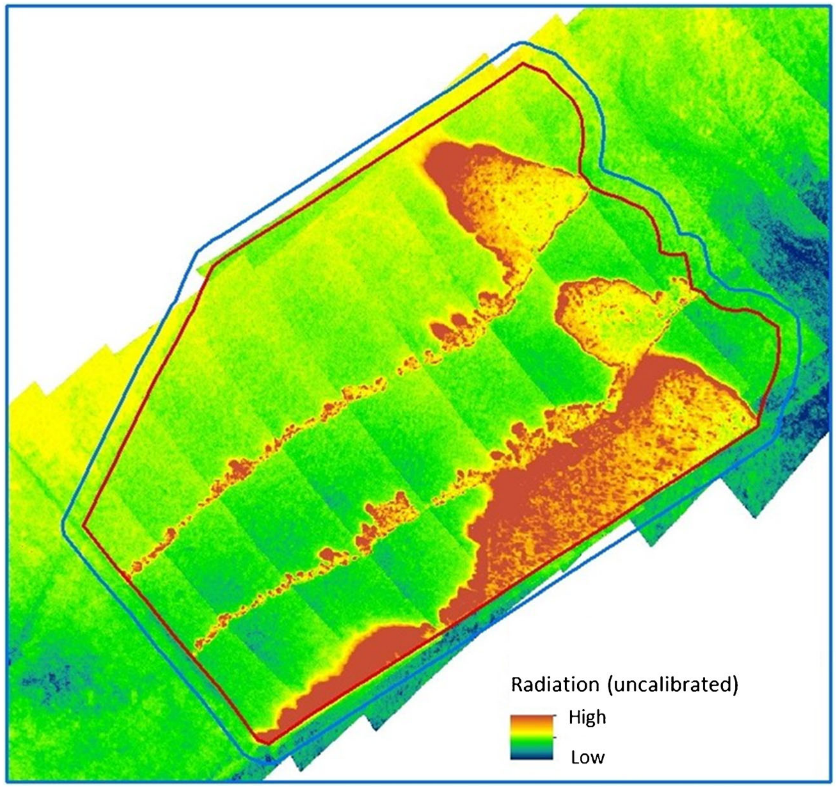

Fig. 6 Uncalibrated relative fire radiated flux density (Wm^{-2}) from a mosaic of Wildfire Airborne Sensor Program longwave IR imagery. Image is from a 151-ha forested unit (L2F) burned during the RxCADRE 2012 campaign [26•]

dependent mortality, though coupled fire-atmosphere modeling can provide a way to overcome these challenges.

Applying highly resolved, physics-based fire models to ecological problems across scales requires adequate and accurate input data. These inputs include three-dimensionally resolved fuels and spatially and temporally resolved weather and fuel moisture. Three-dimensional fuel structure captured through terrestrial laser scanning (TLS, or terrestrial LiDAR, Fig. 7) provides a complete representation of both overstory stand structure and midstory and understory fuels [73]. Good measurements of local turbulence and pre-fire ambient flow data are also critical for understanding convective cooling dynamics which drive energy flux to the canopy [43, 44•].

Any serious effort to bring process-based models into the realm of operational fire effects forecasting will require development of a more robust fire behavior predictive infrastructure at landscape to regional scales given the complexity of the processes involved [138, 139]. The Integrated Fuels Treatment Decision Support System (IFTDSS) models fire effects by combining existing fire (e.g., BehavePlus) and fire effects (e.g., CONSUME, FOFEM) software and datasets including LANDFIRE fuels, forest structure, and biophysical settings layers [140]. LANDFIRE layers were developed for national assessments but are often being used for modeling fire behavior locally [141, 142]. For example, the Wildland Fire Decision Support System (WFDSS) is used on federal fire incidents in the USA [143] and, among other functionality, provides fire spread forecasts using LANDFIRE layers (https://wfdss.usgs.gov/wfdss/WFDSS_Home.shtml accessed April 3, 2018). WFDSS does not currently forecast ecological effects [139]. IFTDSS has incorporated the WindNinja modeling package [144] to extrapolate wind speeds from sparse measurement locations in complex topography, improving fire behavior prediction. However, all these tools are still rooted in semi-empirical fire spread models that are uncoupled to the atmosphere with all their inherent limitations. The increasingly wide availability of airborne LiDAR [145] will ultimately result in better fuels and vegetation description and, thus, fire behavior and effects forecasts. As more sophisticated tree mortality models are incorporated into operational fire effects forecasting, physiologically relevant variables such as site water status and related tree stress could be obtained from coupled hydrology and ecosystem process models [139].

