



**HAL**  
open science

## Integrating plant physiology into simulation of fire behavior and effects

L. Turin Dickman, Alexandra K Jonko, Rodman R Linn, Ilkay Altintas, Adam L Atchley, Andreas Bär, Adam D Collins, Jean-luc Dupuy, Michael R Gallagher, J. Kevin Hiers, et al.

### ► To cite this version:

L. Turin Dickman, Alexandra K Jonko, Rodman R Linn, Ilkay Altintas, Adam L Atchley, et al.. Integrating plant physiology into simulation of fire behavior and effects. *New Phytologist*, 2023, 238 (3), pp.952-970. 10.1111/nph.18770 . hal-04159896

**HAL Id: hal-04159896**

**<https://hal.inrae.fr/hal-04159896v1>**

Submitted on 12 Jul 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License



## Tansley review








# Integrating plant physiology into simulation of fire behavior and effects

Author for correspondence:

L. Turin Dickman  
Email: [lee@lanl.gov](mailto:lee@lanl.gov)

Received: 6 November 2022

Accepted: 20 December 2022

**L. Turin Dickman**<sup>1</sup> , **Alexandra K. Jonko**<sup>1</sup> , **Rodman R. Linn**<sup>1</sup> , **Ilkay Altintas**<sup>2</sup> , **Adam L. Atchley**<sup>1</sup> , **Andreas Bär**<sup>3</sup> , **Adam D. Collins**<sup>1</sup> , **Jean-Luc Dupuy**<sup>4</sup> , **Michael R. Gallagher**<sup>5</sup> , **J. Kevin Hiers**<sup>6</sup> , **Chad M. Hoffman**<sup>7</sup> , **Sharon M. Hood**<sup>8</sup> , **Matthew D. Hurteau**<sup>9</sup> , **W. Matt Jolly**<sup>8</sup> , **Alexander Josephson**<sup>1</sup> , **E. Louise Loudermilk**<sup>10</sup> , **Wu Ma**<sup>1</sup> , **Sean T. Michaletz**<sup>11</sup> , **Rachael H. Nolan**<sup>12,13</sup> , **Joseph J. O'Brien**<sup>10</sup> , **Russell A. Parsons**<sup>8</sup> , **Raquel Partelli-Feltrin**<sup>11</sup> , **François Pimont**<sup>4</sup> , **Víctor Resco de Dios**<sup>14,15</sup> , **Joseph Restaino**<sup>16</sup> , **Zachary J. Robbins**<sup>1</sup> , **Karla A. Sartor**<sup>17</sup> , **Emily Schultz-Fellenz**<sup>1</sup> , **Shawn P. Serbin**<sup>18</sup> , **Sanna Sevanto**<sup>1</sup> , **Jacquelyn K. Shuman**<sup>19</sup> , **Carolyn H. Sieg**<sup>20</sup> , **Nicholas S. Skowronski**<sup>21</sup> , **David R. Weise**<sup>22</sup> , **Molly Wright**<sup>23</sup> , **Chonggang Xu**<sup>1</sup> , **Marta Yebra**<sup>24,25</sup>  and **Nicolas Younes**<sup>24</sup> 

<sup>1</sup>Earth & Environmental Sciences Division, Los Alamos National Laboratory, Los Alamos, NM 87545, USA; <sup>2</sup>San Diego Supercomputer Center and Halicioglu Data Science Institute, University of California San Diego, La Jolla, CA 92093, USA; <sup>3</sup>Department of Botany, University of Innsbruck, 6020 Innsbruck, Austria; <sup>4</sup>Ecologie des Forêts Méditerranéennes (URFM), INRAe, 84914 Avignon, France; <sup>5</sup>USDA Forest Service Northern Research Station, New Lisbon, NJ 08064, USA; <sup>6</sup>Tall Timbers Research Station, Tallahassee, FL 32312, USA; <sup>7</sup>Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, CO 80523, USA; <sup>8</sup>Rocky Mountain Research Station, USDA Forest Service, Missoula, MT 59801, USA; <sup>9</sup>Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA; <sup>10</sup>Southern Research Station, USDA Forest Service, Athens, GA 30602, USA; <sup>11</sup>Department of Botany and Biodiversity Research Centre, The University of British Columbia, Vancouver, BC V6T 1Z4, Canada; <sup>12</sup>Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW 2753, Australia; <sup>13</sup>NSW Bushfire Risk Management Research Hub, Wollongong, NSW 2522, Australia; <sup>14</sup>School of Life Sciences and Engineering, Southwest University of Science and Technology, Mianyang 621010, China; <sup>15</sup>Department of Crop and Forest Sciences and JRU CTFC-AGROTECNIO, Universitat de Lleida, Lleida 25198, Spain; <sup>16</sup>Fire and Resource Assessment Program, California Department of Forestry and Fire Protection, South Lake Tahoe, CA 96155, USA; <sup>17</sup>Environmental Protection and Compliance Division, Los Alamos National Laboratory, Los Alamos, NM 87545, USA; <sup>18</sup>Environmental and Climate Sciences Department, Brookhaven National Laboratory, Upton, NY 11973, USA; <sup>19</sup>Climate and Global Dynamics Laboratory, Terrestrial Sciences Section, National Center for Atmospheric Research, Boulder, CO 80305, USA; <sup>20</sup>Rocky Mountain Research Station, USDA Forest Service, Flagstaff, AZ 86001, USA; <sup>21</sup>Northern Research Station, USDA Forest Service, Morgantown, WV 26505, USA; <sup>22</sup>Pacific Southwest Research Station, USDA Forest Service, Riverside, CA 92507, USA; <sup>23</sup>Cibola National Forest, USDA Forest Service, Albuquerque, NM 87113, USA; <sup>24</sup>Fenner School of Environment and Society, Australian National University, Canberra, ACT 2601, Australia; <sup>25</sup>School of Engineering, Australian National University, Canberra, ACT 2601, Australia

## Contents

|  |     |  |     |
|--|-----|--|-----|
| Summary  | 953 | V. Remote sensing of plant water and carbon to inform process modeling | 963 |
| I. Introduction  | 953 | VI. Conclusions and future directions                                  | 964 |
| II. Existing models of fire behavior and effects         | 955 | Acknowledgements   | 965 |
| III. Physiological controls of fire behavior and effects | 956 | References   | 966 |
| IV. Integrating fine-scale physiology with fire models   | 961 |  |     |

## Summary

*New Phytologist* (2023) **238**: 952–970  
doi: 10.1111/nph.18770

**Key words:** carbon dynamics, fire behavior, fire effects, fire modeling, plant physiology, remote sensing, vegetation–fire interactions, water dynamics.

Wildfires are a global crisis, but current fire models fail to capture vegetation response to changing climate. With drought and elevated temperature increasing the importance of vegetation dynamics to fire behavior, and the advent of next generation models capable of capturing increasingly complex physical processes, we provide a renewed focus on representation of woody vegetation in fire models. Currently, the most advanced representations of fire behavior and biophysical fire effects are found in distinct classes of fine-scale models and do not capture variation in live fuel (i.e. living plant) properties. We demonstrate that plant water and carbon dynamics, which influence combustion and heat transfer into the plant and often dictate plant survival, provide the mechanistic linkage between fire behavior and effects. Our conceptual framework linking remotely sensed estimates of plant water and carbon to fine-scale models of fire behavior and effects could be a critical first step toward improving the fidelity of the coarse scale models that are now relied upon for global fire forecasting. This process-based approach will be essential to capturing the influence of physiological responses to drought and warming on live fuel conditions, strengthening the science needed to guide fire managers in an uncertain future.

## I. Introduction

Wildland fire burns hundreds of millions of hectares of forests, woodlands, and grasslands annually (Giglio *et al.*, 2013), shaping terrestrial ecosystems (Bond & van Wilgen, 1996; Bond & Keeley, 2005; Bond, 2021), and their impacts on global carbon (Bowman *et al.*, 2009) and water (Li & Lawrence, 2017) cycles. To accurately predict fire behavior and resulting effects, we need to understand the influences of vegetation structure and physiology on combustion (e.g. Byram, 1959; Weise & Wright, 2013) and the microenvironment (e.g. Finnigan, 2000; Banerjee *et al.*, 2020; Atchley *et al.*, 2021). Recent studies demonstrate that burned area shows greater increases in forests and shrublands where vegetation moisture is more sensitive to water limitation (Rao *et al.*, 2022), and that hydraulic traits of woody evergreen species are responsible for up to 3.6-fold variation in live fuel moisture content (LFMC, ratio of biomass water content to oven-dry biomass, Table 1; Scarff *et al.*, 2021). These findings emphasize the importance of accounting for ecophysiological controls on woody vegetation in wildfire forecasting and prescribed fire planning, where fuel effects dominate under less extreme fire danger conditions (Cruz *et al.*, 2022). This will be particularly important in fire-susceptible ecosystems which experience significant drought and LFMC declines below thresholds that drive increases in fire behavior (Pimont *et al.*, 2019a). As atmospheric aridity continues

to increase with rising temperatures, compounding plant water stress (Grossiord *et al.*, 2020), the number of regions for which live fuels (i.e. living plants) are important in determining the behavior of fires and their ecological outcomes is likely to expand (Resco de Dios *et al.*, 2021).

Historically, representation of live fuels in fire behavior models has been limited to static fuel models (Table 2) that generalize vegetation into classes, such as grass, shrub, and timber (Albini, 1976; Scott & Burgan, 2005; but see Rothermel & Philpot, 1973; Hough & Albini, 1978 for seasonally- and age-dynamic fuel models). With recent advances in process-based modeling and remote sensing of both fuels and fires, there is now opportunity to capture more realistic fuel heterogeneities, including the physiological dynamics that determine live fuel conditions ('pyro-ecophysiology', Jolly & Johnson, 2018). This will allow exploration of their influence on fire behavior, ecological outcomes (i.e. plant injury, mortality, and recovery; hereafter, 'fire effects') and cascading hazards. Recent work has called for modeling efforts to improve integration of fire behavior and its effects (e.g. Hood *et al.*, 2018; O'Brien *et al.*, 2018; Kleynhans *et al.*, 2021) to better capture fire–vegetation–environment feedbacks. This integration is particularly important in the context of low-intensity and prescribed fire. While fuel heterogeneity has little effect in a high-intensity fire environment (Atchley *et al.*, 2021; Cruz *et al.*, 2022), changes in phenology can make the difference between

**Table 1** Glossary of pyro-ecophysiology terms.

|   |   |
|---|---|
| Canopy bulk density (CBD, mass per unit volume)                           | Measure of how closely canopy fuels are packed, reflects likelihood that fire can move through the forest canopy  |
| Carbon starvation   | Plant mortality resulting from inability of NSC to meet metabolic demands   |
| Cavitation  | Process by which excessive water tension causes expansion of dissolved air to form bubbles; in plants, this causes a break in the water column and a decrease in <i>hydraulic conductivity</i>  |
| Conduction  | Heat transfer through a material from a region of higher temperature to a region of lower temperature   |
| Consumption (mass per unit area)  | Amount of biomass consumed during fire  |
| Convection  | Heat transfer by the movement of a gas or liquid  |
| Embolism  | Blockage of a vessel by a mass; in plants, caused by air bubbles formed in xylem <i>via cavitation</i>  |
| Equivalent water thickness (EWT, g m <sup>-2</sup> )                      | Measure of leaf water content   |
| Fire radiative energy density (FRED, MJ m <sup>-2</sup> )                 | Measure of the intensity of radiative energy released from fuel during a fire   |
| Hydraulic conductivity (water mass or volume per unit time per unit area) | Measure of a system's ability to transport water  |
| Hydraulic failure   | Plant mortality resulting from failure of the water column by exceeding <i>PLC</i> thresholds   |
| Leaf mass per area (LMA, g m <sup>-2</sup> )                              | Measure of leaf thickness and density; inverse of specific leaf area; also called dry matter content (DMC) in remote sensing applications   |
| Live fuel moisture content (LFMC, %)                                      | Ratio of water mass to dry mass in living plants; controlled largely by physiological mechanisms, rather than weather   |
| Non-structural carbohydrates (NSC)  | Plant carbon used for functions other than building structural biomass, such as growth, metabolism, osmoregulation, transport, storage, and defense   |
| Osmotic potential (MPa)   | Potential of water molecules to move from a less concentrated to a more concentrated solution across a semi-permeable membrane  |
| Percent loss of conductivity (PLC)  | A measure of xylem vulnerability to cavitation at a given <i>water potential</i>  |
| Phenology   | Biological cycles resulting from seasonal or interannual climate variations   |
| Physiology  | Dynamic chemical and physical processes that govern function  |
| Pyro-ecophysiology  | Ecophysiology-based approach to live fuel research that considers how plant water and carbon cycles independently and collectively interact at the leaf and whole plant level to regulate flammability and subsequent fire behavior (Jolly & Johnson, 2018) |
| Radiation   | Heat transfer through a gas or vacuum other than by heating of the intervening space  |
| Relative water content (RWC, %)   | Plant water content relative to its fully hydrated state  |
| Senescence  | Process of biological aging; can be stress-induced or developmental   |
| Traits  | Morphological, physiological or phenological features measurable at the individual level (Violle <i>et al.</i> , 2007)  |
| Transpiration   | Loss of water vapor from a living body; in plants, evaporation <i>via</i> stomata   |
| Vapor pressure deficit (VPD, kPa)   | The difference between the amount of moisture in the air and how much moisture the air can hold when saturated; measure of atmospheric aridity  |
| Water potential (MPa)   | Pressure potential required to remove a water molecule from its matrix (e.g. xylem); a measure of plant water status  |

containment and escape for prescribed fires, where combustion dynamics are engineered to achieve desired biological and physical outcomes (e.g. species-specific vegetation survival or mortality, fire risk reduction, soil protection, and smoke management (Hiers *et al.*, 2020)) with implications for future fire and landscape dynamics (Mitchell *et al.*, 2009; Gallagher *et al.*, 2021). Plant water and carbon cycles have been recognized as important to both fire behavior (Nelson, 2001; Macias Fauria *et al.*, 2011; Jolly *et al.*, 2014; Jolly & Johnson, 2018) and ecological fire effects (Michaletz & Johnson, 2007; Hood *et al.*, 2018; Bär *et al.*, 2019). Yet, they have not been considered as an integrating framework mechanistically linking the two.

We argue that plant water and carbon cycles drive live fuel moisture and dry mass dynamics, which influence heat transfer into the plant during a fire and subsequent postfire survival and recovery. This focus on plant water and carbon dynamics provides a mechanistic framework that links plant physiology to fine-scale fire behavior and fire-induced effects on plant tissues, addressing a gap in current approaches to modeling fire and vegetation (Fig. 1). We focus in this review on the interactions of woody plants and fire, due to the availability of literature and to maintain focus on the

underlying argument. However, many of the needs and underlying connections that we recognize have importance to nonwoody systems. Understanding how within-plant physiology and fire interact will allow exploration of mechanisms important to ensuing plant, stand, and landscape-level vegetation dynamics, which influence subsequent fire behavior. To fully capture fire-ecosystem feedbacks, we propose exploring new ways to bring together fire behavior and effects models at fine scales where both fire and physiological processes can be represented in sufficient detail to define important biophysical mechanisms, with heat transfer to vegetation providing the mechanistic linkage from physiology to fire behavior and subsequent effects (Varner *et al.*, 2021). A fundamental understanding of how fire and plants interact at the fine scale is needed to constrain simulations used at management-relevant scales. Under unprecedented future climate conditions, for which we do not have past or present analogs, biophysical process modeling will be essential to understand response to conditions that fall outside the range of variability captured by current empirical models. Linking remotely sensed estimates of plant water and carbon status to models of fire behavior and effects offers a mechanistic approach critical to capturing the influence of

**Table 2** Glossary of models and remote sensing methods.

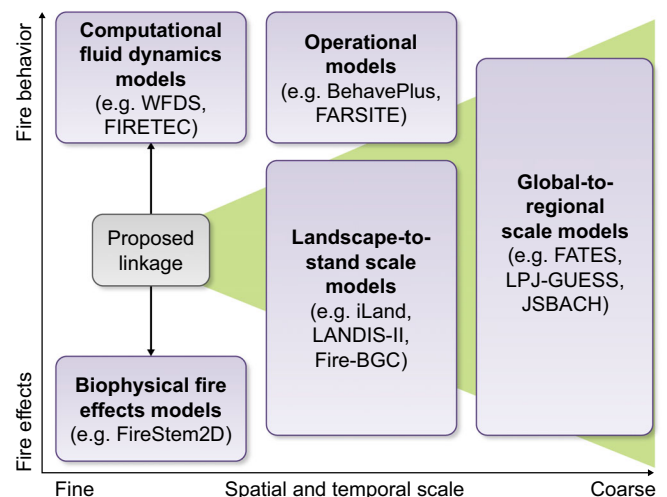
|  |   |
|--|---|
| Models                                     |   |
| 3D Fuel frameworks                         | Models that generate synthetic 3D fuels as inputs for CFD fire models   |
| Computational fluid dynamics (CFD)         | Physics-based models that simulate the interaction of liquids and gases based on fluid mechanics principles; used in simulation of fine-scale fire behavior and fire–atmosphere interactions within individual stands on timescales of minutes to hours |
| Ecosystem process                          | Mechanistic models based on theoretical understanding of ecological processes; for fire applications, can represent both fire behavior and effects on regional to global scales   |
| Empirical fire effects                     | Statistical models that predict tree status (live, dead) as a function of tree characteristics and observed fire injury, often estimated based on flame length  |
| Fire danger rating systems                 | Broad-scale assessments of fire ignition, spread, and hazard potential based on current and antecedent weather, fuels, and topography   |
| Functional structural plant models (FSPMs) | Mechanistic models of 3D plant structure, environment, and physiological response, from gene to community scales  |
| Fuel models                                | Stylized set of fuel bed characteristics used in fire models  |
| Landscape fire succession                  | Spatial simulation models of fire and vegetation dynamics at stand to landscape scales  |
| Operational fire                           | Computationally inexpensive models that rely on empirical representations of fire behavior and fixed, stylized <i>fuel models</i> to determine flame length and resulting mortality   |
| Process-based fire effects                 | Models which predict injury to different plant compartments based on heat transfer  |
| Vegetation demography                      | Models which capture dynamic, size-structured vegetation  |
| Remote sensing                             |   |
| Hyperspectral                              | Acquired in narrow, contiguous wavelength bands; high spectral resolution allows for material characterization, inference of chemical/biological processes, and novel signature identification  |
| Lidar                                      | Light detection and ranging; active <i>optical</i> sensing method using return time of a pulsed laser to measure distance   |
| Microwave                                  | Detects backscattering of actively transmitted radiation in the microwave (1 cm <sup>-1</sup> m) portion of the electromagnetic spectrum; longer wavelengths allow penetration of clouds, rain, and surfaces  |
| Multispectral                              | Acquired in broad, often discontinuous, wavelength bands; low spectral resolution reduces cost and complexity for monitoring known signatures   |
| Optical                                    | Detects <i>reflected</i> radiation in the visible (VIS, 380–780 nm), near- (NIR, 780–1000 nm) and short-wave infrared (SWIR, 1000–2500 nm) portions of the electromagnetic spectrum; primarily passive  |
| Thermal                                    | Detects <i>emitted</i> radiation in the thermal infrared (TIR, 780 nm <sup>-1</sup> mm) portions of the electromagnetic spectrum; primarily passive   |

physiological responses to drought and warming on live fuel conditions under global change.