Linking Fire Behavior to Fire Effects in the Future

Developing operational scale predictions of biophysical fire effects must go beyond a post hoc evaluation of the thermal fire environment. Using models of appropriate dimensions

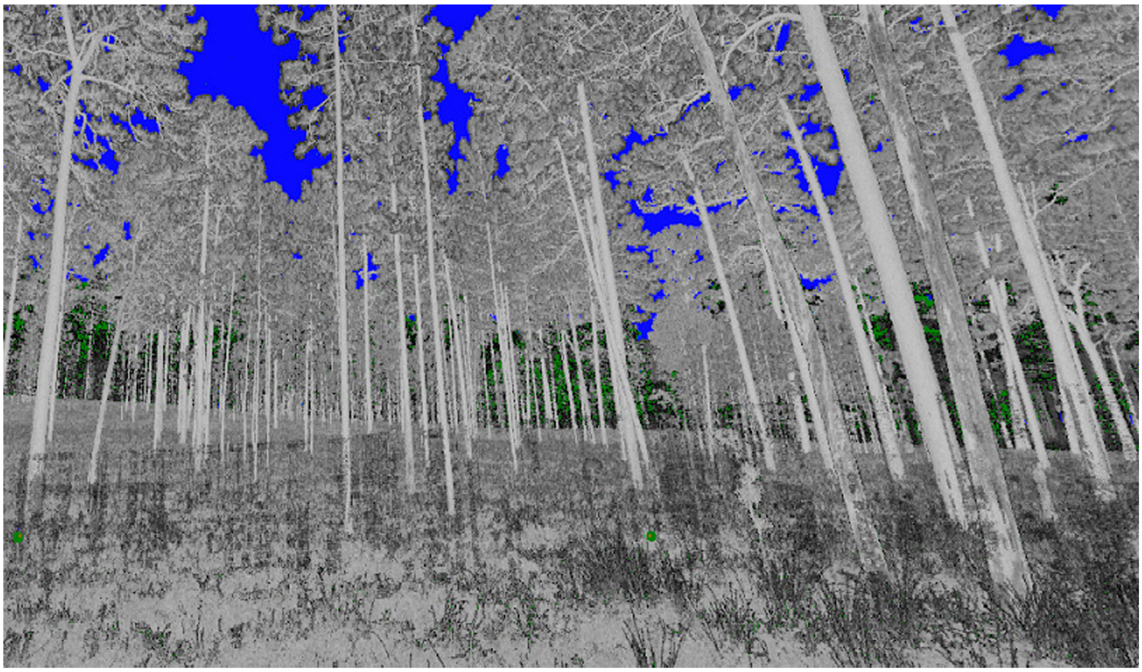

Fig. 7 Example TLS three-dimensional output of a frequently burned longleaf pine area in north Florida, representing the sub-cm scale structure of the surface fuels through the canopy may clarify controls on convective cooling within the crown. The majority of trees in this TLS point cloud are of overstory stature with a height of 30–33 m and diameters ranging from 20 to 100 cm

combined with a dose-dependent relationships of tree injury to predict fire effects will better inform fire management. However, there still will likely be a gap in the ability to achieve desired management results both due to model insufficiency and when the application of fire is constrained by other parameters beyond potential ecological effects. Experienced fire managers intuitively understand that local scale variation in fuels, both in composition, arrangement, and moisture, influences fire behavior, but no decision support tools currently exist that acknowledge the impact and importance of this variation. Recent studies have shown that this fine scale variability in fuels is critical in driving fire behavior [17, 18, 146] and that variation in fire behavior is critical to individual plant and community responses at those fine scales [28••, 67••, 88••, 147].

Even though it has long been recognized that vegetation composition, structure, and pattern are important drivers of fire behavior and effects, the relationship between fuels, fire behavior, and fire effects have still not been well-developed. Previous research has primarily assessed these relationships in isolation and focused on stand averaged values thus preventing the development of tools and frameworks that allow for the spatial prediction of fire effects. Recently developed physically based models [43] are an exception, given that they incorporate multiple interacting controls of fire behavior. Manipulative experimental approaches—and the development of more experimentally tractable model systems for testing theoretical predictions are sorely needed, as is collective insistence upon rigorous standards for field-based model parameterization and validation. Fire ecology as a discipline must see greater efforts to explore interacting elements of fuels, atmospheric flows, fire behavior, and resulting effects on target vegetation. The theoretical drivers of feedbacks seen in mechanistic computational fluid dynamics (CFD) modeling frameworks should be used as a guide to test those assumptions in the field through holistic, empirical sampling of combustion structure within surface fires. Researchers must seek novel and advanced measurements and statistical methods to decompose CFD model outputs to identify drivers of spatial organization in the combustion environment and using model predictions, direct investigations of these complex feedbacks represented in surface fire regimes across scales. Field observations are essential to explore how model results deviate from actual fire behavior and identify other sources of variation that influence combustion but might not be captured by the model. Fire effects on plants should be placed in the context of heat flux, damage as a dose response, and the understanding of wounding as a function of changes in flux at relevant time scales rather than simple integrations of time temperature profiles.

Conclusions

Understanding biophysical mechanisms of fire effects requires observations be scaled to the phenomena under study.

However, many emergent properties such as delayed tree mortality are not necessarily the aggregate effect of small scale phenomena. This reality already challenges the application of mechanistic studies from labs and wind tunnels while overwhelming experiments in the field. The conundrum for advancing our understanding of biophysical fire effects lies in the matching of scales between observable fire behavior and ecological fire effects. Successful evolution of current understanding will be best achieved through interdisciplinary research teams combining ecological and engineering expertise using appropriate methods for characterizing energy, momentum, and mass transport. The complexity of fire has been underappreciated in interpreting biophysical fire effects, as such we conclude in this review that too many studies document ecological effects with incomplete and/or inadequate measurements of antecedent fire behavior. This reliance on post hoc estimates of fire intensity and the heterogeneity of the fire environment has hampered the progress of the discipline. In many fire ecology studies, fire is too often treated as a single uniform disturbance event rather than the recognition that each event represents a range of disturbances whose effects are driven by important sources of heterogeneity at multiple scales. The complexity of fire energy transfer and their ecological effects is both intrinsic, driven by fire-atmosphere-fuels interactions, and extrinsic, driven by the interactions of heat transfer with species traits and their landscape context. Fortunately, emerging technologies combined with spatially and temporally resolved physics-based models of energy transfer promise to help elucidate the mechanisms driving biophysical fire effects and create a dynamic cross-disciplinary interface for advancing wildland fire science. Tools available to managers in the near-term will continue to rely on empirical correlations, while advances in mechanism and modeling tools will gradually offer more operational planning tools to relate variation in fire behavior to management relevant fire effects.