## II. Existing models of fire behavior and effects

There are many existing fire behavior and effects models under use and continuous development. Rather than focusing on any one model or group of models, here we focus on commonly applied scales and model characteristics. We classify these as global to regional-scale models, landscape to stand-scale models, operational models, computational fluid dynamics models, and fine-scale biophysical fire effects models.

On global to regional scales (Fig. 1), fire behavior and effects have been combined within ecosystem process models using various approaches to simulate ecosystem dynamics with fire disturbance (see Rabin *et al.*, 2017 for in-depth review). Simulations commonly span decades to centuries and may include the entire globe. In these models, fire behavior and effects are commonly simulated explicitly at the computational grid level (*c.* 0.1–1°) or implicitly at a subgrid level. Fire spread is a function of fuel characteristics (loading, size distribution, and moisture), ignition patterns, weather, and latent suppression. These models often capture a dimension of vegetation growth and/or demographics which can dynamically inform fuel loads and fuel availability. Fire behavior is usually represented empirically based on experimental and modeling studies by Rothermel (1972) and



**Fig. 1** Model classification according to scale and process representation. In this conceptual figure, we show the classification applied to different models of fire behavior and effects discussed in this review. We also highlight our proposed linkage between fine-scale computational fluid dynamics (CFD) and biophysical fire effects models.

Van Wagner (1973). Fire effects are determined by total energy release and thresholds for mortality by either individuals, cohorts, or by fractioning existing vegetation. For example, recent advances in vegetation demography modeling include the addition of plant

hydraulics in FATES (Christoffersen *et al.*, 2016), allowing decoupling of water and carbon dynamics for more direct determination of live fuel vulnerability to fire at multiple timescales. Live fuel moisture content dynamics are captured by simulating water- and carbon-cycle processes directly at subdaily time scales, allowing for assessment of climate impacts (e.g. change in CO<sub>2</sub>, temperature, and precipitation) on future LFMC trends under different climate scenarios (Ma *et al.*, 2021). However, simplified representation of fire precludes mechanistic understanding of fire–physiology interactions.

At stand to landscape scales, a large number of models were developed for spatial plant ecology and fire occurrence at the scale relevant to forest management (10–100 km<sup>2</sup>; e.g. FIRE-BGC (Keane *et al.*, 2004), LANDIS-II (Sturtevant *et al.*, 2009; Scheller *et al.*, 2019)). These models are applied to decadal to century-long simulations. Observed or modeled fire dynamics account for stand-to-stand fire spread probabilistically or through the estimation of mechanistic processes. These models simulate cohorts or representative sets of individual plants/trees to estimate vegetation development and demography which inform fuel loading and availability. While this class of models can be leveraged to explore fire behavior and effects, they do not mechanistically link the two (Keane *et al.*, 2004). Within the stand (1–10 km<sup>2</sup>), fire effects are usually homogenous or stochastically based on homogenous traits of the stand (Furniss *et al.*, 2022). For example, FIRE-BGCv2 (Keane *et al.*, 2011) links biogeochemical processes with stand-scale fire behavior and effects based on live and dead fuel loading, leveraging FARSITE (Finney, 1998), but does not address within-stand variability. Keane *et al.* (2004) and Sturtevant & Fortin (2021) provide extensive reviews of landscape to stand-scale models.

Operational fire models such as BehavePlus (Andrews, 2013), FARSITE, FLAMMAP (Finney, 1998), or FFE-FVS (Reinhardt & Crookston, 2003) also represent fire behavior and effects. However, these models, which need to be computationally inexpensive to be useful, rely on empirical representations of fire behavior (Rothermel, 1972), and use fixed, stylized fuel models (Scott & Burgan, 2005) to determine flame length and resulting mortality. Their linkage between fire behavior and effects is thus very simple, and largely does not account for dynamic plant physiology or demography.

At the substand scale (<1 m–1 km), the most advanced representations of fire behavior and effects are currently found in distinct classes of models. Fire behavior is best captured with Computational Fluid Dynamics (CFD) models such as FIRETEC (Linn *et al.*, 2002) or the Wildland–Urban Interface Fire Dynamics Simulator (WFDS, Mell *et al.*, 2009). These models simulate individual fire events, or portions thereof, on short timescales of minutes to hours. Fuel parameters are static, with exception of moisture mass and dry mass of the fuel, which may decrease through dehydration and consumption, respectively. These models do not represent fire effects, as they do not explicitly distinguish between live and dead fuels, or between different vegetation species or functional groups. In absence of explicit vegetation response to changing meteorological conditions, they cannot resolve changes in LFMC or the sensitivity of fire behavior to live fuel moisture dynamics (Jolly, 2007).

Prediction of fine-scale ecological fire effects (postfire vegetation injury, mortality, and recovery) has been approached using both empirical and process-based models, with fire intensity provided as input from other models or measurements. Most postfire mortality models rely on empirical correlations (Woolley *et al.*, 2012; Hood *et al.*, 2018) which predict vegetation status (live or dead) as a function of plant characteristics (e.g. species, bark thickness, height, and diameter) and observed fire injury (e.g. crown scorch, and bark char), often estimated based on flame scorch height (Van Wagner, 1973). A number of process-based biophysical fire effects models predict injury to different woody plant compartments (e.g. stem (FireStem2D, Chatziefstratiou *et al.*, 2013) or crown (Michaletz & Johnson, 2006) heating models). Few, however, have considered injuries to more than one part of the plant (Michaletz & Johnson, 2008), and none address the influence of interacting injuries across multiple woody plant compartments on postfire plant function.

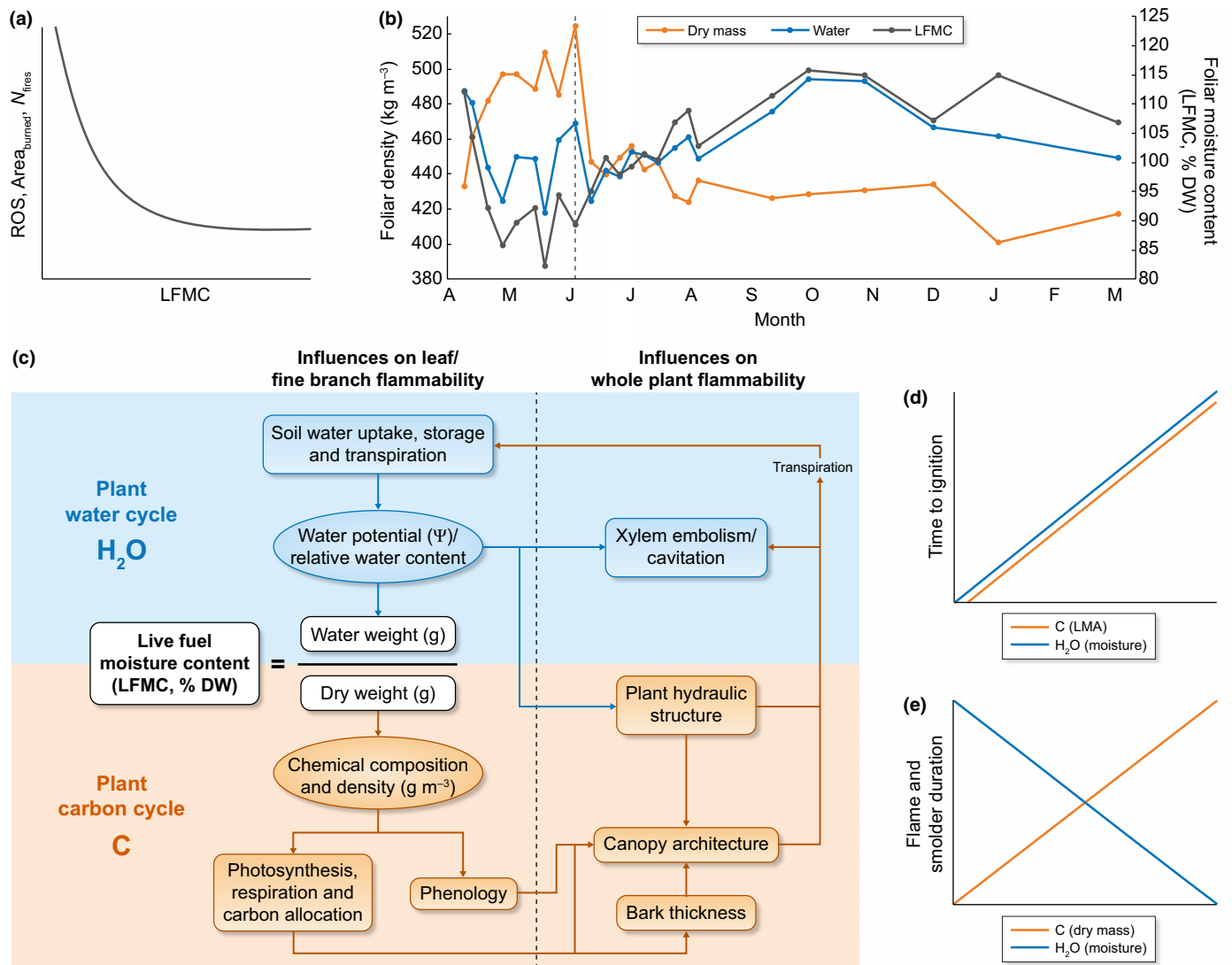
Direct coupling of fine-scale fire behavior and effects models remains challenging due to the different temporal scales that are relevant for both. As an alternative to solve this challenge, we propose exploring nested modeling frameworks (Gettelman *et al.*, 2022; Shuman *et al.*, 2022) which can transfer information across models at scales where both fire and physiological processes can be represented in sufficient detail to define important biophysical mechanisms. Recent work has made strides in mechanistically linking fire behavior to ecological effects through plant traits (Zylstra, 2021), but without mechanistic determination of vegetation density and moisture content resulting from plant water and carbon dynamics. By incorporating fine-scale physiology, we can capture dynamic water and carbon to represent these properties more realistically.