Acknowledgements The authors would like to thank Dr. Marty Alexander for the opportunity to develop this review article and recognize his helpful reviews for its thoroughness and clarity. We also recognize two anonymous reviewers for their improvements to drafts of this manuscript.

Funding Funding was provided by Tall Timbers Research Station, Tallahassee, FL, and the USDA Forest Service Center for Disturbance Science, Athens GA.

Compliance with Ethical Standards

Conflict of Interest The authors declare they have no conflict of interest.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

References

Papers of particular interest, published recently, have been highlighted as:
- Of importance
•• Of major Importance

1. Byram GM. Combustion of forest fuels. In: Davis KP, editor. Forest fire: control and use. New York: McGraw-Hill; 1959. p. 61–89.
2. McArthur AG, Cheney NP. The characterization of fires in relation to ecological studies. Fire Ecology. 2015;11(1):3–9.
3. Van Wagner CE. Height of crown scorch in forest fires. Can J For Res. 1973;3:373–8.
4. Van Wagner CE, Methven IR. Two recent articles on fire ecology. Can J For Res. 1978;8:491–2.
5. Methven IR. Fire research at the Petawawa Forest Experiment Station: the integration of fire behaviour and forest ecology for management purposes. In: Dubè DE, editor. Fire Ecology in Resource Management: Workshop Proceedings. Canadian Forestry Service, Northern Forest Research Centre Information Report NOR-X-210; 1978. p. 23–27.
6. Alexander ME. Calculating and interpreting forest fire intensities. Can J Bot. 1982;60:349–57.
7. Wade DD. Linking fire behavior to its effects on living plant tissue. In: Proceedings of the Society of American Foresters 1986 National Convention, Birmingham, 1986; p. 112–116.
8. Burrows ND. A framework for assessing acute impacts of fire in jarrah forests for ecological studies. CALM Science Supplement. 1995;4:59–66.
9. Johnson E, Miyanishi K. Strengthening fire ecology's roots. In: Johnson E, Miyanishi K, editors. Forest fires: behavior and ecological effects. San Diego: Academic Press; 2001. p. 1–9.
10. Michaletz ST, Johnson E, Tyree M. Moving beyond the cambium necrosis hypothesis of post-fire tree mortality: cavitation and deformation of xylem in forest fires. New Phytol. 2012;194:254–63.
11. Michaletz ST, Johnson EA. How forest fires kill trees: a review of the fundamental biophysical processes. Scand J For Res. 2007;22: 500–15.
12. Dickinson M, Johnson E. Fire effects on trees. In: Johnson E, Miyanishi K, editors. Forest fires: behaviour and ecological effects. San Diego: Academic Press; 2001. p. 477–525.
13. Butler BW, Dickinson MB. Tree injury and mortality in fires: developing process-based models. Fire Ecology. 2010;6(1):55–79.
14. Jones JL, Webb BW, Jimenez D, Reardon J, Butler B. Development of an advanced one-dimensional stem heating model for application in surface fires. Can J For Res. 2004;34:20–30.
15. Kavanaugh KL, Dickinson MB, Bova AS. A way forward for fire-caused tree mortality prediction: modeling a physiological consequence of fire. Fire Ecology. 2010;6(1):80–94.
16. Stephan K, Miller M, Dickinson M. First-order fire effects on herbs and shrubs: present knowledge and modeling needs. Fire Ecology. 2010;6(1):95–114.
17. Hiers JK, O'Brien JJ, Mitchell RJ, Grego JM, Loudermilk EL. The wildland fuel cell concept: an approach to characterize fine-scale variation in fuels and fire in frequently burned longleaf pine forests. Int J Wildland Fire. 2009;18:315–25.
18. Loudermilk EL, O'Brien JJ, Mitchell RJ, Cropper WP, Hiers JK, Grunwald S, et al. Linking complex forest fuel structure and fire behaviour at fine scales. Int J Wildland Fire. 2012;21:882–93.
19. Loudermilk EL, Achtemeier GL, O'Brien JJ, Hiers JK, Hornsby BS. High-resolution observations of combustion in heterogeneous surface fuels. Int J Wildland Fire. 2014;23:1016–26.