### III. Physiological controls of fire behavior and effects

#### 1. Evidence for the role of plant water and carbon in fire behavior

Fire behavior is broadly controlled by complex interactions among fuel density and moisture content, topography, and the atmosphere (Countryman, 1966). These factors not only interact, but also can be highly variable in space and time, resulting in dynamic fire environments. Live fuel moisture content is a key fuel property governing fire behavior (Fig. 2a). Declining LFMC is associated with an increase in area burned (Dennison & Moritz, 2009; Nolan *et al.*, 2016; Pimont *et al.*, 2019b), and LFMC below 100% sharply increases fire rate of spread (ROS, Pimont *et al.*, 2019a) and the probability of large fires (Martin-StPaul *et al.*, 2018) (Fig. 2a). Given its impact on fire behavior, LFMC has been incorporated into fire danger rating systems (e.g. Deeming *et al.*, 1977; Stocks *et al.*, 1989) and fire behavior models (e.g. Rothermel, 1972).

The water and dry mass components of LFMC are outcomes of plant water- and carbon-cycle processes, respectively, and are controlled by environmental conditions, soil properties, and plant physiology (Fig. 2b,c; Macias Fauria *et al.*, 2011; Jolly & Johnson, 2018; Ruffault *et al.*, 2018). Plant water and carbon can vary independently in both space and time, with opposing



**Fig. 2** Live fuel moisture content (LFMC, black), an important driver of landscape-scale fire behavior (a), is a function of plant carbon (C, orange) and water (H<sub>2</sub>O, blue) (b, c), which can have opposing influences on fire behavior in leaf level burn experiments (d, e). (a) Rate of spread (ROS), area burned, and fire occurrence ( $N_{\text{fires}}$ ) as a function of LFMC, as shown by Dennison & Moritz (2009), Martin-StPaul *et al.* (2018), Pimont *et al.* (2019a,b), and others. (b) Monthly variation in foliar dry mass (orange) and water (blue) density, and foliar moisture content (dry mass/water mass, LFMC; black) extracted from Jolly *et al.* (2016) with WEBPLOTDIGITIZER (Rohatgi, 2021). Dashed vertical line indicates divergence between LFMC and water density driven by increasing dry mass. (c) Conceptual model of LFMC as a function of plant water and carbon cycles redrawn from Jolly & Johnson (2018). (d) Time to ignition as a function of leaf carbon (leaf mass per area, LMA) and water (moisture) as shown in Grootemaat *et al.* (2015) and Bianchi *et al.* (2019). (e) Flame and smolder duration as a function of leaf carbon (dry mass) and water (moisture), as shown in Grootemaat *et al.* (2015) and Bianchi *et al.* (2019).

effects on LFMC. For example, a sharp prebuddburst (early June) increase in foliar dry mass of older, live pine needles has been shown to reduce LFMC despite increasing foliar water mass (Fig. 2b; Jolly *et al.*, 2014, 2016). Based on these findings, Jolly & Johnson (2018) proposed a framework decomposing LFMC into plant water and carbon cycle processes (Fig. 2c), where the numerator is determined by whole plant hydraulics (e.g. transpiration; relative water content; and xylem embolism), and the denominator by carbon allocation (e.g. chemical composition/density; phenology; and canopy architecture). These processes influence fire behavior both by changing tissue- and canopy-level properties that influence heat transfer, and by altering the proportion of dead biomass in fuels and on the ground surface. Seasonal or drought-induced senescence and

shedding are examples of physiological processes that alter leaf, fine branch, and whole plant flammability, transforming live fuels into dead fuels and increasing litter accumulation. Tissue senescence is associated with shifts in osmolytes and water content (Milla *et al.*, 2007), which can increase or decrease LFMC. Tissue mortality also increases the dead to live fuel ratio, causing a strong increase in fire spread and intensity (e.g. Cruz *et al.*, 2015; Sieg *et al.*, 2017; Balaguer-Romano *et al.*, 2020). When senesced tissues are shed, litter accumulates in the surface fuel-bed and may increase the likelihood of surface fire.

The importance of both plant water- and carbon-cycle processes for fire behavior becomes clear when examining their effects on heat transfer and combustion (Michaletz & Johnson, 2007; Bär

*et al.*, 2019; Diatenberger *et al.*, 2020; Kleynhans *et al.*, 2021). Preheating, the process by which heat transfer evaporates water, dries, and decomposes carbon-containing polymers in unburned fuels, occurs *via* conduction, convection, and radiation. Thermal conductivity varies with material density, temperature, and water content, while convection depends on geometry and orientation of the fuel surface. The proportion of radiation absorbed by unburned fuel depends on both its thermal absorptance as well as geometry and orientation. Fuel chemistry and water content are therefore important to both conductive and radiative heat transfer through their influence on thermal conductivity and absorptance, while convection and radiative heat transfer to the fuel surface depend on vegetation geometry and orientation, including leaf, branch, crown, or canopy structure (Michaletz & Johnson, 2006; Pausas & Moreira, 2012). The rate at which the temperature increases in response to heat transfer depends on the mass and specific heat of the biomass, which depend on plant tissue water content and composition (Boardman *et al.*, 2021). Water content also determines how much energy is required to heat the fuel to evaporation and combustion temperatures (Yashwanth *et al.*, 2016), while the content of carbon-based polymers determines the amount and rate of thermal decomposition, influencing the rate of preheating and time to combustion (Kilzer & Broido, 1965). Fuel chemistry and water content are also critical in determining whether combustion reactions are self-sustaining and how they will contribute to fire intensity and rate of spread (Quintiere, 2006; Matt *et al.*, 2020). During combustion, the content of organic polymers determines how much energy can be released, and water content can determine whether flaming or smoldering combustion occurs. Higher rates of fire spread and probability of flaming combustion, which occurs at high temperature and/or low moisture, are therefore more likely when live fuels are water stressed and the ratio of water mass to dry mass (LFMC) is lower.

Results from leaf-level burn experiments support the influence of plant water and carbon processes on preheating. Time to ignition (Fig. 2d) has been shown to increase with moisture (Grootemaat *et al.*, 2015; Bianchi *et al.*, 2019; but see Fletcher *et al.*, 2007) and leaf mass per area (LMA, inverse of specific leaf area, Grootemaat *et al.*, 2015), which is associated with accumulation of total structural carbohydrates and lignin (Poorter *et al.*, 2009). Flame and smolder duration (Fig. 2e) also increase with dry mass (Grootemaat *et al.*, 2015), but decrease with moisture (Bianchi *et al.*, 2019). These contrasting effects of leaf-level water and carbon on different fire behavior characteristics underscore the importance of capturing LFMC components independently. Despite evidence from Alam *et al.* (2020) that certain leaf and shoot flammability metrics (e.g. ignitibility and combustibility) are decoupled, the same study showed a positive relationship of leaf dry matter content with shoot and species-level flammability, suggesting that effects of leaf water and carbon on fire behavior are scalable. At canopy scales, Jolly *et al.* (2016) found that increased leaf density, which accounts for changes in dry mass associated with phenological change in foliar chemistry and carbon allocation, increased modeled crown fire propagation and area burned. Additionally, canopy bulk density, a measure of canopy architecture influenced by water- and

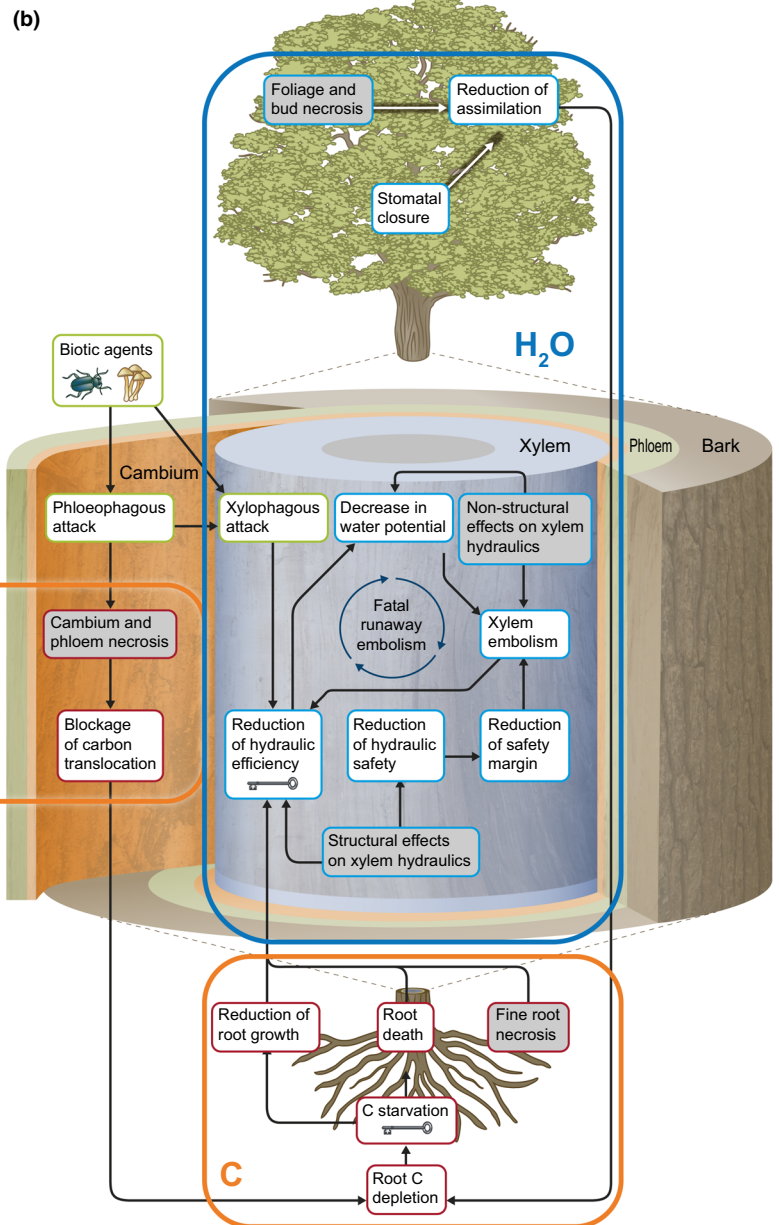
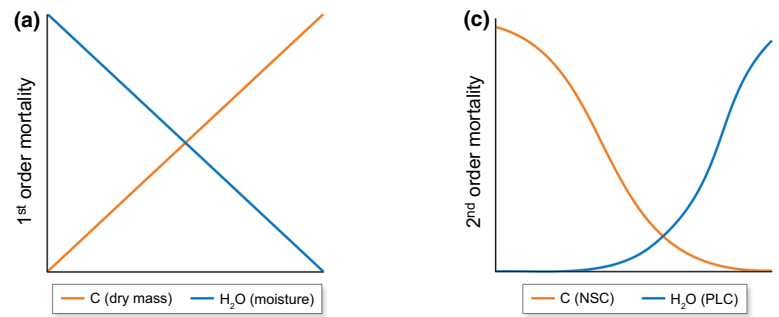
carbon-cycle processes *via* growth rate, environment, and phenology, has long been recognized as an important driver of spread rate in active crown fires (Van Wagner, 1977; Resco de Dios, 2020). The independent relationships of water- and carbon-cycle processes with fire behavior, and their complex interdependence, highlight the need for a more mechanistic representation of LFMC that accounts for underlying physiology and allows for dynamic change.

## 2. Evidence for the role of plant water and carbon in fire effects

First-order effects of fire on vegetation are the direct result of combustion and heat transfer to plant tissues (Michaletz & Johnson, 2007), and can be modulated by plant physiological characteristics. The same traits that influence fire behavior through controls on heat transfer also influence fire effects by modulating tissue temperatures and exposure times, particularly in low and mixed-severity fire regimes where vegetation is not combusted and immediately killed (O'Brien *et al.*, 2018; Varner *et al.*, 2021). Percent mortality has been demonstrated to increase with fire radiative energy density (Smith *et al.*, 2017; Steady *et al.*, 2019), or time-integrated radiative flux density from ignition to cessation of the fire. Since absorbed fire radiative energy is tied to flame and smolder duration (O'Brien *et al.*, 2016), which increases with dry mass and decreases with moisture (Fig. 2e), we expect first-order mortality to increase with dry mass and decrease with moisture content (Fig. 3a). This is consistent with significant increases in simulated canopy fuel consumption with reduced canopy fuel moisture, particularly under low-wind scenarios (Sieg *et al.*, 2017). While the physical relationship between moisture and flame and smolder duration should hold across species and ecosystems, further research is required to validate the relationship between moisture content and first-order mortality, as tissues with higher moisture contents can also be more heat sensitive (Wright & Bailey, 1982).

When vegetation is not consumed, fire-induced injuries, including hydraulic dysfunction, cambium and apical meristem necrosis, leaf and fine root necrosis, are proposed to influence whole-plant carbon and water budgets resulting in hydraulic failure and/or carbon starvation (Fig. 3b; Midgley *et al.*, 2011; Michaletz *et al.*, 2012; Hood *et al.*, 2018; Michaletz, 2018; Silva *et al.*, 2018; Bär *et al.*, 2019; Berenguer *et al.*, 2021). This framework suggests that second-order effects on live vegetation are driven, in part, by postfire water and carbon availability, along with integrity of the water and carbon uptake and transport systems (Fig. 3b,c; Michaletz & Johnson, 2007; Hood *et al.*, 2018; Michaletz, 2018; Bär *et al.*, 2019). Postfire environmental conditions and species-specific traits determine whether resulting functional and growth limitations will lead to vegetation recovery or mortality (Bär *et al.*, 2019; Sayer *et al.*, 2020; Hood, 2021; Ruswick *et al.*, 2021). For instance, traits such as water stress resistance are observed to differ between disturbance-dependent and obligate sprouters in Mediterranean-type climate regions (Pratt *et al.*, 2012), with implications for postfire community composition. Franco *et al.* (2014) note that in neotropical savannas, where fire is common and accelerated fire frequencies and prolonged droughts





**Fig. 3** Plant carbon (C, orange) and water (H<sub>2</sub>O, blue) determine fire effects. (a) First-order effects are the direct result of heat transferred to plant tissues (Michaletz & Johnson, 2007), as modulated by plant tissue properties (water and carbon content). Percent mortality increases with time integrated from ignition to cessation of fire (fire radiative energy density (FRED); Smith *et al.*, 2017; Steady *et al.*, 2019), which should approximate flame and smolder duration (Fig. 1e), which increase with leaf carbon (dry mass) and decrease with leaf water (moisture) content (Grootemaat *et al.*, 2015; Bianchi *et al.*, 2019). (b) Conceptual diagram illustrating the cascade of potential physiological responses to post-fire injuries in plant roots, stems, and crowns adapted from Bär *et al.* (2019). Blue frame captures processes impacting the plant water cycle leading to reduction in hydraulic efficiency and ultimate hydraulic failure (fatal runaway embolism). Orange frames capture processes impacting the plant carbon cycle, leading to carbon starvation. (c) Second-order effects are modulated by post-fire water and carbon availability, along with integrity of the water and carbon uptake and transport systems (Hood *et al.*, 2018; Bär *et al.*, 2019). Mortality thresholds for hydraulic failure and carbon starvation are defined based on percent loss of conductivity (PLC, Hammond *et al.*, 2019) and non-structural carbohydrate (NSC) concentrations (Barker Plotkin *et al.*, 2021), both of which are impacted by fire (Varner *et al.*, 2009; Michaletz *et al.*, 2012; West *et al.*, 2016).

are expected under climate change, the interplay between temperature optima and CO<sub>2</sub> fertilization effects on photosynthesis, photorespiration, and respiration will define how much carbon is available for postfire plant growth and resprouting, determining the acclimation potential of a given species, plant community or

ecosystem. Indeed, from Mediterranean to Tropical ecosystems, the balance between forest expansion and retreat, between seedling recruitment and mortality, has been attributed to species differences in drought sensitivity (e.g. embolism resistance, rooting depth, and stomatal regulation) and carbon balance (e.g. stomatal

regulation, osmotic adjustment, and carbon allocation) (Keeley, 1998; Franco *et al.*, 2014).