20. Jones JL, Webb BW, Butler BW, Dickinson MB, Jimenez D, Reardon J, et al. Prediction and measurement of thermally induced cambial tissue necrosis in tree stems. Int J Wildland Fire. 2006;15:3–17.
21. Skowronski N, Clark K, Nelson R, Hom J, Patterson M. Remotely sensed measurements of forest structure and fuel loads in the pinelands of New Jersey. Remote Sens Environ. 2007;108:123–9.
22. Kremens R, Smith A, Dickinson M. Fire metrology: current and future directions in physics-based methods. Fire Ecol. 2010;6(1):13–35.
23. Chatziefstratiou EK, Bohrer G, Bova AS, Subramanian R, Frasson RP, Scherzer A, et al. Firestem2d—a two-dimensional heat transfer model for simulating tree stem injury in fires. PLoS One. 2013;8(7):e70110.
24. Michaletz S, Johnson E, Mell W, Greene D. Timing of fire relative to seed development may enable non-serotinous species to recolonize from the aerial seed banks of fire-killed trees. Biogeosciences. 2013;10:5061–78.
25.• Pimont F, Parsons R, Rigolot E, de Coligny F, Dupuy J-L, Dreyfus P, et al. Modeling fuels and fire effects in 3D: model description and applications. Environ Model Softw. 2016;80:225–44. **Describes the utility of 3D representations of fuels.**
26.• Dickinson MB, Hudak AT, Zajkowski T, Loudermilk EL, Schroeder W, Ellison L, et al. Measuring radiant emissions from entire prescribed fires with ground, airborne and satellite sensors—RxCADRE 2012. Int J Wildland Fire. 2016;25:48–61. **Contrasts measurements of fire radiant heat using different platforms and different scales.**
27.• O'Brien JJ, Loudermilk EL, Hornsby B, Hudak AT, Bright BC, Dickinson MB, et al. High-resolution infrared thermography for capturing wildland fire behaviour: RxCADRE 2012. Int J Wildland Fire. 2016;25:62–75. **Details techniques and utility of spatially and temporally explicit measurements of fire heat release.**
28.•• O'Brien JJ, Loudermilk EL, Hiers JK, Hornsby B, Pokswinski S, Hudak AT, et al. Canopy derived fuels drive patterns of in-fire energy release and understory plant mortality in a longleaf pine (*Pinus palustris*) sandhill in Northwest FL, USA. Can J Remote Sens. 2016;42:489–500. **Captures the explicit link between spatial variation in fire heat release, overstory derived fuels, and plant community dynamics for the first time.**
29. Clements CB, Lareau NP, Seto D, Contezac J, Davis B, Teske C, et al. Fire weather conditions and fire–atmosphere interactions observed during low-intensity prescribed fires—RxCADRE 2012. Int J Wildland Fire. 2016;25:90–101.
30. Mitchell RJ, Hiers JK, O'Brien J, Starr G. Ecological forestry in the southeast: understanding the ecology of fuels. J For. 2009;107:391–7.
31. Sugihara NG, Van Wagtendonk JW, Fites-Kaufman J. Fire as an ecological process. In: Sugihara NG, van Wagtendonk JW, Fites-Kaufman J, Shaffer KE, Thode AE, editors. Fire in California's ecosystems. Berkely: University of California Press; 2006. p. 58–74.
32. Waldrop TA, Brose PH. A comparison of fire intensity levels for stand replacement of table mountain pine (*Pinus pungens* lamb.). For Ecol Manag. 1999;113:155–66.
33. Menges ES, Deyrup MA. Postfire survival in South Florida slash pine: interacting effects of fire intensity, fire season, vegetation, burn size, and bark beetles. Int J Wildland Fire. 2001;10:53–63.
34. Arthur MA, Blankenship BA, Schörgendorfer A, Loftis DL, Alexander HD. Changes in stand structure and tree vigor with repeated prescribed fire in an Appalachian hardwood forest. For Ecol Manag. 2015;340:46–61.
35. Varner JM, Hiers JK, Ottmar RD, Gordon DR, Putz FE, Wade DD. Overstory tree mortality resulting from reintroducing fire to long-unburned longleaf pine forests: the importance of duff moisture. Can J For Res. 2007;37:1349–58.