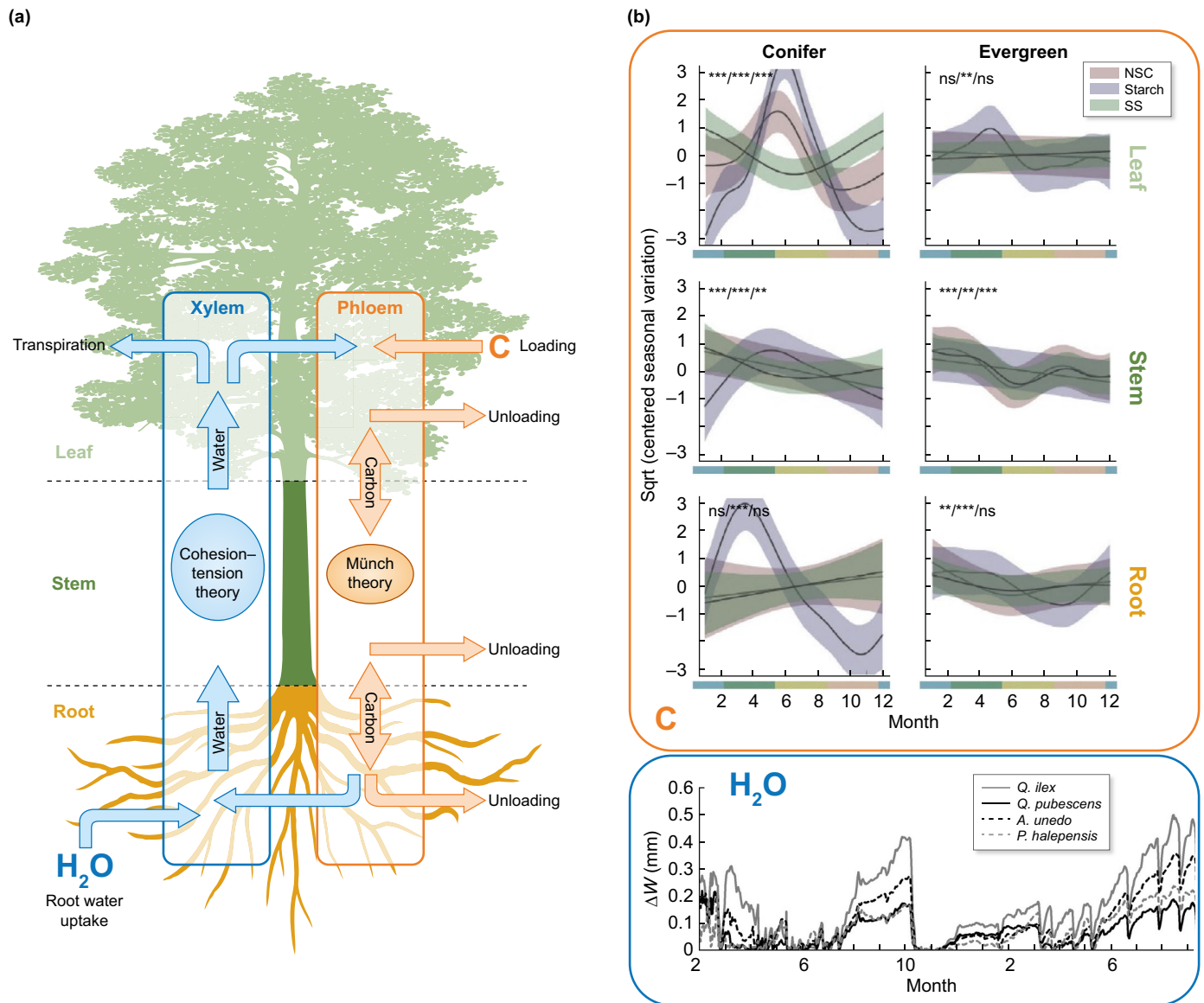
Drought and herbivory research, where tree mortality has a long history of study, has defined mortality thresholds for hydraulic failure in terms of percent loss of hydraulic conductivity (PLC; Hammond *et al.*, 2019), and for carbon starvation in terms of nonstructural carbohydrate (NSC) depletion (Barker Plotkin *et al.*, 2021). Evidence of increased PLC from laboratory experiments (Michaletz *et al.*, 2012; West *et al.*, 2016; Partelli-Feltrin *et al.*, 2021), as well as from forest fires (Bär *et al.*, 2018), indicates that fire increases vulnerability to cavitation (Midgley *et al.*, 2011; Hood, 2021). In addition, fire can decrease root NSC (Varner *et al.*, 2009), reducing stores available to support metabolism, growth, and subsequent stress response, resulting in mortality independent of canopy damage. Together, this research suggests similar relationships for second-order fire mortality (Fig. 3c) as for mortality from drought and herbivory, where sufficiently high PLC or low NSC results in mortality. This is consistent with recent work linking mortality and recovery from low-intensity fire to prefire water status (van Mantgem *et al.*, 2018; Partelli-Feltrin *et al.*, 2020) and concentrations of NSC (Zhu *et al.*, 2012; Sayer *et al.*, 2020). In addition, smoldering consumption can impact water uptake directly through root loss (O'Brien *et al.*, 2010). In conifers, trade-offs have also been documented between resistance to cavitation and to fire, likely mediated by allocation of carbon to either building thick bark or dense xylem, but not both (Resco de Dios *et al.*, 2018). These trade-offs have implications for woody vegetation recovery from fire under climate change, where drought conditions can predispose woody vegetation to hydraulic (Partelli-Feltrin *et al.*, 2020) and carbon (Sayer *et al.*, 2020) limitations, impacting capacity to recover from fire-induced injury and/or resprout. Indeed, intense postfire drought can also cause significant resprout mortality resulting from simultaneous loss of hydraulic conductivity and depletion of root starch (Pratt *et al.*, 2014).

### 3. Importance of plant water and carbon dynamics

Given the demonstrated role of plant water and carbon status in both fire behavior (Fig. 2) and effects (Fig. 3), accurately capturing their dynamics (seasonal variation, differences across species or functional types, with topography, and natural disturbance) will lead to improvements in fire behavior and effects models. Carbon and water status of live fuels change dynamically through time with environmental conditions and seasonal phenology (Baffoin *et al.*, 2021). Variation in plant dry matter is driven by changes in organic molecules, largely NSC and lipids synthesized in the leaf and allocated to different plant organs (i.e. roots, stems, leaves, and reproductive structures) as needed for respiration and storage (Chapin *et al.*, 1990). Diurnal variation results from daily synthesis and export patterns, while seasonal variation is largely driven by re-allocation to meet seasonal demands associated with phenology or source limitation (e.g. drought-induced reduction in photosynthesis; Martínez-Vilalta *et al.*, 2016). Changes in water content are driven by the interplay between soil water availability, physiological and morphological regulation, and atmospheric vapor pressure

deficit through the soil–plant–atmosphere continuum (Nelson, 2001; Macias Fauria *et al.*, 2011). Water and carbon status differ across organs and over time as water moves from root to leaf *via* transpiration and as carbon is assimilated and transported across organs *via* the phloem (Fig. 4a, Zhou *et al.*, 2020), and these dynamics differ by species and/or plant functional type. For instance, while evergreen conifers show strong seasonal variation in leaf NSC and dampened variation in stem NSC and water deficit ( $\Delta W$ ), the opposite is true for evergreen angiosperms (Fig. 4b, Sánchez-Costa *et al.*, 2015; Martínez-Vilalta *et al.*, 2016). Topographic variation (microclimates, water availability, and soil resources available for growth) can also modify physiology, and fuel availability and loading, and has been shown to govern fire behavior and effects (Knapp *et al.*, 1993; Krawchuk *et al.*, 2016; Swann *et al.*, 2022). Different functional strategies in relation to seasonal water deficit and disturbance, such as those defined by leaf lifespan (deciduous vs evergreen) and minimum water potential (Ackerly, 2004), will determine how these water and carbon dynamics manifest across species. Even within an individual species, plants can modulate the effects of variability in water resources by modifying leaf area, rooting depth, and/or stomatal conductance (Rambal, 1993). Among co-occurring chaparral shrubs, differences in rooting depth can drive differential responses of leaf water potential to seasonal drought (Davis & Mooney, 1986; Smith & Richardson, 1990), and those with similar responses may use different modes of seasonal osmotic adjustment to accomplish changes in osmotic potential (i.e. shift in water volume vs solute concentration; Bowman & Roberts, 1985), with strong implications for LFMC. Species differences in drought response and associated leaf senescence and shedding have implications for litter accumulation and fuel-bed flammability as well due to species variation in litter flammability and nonadditive effects in multi-species litter mixtures (de Magalhães & Schwilk, 2012, 2021).

Climate and phenology drive seasonal change in these fire-relevant traits, regulating water and NSC balances. Under future climate conditions, drought and phenological shifts can affect greenup, senescence, and susceptibility to mortality, all of which impact fuel load and flammability (Jolly *et al.*, 2016). For instance, prefire drought increases the likelihood of mortality (van Mantgem *et al.*, 2018; Partelli-Feltrin *et al.*, 2020) and of resprouting failure (Karavani *et al.*, 2018; Resco de Dios *et al.*, 2020). Topographic variation can be an important control on drought induced mortality and resulting fuel loads. For example, increased water availability in concave areas can mediate the increase in hydraulic stress typical at lower elevations (Tai *et al.*, 2017). Prefire drought and heat stress may also diminish flowering and seed production, negatively impacting species with fire-cued recruitment (Nolan *et al.*, 2021). Heat susceptibility of tissues (Bär *et al.*, 2021) and probability of vegetation survival can also be influenced by plant phenological stage during a burn (Trabaud, 1991; Knapp *et al.*, 2009; Ruckman *et al.*, 2012; Pratt *et al.*, 2014), highlighting the importance of capturing seasonal variation in prediction of mortality (Bond & van Wilgen, 1996). Beyond drought, other natural disturbances can cause physical damage to vegetation (e.g. pathogens and herbivory), change in fuel loads and availability due to rapid mortality (e.g. bark beetles and tropical cyclones), or



**Fig. 4** Plant carbon (C, orange) and water (H<sub>2</sub>O, blue) are constantly varying across organs (a), species and time (b). (a) Plant water (H<sub>2</sub>O, blue) and carbon (C, orange) exchange across organs (leaf, root, stem) by cohesion-tension and Münch flow through xylem and phloem adapted from Zhou *et al.* (2020). (b, Carbon) Global patterns of seasonal variation (centered smooths, square-root transformed mg g<sup>-1</sup> dry mass) in total non-structural carbohydrates (NSC), starch, and soluble sugars (SS) as a function of month, functional type (columns; conifer, evergreen angiosperm), and organ (rows; leaf, stem, root) adapted from Martínez-Vilalta *et al.* (2016). (b, H<sub>2</sub>O) Seasonal course of tree water deficit (ΔW, de-trended stem diameter variation) for four species representing three different Mediterranean forest functional types: evergreen sclerophyllous (*Quercus ilex* L., *Arbutus unedo* L.); winter deciduous (*Quercus pubescens* Willd.); early successional, drought-adapted conifer (*Pinus halepensis* Mill.) (adapted from Sánchez-Costa *et al.*, 2015).

increased resource availability for plant growth (e.g. windfall), all of which can be incorporated into plant physiology models to understand their feedbacks on fire behavior and effects (Karp *et al.*, 2021; Rouet-Leduc *et al.*, 2021; Fettig *et al.*, 2022; Ibanez *et al.*, 2022; Lee *et al.*, 2022). Acknowledging dynamic physiology recognizes that fire behavior and its effects will vary, within and across species, with plant water status (Nolan *et al.*, 2018), carbon dynamics (photosynthesis, respiration, allocation), phenology (Bär *et al.*, 2021), species (McAllister & Weise, 2017; Nolan *et al.*, 2018; Resco de Dios, 2020), and time (Fig. 4).