36. Rossi J-L, Simeoni A, Moretti B, Leroy-Cancellieri V. An analytical model based on radiative heating for the determination of safety distances for wildland fires. Fire Saf J. 2011;46:520–7.
37. Kennard DK, Outcalt KW, Jones D, O'Brien JJ. Comparing techniques for estimating flame temperature of prescribed fires. Fire Ecology. 2005;1(1):75–84.
38. Van Wagner CE. Two solitudes in forest fire research. Petwawa Forest Experiment Station, Chalk River, ON: Canadian Forestry Service; 1971. Information Report PS-X-29.
39. Levin SA. The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. Ecology. 1992;73:1943–67.
40. Fernandes PA, Loureiro CA, Botelho HS. Fire behaviour and severity in a maritime pine stand under differing fuel conditions. Ann For Sci. 2004;61:537–44.
41. Linn RR, Cunningham P. Numerical simulations of grass fires using a coupled atmosphere–fire model: basic fire behavior and dependence on wind speed. Journal of Geophysical Research: Atmospheres. 2005;110(D13).
42. Nunes MC, Vasconcelos MJ, Pereira JM, Dasgupta N, Alldredge RJ, Rego FC. Land cover type and fire in Portugal: do fires burn land cover selectively? Landsc Ecol. 2005;20:661–73.
43. Linn RR, Sieg CH, Hoffman CM, Winterkamp JL, McMillin JD. Modeling wind fields and fire propagation following bark beetle outbreaks in spatially-heterogeneous pinyon-juniper woodland fuel complexes. Agric For Meteorol. 2013;173:139–53.
44.• Hoffman C, Canfield J, Linn R, Mell W, Sieg C, Pimont F, et al. Evaluating crown fire rate of spread predictions from physics-based models. Fire Technol. 2016;52:221–37. **Evaluates the performance of mechanistic models of crown fire spread.**
45. Morvan D, Meradji S, Accary G. Physical modelling of fire spread in grasslands. Fire Saf J. 2009;44:50–61.
46. Dupuy J-L, Linn R, Konovalov V, Pimont F, Vega J, Jiménez E. Exploring three-dimensional coupled fire–atmosphere interactions downwind of wind-driven surface fires and their influence on backfires using the HIGRAD-FIRETEC model. Int J Wildland Fire. 2011;20:734–50.
47. Andrews PL. BehavePlus fire modeling system, version 5.0: Variables. Rocky Mountain Research Station, Fort Collins, CO: USDA Forest Service; 2009. General Technical Report RMRS-GTR-213 Revised.
48. Linn R, Winterkamp J, Colman JJ, Edminster C, Bailey JD. Modeling interactions between fire and atmosphere in discrete element fuel beds. Int J Wildland Fire. 2005;14:37–48.
49. Mell W, Jenkins MA, Gould J, Cheney P. A physics-based approach to modelling grassland fires. Int J Wildland Fire. 2007;16:1–22.
50. Cunningham P, Linn RR. Numerical simulations of grass fires using a coupled atmosphere-fire model: dynamics of fire spread. Journal of Geophysical Research: Atmospheres. 2007;112(D5).
51. Parsons RA, Mell WE, McCauley P. Linking 3D spatial models of fuels and fire: effects of spatial heterogeneity on fire behavior. Ecol Model. 2011;222:679–91.
52.• Parsons RA, Linn RR, Pimont F, Hoffman C, Sauer J, Winterkamp J, et al. Numerical investigation of aggregated fuel spatial pattern impacts on fire behavior. Land. 2017;6(2):43. **Connects spatial variability in fuels to fire behavior.**
53.• Lodge AG, Dickinson MB, Kavanagh KL. Xylem heating increases vulnerability to cavitation in longleaf pine. Environ Res Lett. 2018;13:055007. **A mechanistic investigation to how heat influences tree physiology.**
54. Alexander ME, Cruz MG. Are the applications of wildland fire behaviour models getting ahead of their evaluation again? Environ Model Softw. 2013;41:65–71.