#### IV. Integrating fine-scale physiology with fire models

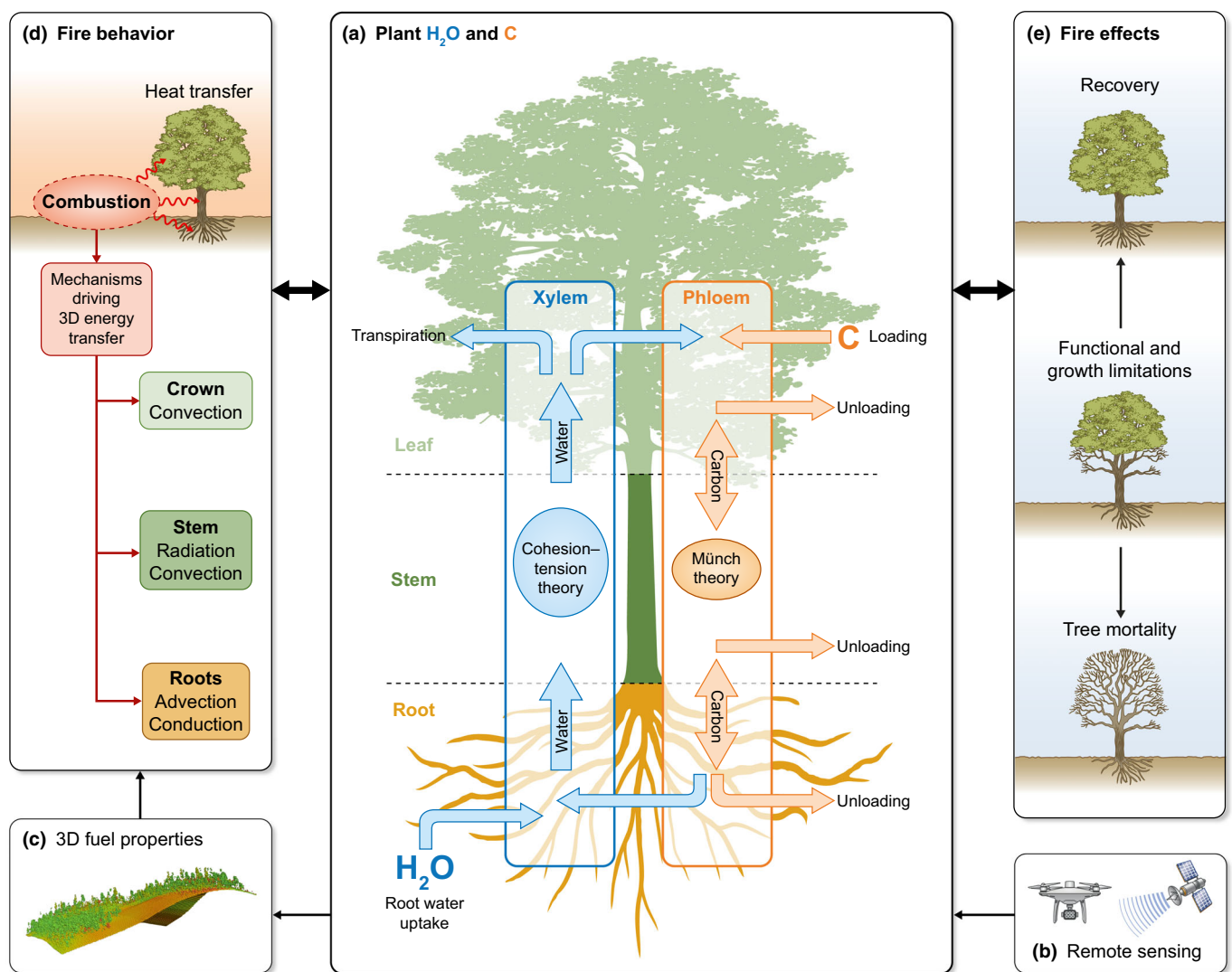
The wildland fire research community has called for the use of process-based models to explore the potential mechanisms and interactions driving fire dynamics and effects and to conduct virtual experiments that allow for consideration of no-analog future climate conditions (Michaletz *et al.*, 2013; Hoffman *et al.*, 2018; O'Brien *et al.*, 2018). The demonstrated importance of plant water and carbon to fire behavior and effects, and their variability across species and time, underscore the value in applying plant carbon and

water process models to explore the biophysical mechanisms linking vegetation to fire behavior and effects under present and future conditions.

Recent advances in whole-plant modeling offer a promising framework for linking simulations of plant water- and carbon-related processes to finer-scale models of fire behavior and effects. Nolan *et al.* (2018, 2020) suggested a physiological basis to model LFMC for fire behavior applications using leaf water potential as a proxy. This approach allows for species-specific variation with environmental drivers, while acknowledging the importance of capturing variation in leaf mass to account for decoupling of seasonal changes in the water and carbon contents that comprise LFMC. Mechanistic functional structural plant models (FSPMs)

(Vos *et al.*, 2010; Louarn & Song, 2020; de Vries, 2021), of 3D plant structure, environment, and physiological response, from gene to community scales, offer a potential solution to capture both water and carbon cycle processes. Functional structural plant models, which can simulate water and carbon flows across 3D plant compartments (root, stem, and leaf) in response to environmental conditions, have been demonstrated for use in simulation of both small plants and trees and include open-source platforms that enable coupling with external modeling tools (e.g. Zhou *et al.*, 2020).

Such a model could be coupled to fine-scale fire behavior models using fuel modeling frameworks such as Fuel3D (Parsons *et al.*, 2011), FuelManager (Pimont *et al.*, 2016), STANDFIRE



**Fig. 5** Plant carbon (C) and water ( $H_2O$ ) dynamics provide the mechanistic linkage between fire behavior and effects. In our conceptual framework, plant carbon and water process models (a; adapted from Zhou *et al.*, 2020), which can be parameterized by remotely sensed estimates of canopy carbon and water contents (b; e.g. Dahlin *et al.*, 2013; Singh *et al.*, 2015), provide input to 3D fuel models (c; e.g. Pimont *et al.*, 2016; Parsons *et al.*, 2018). Detailed fuel properties are then exported to physics-based fire models (d; adapted from O'Brien *et al.*, 2018; Bär *et al.*, 2019) that provide heat transfer estimates for input to the plant water and carbon model (a), which feeds into simulation of fire effects (e; adapted from Bär *et al.*, 2019). These effects, along with remotely sensed estimates (b), drive subsequent plant water and carbon (a), feeding 3D fuels (c), and the cycle repeats.

(Parsons *et al.*, 2018), or FastFuels (Parsons *et al.*, 2020). These frameworks can generate the 3D structure of canopy, mid-, and under-story vegetation for input to physics-based fire models, such as FIRETEC or WFDS, allowing examination of within-stand 3D fuel–fire interactions. Currently, meteorological or remotely sensed data (see the [Remote sensing of plant water and carbon to inform process modeling](#) section) can be used to set the moisture properties in these fuel models. Moisture is most often assigned a fixed value by the user for the course of the simulation across minutes to hours, and only FuelManager allows for assignment of alive vs dead status. As an advance to enable mechanistic evaluation of fine-scale interactions between physiological and heat transfer processes and their influence on fire behavior and effects, we propose incorporation of a physiological process model to determine fuel condition based on physiological descriptions (plant water and carbon-related processes) of individual plants (e.g. Cochard *et al.*, 2021; Ruffault *et al.*, 2022a,b). This could be achieved through use of a FSPM with remotely sensed parameterization (Fig. 5a,b) to inform 3D fuel properties (Fig. 5c). These properties would provide the necessary inputs to parameterize fire behavior models (Fig. 5d), the outputs of which could inform predictions of subsequent plant water and carbon dynamics (Fig. 5a). Model representations of these postfire physiological processes could then inform second-order fire effects (Fig. 5e) through a process-based mortality model (e.g. Michaletz & Johnson, 2008; Butler & Dickinson, 2010) and subsequent 3D fuel properties (Fig. 5c). This approach will require parallel advances in mechanistic modeling of whole-plant fire injury processes to determine whether interacting injuries result in ultimate recovery, mortality, or functional limitations (Hood *et al.*, 2018; Bär *et al.*, 2019), which will be essential to determining subsequent fuel properties.