55. Ducrey M, Duhoux F, Huc R, Rigolot E. The ecophysiological and growth responses of Aleppo pine (*Pinus halepensis*) to controlled heating applied to the base of the trunk. Can J For Res. 1996;26:1366–74.
56. Bova A, Dickinson M. Linking surface-fire behavior, stem heating, and tissue necrosis. Can J For Res. 2005;35:814–22.
57. O'Brien JJ, Hiers JK, Mitchell RJ, Varner JM, Mordecai K. Acute physiological stress and mortality following fire in a long-unburned longleaf pine ecosystem. Fire Ecology. 2010;6(2):1–12.
58.•• West AG, Nel JA, Bond WJ, Midgley JJ. Experimental evidence for heat plume-induced cavitation and xylem deformation as a mechanism of rapid post-fire tree mortality. New Phytol. 2016;211:828–38. **Critically examines the physiological link between fire energy release and mortality.**
59. Varner JM, Putz FE, O'Brien JJ, Hiers JK, Mitchell RJ, Gordon DR. Post-fire tree stress and growth following smoldering duff fires. For Ecol Manag. 2009;258:2467–74.
60. Lorio PL Jr. Growth-differentiation balance: a basis for understanding southern pine beetle-tree interactions. For Ecol Manag. 1986;14:259–73.
61.• Slack AW, Zeibig-Kichas NE, Kane JM, Varner JM. Contingent resistance in longleaf pine (*Pinus palustris*) growth and defense 10 years following smoldering fires. For Ecol Manag. 2016;364:130–8. **Examines a long term physiological response to smoldering combustion.**
62. Johansen RW, Wade DD. Effects of crown scorch on survival and diameter growth of slash pines. South J Appl For. 1987;11:180–4.
63. Aubrey DP, Mortazavi B, O'Brien JJ, McGee JD, Hendricks JJ, Kuehn KA, et al. Influence of repeated canopy scorching on soil CO_2 efflux. For Ecol Manag. 2012;282:142–8.
64. Hood SM, McHugh CW, Ryan KC, Reinhardt E, Smith SL. Evaluation of a post-fire tree mortality model for western USA conifers. Int J Wildland Fire. 2008;16:679–89.
65. Michaletz S, Johnson E. A heat transfer model of crown scorch in forest fires. Can J For Res. 2006;36:2839–51.
66.•• Smith AMS, Sparks AM, Kolden CA, Abatzoglou JT, Talhelm AF, Johnson DM, et al. Towards a new paradigm in fire severity research using dose–response experiments. Int J Wildland Fire. 2016;25:158–66. **Suggests a novel approach for linking fire energy transfer to physiological impacts.**
67.•• Smith AM, Talhelm AF, Johnson DM, Sparks AM, Kolden CA, Yedinak KM, et al. Effects of fire radiative energy density dose on *Pinus contorta* and *Larix occidentalis* seedling physiology and mortality. Int J Wildland Fire. 2017;26:82–94. **Tests the utility of the dose dependence approach on mechanisms driving fire effects.**
68. Canham CDW, Cole J, Lauenroth WK. Models in ecosystem science. Princeton: Princeton University Press; 2003.
69. Finney MA, Cohen JD, Forthofer JM, McAllister SS, Gollner MJ, Gorham DJ, et al. Role of buoyant flame dynamics in wildfire spread. Proc Natl Acad Sci. 2015;112:9833–8.
70. Hudak AT, Strand EK, Vierling LA, Byrne JC, Eitel JU, Martinuzzi S, et al. Quantifying aboveground forest carbon pools and fluxes from repeat LiDAR surveys. Remote Sens Environ. 2012;123:25–40.
71.• Hudak AT, Dickinson MB, Bright BC, Kremens RL, Loudermilk EL, O'Brien JJ, et al. Measurements relating fire radiative energy density and surface fuel consumption–RxCADRE 2011 and 2012. Int J Wildland Fire. 2016;25:25–37. **Connects fire radiative energy to fuel consumption and thus total energy release.**
72. Silva C, Hudak AT, Lieberman R, Satterberg K, Carlos L, Rodriguez E. LiDAR remote sensing to individual tree processing: a comparison between high and low pulse density in Florida, United States of America. In: XVI Brazilian Remote Sensing Symposium, Foz do Iguaçú, Brazil. 2013. p. 6073–6080.
73. Rowell E, Loudermilk EL, Seielstad C, O'Brien JJ. Using simulated 3D surface fuelbeds and terrestrial laser scan data to develop inputs to fire behavior models. Can J Remote Sens. 2016;42:443–59.
74. Rowell EM, Seielstad CA, Ottmar RD. Development and validation of fuel height models for terrestrial lidar—RxCADRE 2012. Int J Wildland Fire. 2015;25:38–47.
75. Raffel M. Background-oriented schlieren (BOS) techniques. Exp Fluids. 2015;56(3):60.
76. Atcheson B, Ihrke I, Heidrich W, Tevs A, Bradley D, Magnor M, et al. Time-resolved 3d capture of non-stationary gas flows. ACM Transactions on graphics (TOG). 2008;27:132.
77. Bova AS, Dickinson MB. Beyond "fire temperatures": calibrating thermocouple probes and modeling their response to surface fires in hardwood fuels. Can J For Res. 2008;38:1008–20.
78. Bova AS, Dickinson MB. An inverse method to estimate stem surface heat flux in wildland fires. Int J Wildland Fire. 2009;18:711–21.
79. Swezy DM, Agee JK. Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. Can J For Res. 1991;21:626–34.
80. Campbell GS, Jungbauer J Jr, Bristow KL, Hungerford RD. Soil temperature and water content beneath a surface fire. Soil Sci. 1995;159:363–74.
81. Massman WJ, Frank JM, Mooney SJ. Advancing investigation and physical modeling of first-order fire effects on soils. Fire Ecology. 2010;6(1):36–54.
82. Massman W. A non-equilibrium model for soil heating and moisture transport during extreme surface heating: the soil (heat–moisture–vapor) HMV-model version 1. Geosci Model Dev. 2015;8(11):3659–80.
83. Smits KM, Kirby E, Massman WJ, Baggett LS. Experimental and modeling study of forest fire effect on soil thermal conductivity. Pedosphere. 2016;26:462–73.
84. Belov S. Forest pyrology (in Russian), Leningrad forestry academy of the USSR, St. Petersburg. 1976.
85. Furyaev VV, VAganov EA, Tchebakova NM, Valendik EN. Effects of fire and climate on successions and structural changes in the Siberian boreal forest. Eurasian Journal of Forest Research. 2001;2:1–15.
86. Korovin G. Analysis of the distribution of forest fires in Russia. In: Goldammer JG, Furyaev V, editors. Fire in ecosystems of boreal Eurasia. Dordrecht: Springer; 1996. p. 112–28.
87. Conard SG, Ivanova GA. Wildfire in Russian boreal forests—potential impacts of fire regime characteristics on emissions and global carbon balance estimates. Environ Pollut. 1997;98:305–13.
88.•• Dell JE, Richards LA, O'Brien JJ, Loudermilk EL, Hudak AT, Pokswinski SM et al. Overstory-derived surface fuels mediate plant species diversity in frequently burned longleaf pine forests. Ecosphere. 2017;8(10). **Explicitly connects spatial variation of vegetation to fuels then subsequently to post-fire effects.**
89. Bond WJ, Keeley JE. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends Ecol Evol. 2005;20:387–94.
90. Hillel D, editor. Environmental soil physics: fundamentals, applications, and environmental considerations. San Diego, CA: Academic Press; 1998.
91. Miyanishi K. Duff consumption. In: Johnson E, Miyanishi K, editors. Forest fires: behavior and ecological effects. San Diego: Academic Press; 2001. p. 437–75.
92. Coleman D. Through a ped darkly: an ecological assessment of root-soil-microbial-faunal interactions. In: Fitter AH, Atkinson D, Read DJ, Usher MB, editors. Ecological interactions in soil: plants, microbes and animals. Oxford: Blackwell. British Ecological Society special publication,1985;4:1–21.

93. Hartford RA, Frandsen WH. When it's hot, it's hot... or maybe it's not! (Surface flaming may not portend extensive soil heating). Int J Wildland Fire. 1992;2:139–44.
94. Reardon J, Hungerford R, Ryan K. Factors affecting sustained smouldering in organic soils from pocosin and pond pine woodland wetlands. Int J Wildland Fire. 2007;16:107–18.
95. DeBano LF, Neary DG, Ffolliott PF, editors. Fire effects on ecosystems. New York: John Wiley & Sons, Inc.; 1998.
96. Smith NR, Kishchuk BE, Mohn WW. Effects of wildfire and harvest disturbances on forest soil bacterial communities. Appl Environ Microbiol. 2008;74:216–24.
97. Ryan KC, Frandsen WH. Basal injury from smoldering fires in mature *Pinus ponderosa* Laws. Int J Wildland Fire. 1991;1:107–18.
98. Gill A, Ashton D. The role of bark type in relative tolerance to fire of three central Victorian eucalypts. Aust J Bot. 1968;16:491–8.
99. Gutsell S, Johnson E. How fire scars are formed: coupling a disturbance process to its ecological effect. Can J For Res. 1996;26:166–74.
100. Cochrane MA, Alencar A, Schulze MD, Souza CM, Nepstad DC, Lefebvre P, et al. Positive feedbacks in the fire dynamic of closed canopy tropical forests. Science. 1999;284:1832–5.
101. Pinard MA, Huffman J. Fire resistance and bark properties of trees in a seasonally dry forest in eastern Bolivia. J Trop Ecol. 1997;13:727–40.
102. Balfour DA, Midgley JJ. Fire induced stem death in an African acacia is not caused by canopy scorching. Austral Ecology. 2006;31:892–6.
103. Midgley J, Kruger L, Skelton R. How do fires kill plants? The hydraulic death hypothesis and cape Proteaceae "fire-resisters". S Afr J Bot. 2011;77:381–6.
104. McDowell NG, Michaletz ST, Bennett KE, Solander KC, Xu C, Maxwell RM, et al. Predicting chronic climate-driven disturbances and their mitigation. Trends Ecol Evol. 2017;33:15–27.
105. Sevanto S, McDowell NG, Dickman LT, Pangle R, Pockman WT. How do trees die? A test of the hydraulic failure and carbon starvation hypotheses. Plant Cell Environ. 2014;37:153–61.
106. Dickinson M, Jolliff J, Bova A. Vascular cambium necrosis in forest fires: using hyperbolic temperature regimes to estimate parameters of a tissue-response model. Aust J Bot. 2005;52:757–63.
107.•• Michaletz ST. Xylem dysfunction in fires: towards a hydraulic theory of plant responses to multiple disturbance stressors. New Phytol. 2018;217:1391–3. **Defines a biophysical mechanism for fire damage to tree physiology.**
108. Smith KT, Sutherland EK. Fire-scar formation and compartmentalization in oak. Can J For Res. 1999;29:166–71.
109. Smith KT, Arbellay E, Falk DA, Sutherland EK. Macroanatomy and compartmentalization of recent fire scars in three north American conifers. Can J For Res. 2016;46:535–42.
110.•• Thompson MT, Koyama A, Kavanagh KL. Wildfire effects on physiological properties in conifers of Central Idaho forests, USA. Trees. 2017;31:545–55. **Connects fire energy release to physiological impacts.**
111. Brando PM, Nepstad DC, Balch JK, Bolker B, Christman MC, Coe M, et al. Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. Glob Chang Biol. 2012;18:630–41.
112. Bär A, Nardini A, Mayr S. Post-fire effects in xylem hydraulics of *Picea abies*, *Pinus sylvestris* and *Fagus sylvatica*. New Phytol. 2018;217:1484–93.
113. Brando PM, Balch JK, Nepstad DC, Morton DC, Putz FE, Coe MT, et al. Abrupt increases in Amazonian tree mortality due to drought–fire interactions. Proc Natl Acad Sci. 2014;111:6347–52.
114. Anderegg WR, Plavcová L, Anderegg LD, Hacke UG, Berry JA, Field CB. Drought's legacy: multiyear hydraulic deterioration underlies widespread aspen forest die-off and portends increased future risk. Glob Chang Biol. 2013;19:1188–96.
115. Battipaglia G, Savi T, Ascoli D, Castagneri D, Esposito A, Mayr S, et al. Effects of prescribed burning on ecophysiological, anatomical and stem hydraulic properties in *Pinus pinea* L. Tree Physiol. 2016;36:1019–31.
116. Kelley SS, Rials TG, Glasser WG. Relaxation behaviour of the amorphous components of wood. J Mater Sci. 1987;22:617–24.
117. Michaletz ST, Johnson EA. A biophysical process model of tree mortality in surface fires. Can J For Res. 2008;38:2013–29.
118. Woolley T, Shaw DC, Ganio LM, Fitzgerald S. A review of logistic regression models used to predict post-fire tree mortality of western north American conifers. Int J Wildland Fire. 2012;21:1–35.
119. Alexander ME, Cruz MG. Interdependencies between flame length and fireline intensity in predicting crown fire initiation and crown scorch height. Int J Wildland Fire. 2012;21:95–113.
120. Cohen WB, Omi PN, Kaufmann MR. Heating-related water transport to intact lodgepole pine branches. For Sci. 1990;36:246–54.
121. Cohen WB, Omi PN. Water-stress effects on heating-related water transport in woody plants. Can J For Res. 1991;21:199–206.
122. Michaletz S, Johnson E. Foliage influences forced convection heat transfer in conifer branches and buds. New Phytol. 2006;170:87–98.
123. Haines DA. Horizontal roll vortices and crown fires. J Appl Meteorol. 1982;21:751–63.
124. Hudak A, Bright B, Pokswinski S, Loudermilk EL, O'Brien J, Hornsby B, et al. Mapping forest structure and composition from low density lidar for informed forest, fuel, and fire management across Eglin Air Force Base, Florida. USA Can J Remote Sens. 2016;42:411–27.
125. Tanase M, de la Riva J, Pérez-Cabello F. Estimating burn severity at the regional level using optically based indices. Can J For Res. 2011;41:863–72.
126. Mercer G, Weber R. Plumes above line fires in a cross-wind. Int J Wildland Fire. 1994;4:201–7.
127. Hudak AT, Freeborn PH, Lewis SA, Hood SM, Smith HY, Hardy CC, et al. The Cooney ridge fire experiment: an early operation to relate pre-, active, and post-fire field and remotely sensed measurements. Firehouse. 2018;1(1):10.
128. Frankman D, Webb BW, Butler BW, Jimenez D, Forthofer JM, Sopko P, et al. Measurements of convective and radiative heating in wildland fires. Int J Wildland Fire. 2013;22:157–67.
129. Peterson DL, Ryan KC. Modeling postfire conifer mortality for long-range planning. Environ Manag. 1986;10:797–808.
130. Dickinson MB, Ryan KC. Introduction: strengthening the foundation of wildland fire effects prediction for research and management. Fire Ecology. 2010;6(1):1–12.
131. Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, et al. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For Ecol Manag. 2010;259:660–84.
132. van Mantgem PJ, Nesmith JC, Keifer M, Brooks M. Tree mortality patterns following prescribed fire for *Pinus* and *Abies* across the southwestern United States. For Ecol Manag. 2013;289:463–9.
133. McDowell NG, Sevanto S. The mechanisms of carbon starvation: how, when, or does it even occur at all? New Phytol. 2010;186:264–6.
134. Kane JM, Varner JM, Metz MR, van Mantgem PJ. Characterizing interactions between fire and other disturbances and their impacts on tree mortality in western U.S. forests. For Ecol Manag. 2017;405:188–99.
135. Riggan PJ, Tissell RG, Lockwood RN, Brass JA, Pereira JAR, Miranda HS, et al. Remote measurement of energy and carbon flux from wildfires in Brazil. Ecol Appl. 2004;14:855–72.

136. Kremens R, Dickinson M, Bova A. Radiant flux density, energy density and fuel consumption in mixed-oak forest surface fires. Int J Wildland Fire. 2012;21:722–30.
137. Bova A, Bohrer G, Dickinson M. A model of gas mixing into single-entrance tree cavities during wildland fires. Can J For Res. 2011;41:1659–70.
138. Reinhardt ED, Dickinson MB. First-order fire effects models for land management: overview and issues. Fire Ecology. 2010;6(1): 131–50.
139. Hyde K, Dickinson MB, Bohrer G, Calkin D, Evers L, Gilbertson-Day J, et al. Research and development supporting risk-based wildfire effects prediction for fuels and fire management: status and needs. Int J Wildland Fire. 2013;22:37–50.
140. Drury SA, Huang S, Lavezzo TL, Banwell EM, Michael RH. The interagency fuels treatment decision support system: functionality for fuels treatment planning. Fire Ecology. 2016;12(1):103–23.
141. Ryan KC, Opperman TS. LANDFIRE—A national vegetation/fuels data base for use in fuels treatment, restoration, and suppression planning. For Ecol Manag. 2013;294:208–16.
142. Nelson KJ, Connot J, Peterson B, Martin C. The LANDFIRE refresh strategy: updating the national dataset. Fire Ecology. 2013;9(2):80–101.
143. Noonan-Wright EK, Opperman TS, Finney MA, Zimmerman GT, Seli RC, Elenz LM et al. Developing the US wildland fire decision support system. Journal of Combustion. 2011; Article ID 168473.
144. Wagenbrenner NS, Forthofer JM, Lamb BK, Shannon KS, Butler BW. Downscaling surface wind predictions from numerical weather prediction models in complex terrain with WindNinja. Atmos Chem Phys. 2016;16:5229–41.
145. Andersen H-E, McGaughey RJ, Reutebuch SE. Estimating forest canopy fuel parameters using LIDAR data. Remote Sens Environ. 2005;94:441–9.
146. Hoffman CM, Morgan P, Mell W, Parsons R, Strand E, Cook S. Surface fire intensity influences simulated crown fire behavior in lodgepole pine forests with recent mountain pine beetle-caused tree mortality. For Sci. 2013;59:390–9.
147. Wiggers MS, Kirkman LK, Boyd RS, Hiers JK. Fine-scale variation in surface fire environment and legume germination in the longleaf pine ecosystem. For Ecol Manag. 2013;310:54–63.