The individual plant (or within-plant) detail of this approach will enable further exploration of the plant traits most critical to the process of, and sensitivity to, heat transfer, allowing for determination of scale-relevant parameters. A model sensitivity approach varying plant physiological input parameters could be used to define functional groupings, based on species traits (response of tissue-level water and carbon to environmental drivers) that influence fire behavior and effects, which may allow for more generalized response functions to reduce computational resource requirements for use at larger scales.

By directly linking combustion, physiological process, and fire-injury plant-mortality models to hydrologic and plant succession models in a spatially explicit way, this framework could potentially be extended to simulate landscape-scale ecohydrology, and its response to fire disturbance under present and future climate conditions. By calculating transient heterogeneous fuel moistures and temperatures based on incident radiation, heat fluxes, and topographic variation, this model extension could capture species- (or functional type-) dependent responses to soil moisture at different depths. Landscape-scale models of ecohydrology could use available downscaled climate reconstructions and models and spatially explicit maps of soil characteristics, topography, and aspect (e.g. Thornton *et al.*, 2014; Soil Survey Staff, 2022) to simulate plant and fire response to landscape heterogeneity. This would allow plant water and carbon to vary spatially, influencing

both fire behavior and vegetation mortality, which feedback to alter hydrology and plant succession, influencing ecosystem trajectory and response to subsequent fire disturbance. Such a framework could also allow for exploration of the role of other natural disturbance, alongside species composition and competitive interactions, in determining fuel load and the likelihood of future fire.

Another way to link fine-scale mechanistic models to coarser scale outcomes is through metamodelling and nested model design. These techniques aim to find the crucial aspects of the mechanism that would be propagated at a higher level of spatial or temporal coarseness. Traditional or machine-learning metamodelling can emulate nonlinear processes at scales where simulation would be unfeasible (Sparks *et al.*, 2011; Huang *et al.*, 2016). These can be integrated into existing coarse-scale models to propagate fine-scale understanding in a more computationally efficient manner (Lu & Ricciuto, 2019). A nested model design can allow for experimentation at relevant scales of physiology and mechanism to constrain coarser models or metamodelling. For example, species trait-based functional types of fire behavior and effects can be created and used at coarser scales; while separately simulating component species at scales relevant to physiology, combustion, or fire injury (Neilson *et al.*, 2005). Bayesian methods can further allow for integrating multiple nested models with observational data to constrain the performance of coarse-scale models along with the propagation of uncertainty (Talluto *et al.*, 2016).

## V. Remote sensing of plant water and carbon to inform process modeling

Remote sensing of vegetation exploits the biophysical links between spectral information contained in the electromagnetic radiation reflected or emitted from the earth's surface and vegetation state, function, and dynamics. Optical data have been used to map LFMFC using multispectral sensors at local (Marino *et al.*, 2020), continental (Yebra *et al.*, 2018a), and global (Quan *et al.*, 2021) scales, producing mapping products at spatial resolutions from tens to thousands of meters. Visible spectrum reflectance is collected by many remote sensing platforms for vegetation monitoring purposes; but alone is insufficient for the prediction of LFMFC. Addition of spectral data from the shortwave infrared (SWIR) region of the electromagnetic spectrum, currently collected by only a limited number of platforms, increases the accuracy of optical LFMFC estimations (Yebra *et al.*, 2018a). One challenge with direct optical estimation of fuel moisture is that satellite and airborne platforms output reflectance data as two-dimensional coverages. In forested areas, these 2D data typically capture canopy conditions while obscuring understory characteristics (Yebra *et al.*, 2018b), which are likely to differ widely from the overstory due to compositional and physiological differences. Similarly, these data are confounded by the presence of clouds, which are transient, yet exceedingly common, in many fire-frequent areas of the world.

Acknowledgment of these challenges has led to research on the application of microwave remote sensing for direct and indirect fuel

moisture content estimation (Fan *et al.*, 2018; Wang *et al.*, 2019). Typically, LFMC is estimated using radar-derived vegetation optical depth, a proxy for vegetation water content (Moesinger *et al.*, 2020). Radar systems operate in the microwave portion of the electromagnetic spectrum and can penetrate cloud cover and the upper canopy to detect the volume of liquid water in vegetation, offering an advantage relative to optical data. Nonetheless, a problem shared by direct microwave and passive optical measurements of LFMC in forests is the discrimination of signals related to the forest canopy, understory, surface litter, and soil (Gale *et al.*, 2021). Merging microwave and optical data is a promising way forward. Rao *et al.* (2020) demonstrated that radar backscatter observations (from Sentinel-1) directly enhanced LFMC predictability in comparison with only using optical reflectance (from Landsat-8) for foliar, herbaceous and fine woody fuels. However, LFMC of denser woody fuels can only be estimated using longer wavelengths (i.e. L-band radar; Tanase *et al.*, 2015).

Despite these advances in mapping LFMC, little has been done to provide independent measures of dry mass and water content in the estimation of LFMC. To this end LMA ( $\text{g m}^{-2}$ ; also called dry matter content for remote sensing applications) and equivalent water thickness (EWT,  $\text{g m}^{-2}$ ) are appropriate target traits for optical sensing, capturing the effects of changing carbon allocation and moisture, respectively. Detection of EWT using optical sensors has a strong physical basis because water absorbs near infrared and short-wave infrared radiation (Yebra *et al.*, 2013). At the leafscale, variation in LMA has a moderate influence on reflectance in the short-wave infrared wavelengths (Feret *et al.*, 2008) given the absorption features of structural properties found in leaves (Curran, 1989). For example, estimation of morphological and structural biochemical properties, including LMA, using reflectance spectroscopy of dried leaf material has been shown to be highly effective (e.g. Serbin *et al.*, 2014). However, the presence of water in hydrated leaves can make the spectral estimation of dry matter content more challenging because water absorption masks the contribution of dry matter to the spectral response (Bowyer & Danson, 2004; Riano *et al.*, 2005). Despite these challenges, the estimation of LMA at leaf and canopy scales has been shown to have reasonable accuracy using hyperspectral instruments (Ely *et al.*, 2019; Chlus *et al.*, 2020; Kamoske *et al.*, 2021), likely due to covariance between EWT and LMA, as well as between leaf-level functional properties and plant and canopy growth form and structure (Ollinger, 2011). Radiative transfer models have also been inverted using multispectral optical data to simultaneously estimate LMA and EWT and, therefore, LFMC (Yebra *et al.*, 2013).

At smaller scales, techniques exist that allow for high-temporal resolution vegetation carbon and water inventories. For instance, novel spectroscopic approaches leveraging high-resolution spectra-trait modeling (Serbin & Townsend, 2020; Burnett *et al.*, 2021) provide the opportunity to more directly link spectral signatures with underlying physiology and plant condition (e.g. water and carbon content) in 2D (e.g. Dahlin *et al.*, 2013; Singh *et al.*, 2015) and 3D (Chlus *et al.*, 2020; Kamoske *et al.*, 2021). Likewise, dual-wavelength lidar shows promise in moisture content estimation due to its ability to distinguish forest layers through ranging (Gale *et al.*, 2021). These approaches are currently not available on space-

based platforms, limiting spatial coverage. However, these systems can be used together with ground-based systems (e.g. imaging spectroscopy) to calibrate airborne and spaceborne hyperspectral (e.g. EnMAP, Guanter *et al.*, 2016; SBG, Cawse-Nicholson *et al.*, 2021; OzFuel, ANU Institute for Space, 2021), thermal (ECOSTRESS, Anderson *et al.*, 2021), and lidar (GEDI, Rishmawi *et al.*, 2021) missions.

While current remote sensing LFMC products lack immediate predictive capability beneficial for fire management, they can be used to improve next-generation process models directly (parameterization) or indirectly (benchmarking predictions). This will lead to improved simulations of fire behavior and spread under changing climate conditions. A challenge posed by the availability of remote sensing data is ensuring integration of data from disparate sources with existing databases for fuel characteristics and LFMC. New 'big' data systems are needed for standardized fusion of data and scalable dynamic updates to fuel data in a changing environment.

## VI. Conclusions and future directions

Fire behavior and effects are intrinsically associated with plant physiology through water and carbon cycles. Integration of plant water and carbon process models with fine-scale fire models will allow for the representation of process-level feedbacks between fire behavior and effects, enabling the use of virtual experiments to explore vegetation responses to global change scenarios (increased temperature and vapor pressure deficit, change in precipitation) and resulting fire outcomes. Recent advances in remote sensing, in combination with upcoming sensor deployments, will enable high-resolution mapping of plant water and carbon status across regions and seasons, providing parameterization and benchmarking for next-generation models. Several areas are ripe for development across the disciplines of plant physiology, fire modeling, and remote sensing to fully enable these advances in understanding and simulation of vegetation–fire interactions. Furthermore, while the research presented here focuses on woody plants (trees and shrubs), additional efforts are needed to understand the interactions between climate, fire, and physiology of other vegetation types that contribute to fire regimes (Knapp, 1985; D'Antonio & Vitousek, 1992; Taylor *et al.*, 2014; Simpson *et al.*, 2016). Parallel advances on all frontiers will be critical to meet the urgency of the wildfire crisis.

With respect to fire behavior, we need to better understand the impacts of plant carbon and water on heat transfer and their interaction with fuel structure beyond the leaf scale. For fire effects, more studies are necessary to disentangle the physiological impacts of fire on tissue-level water and carbon status, along with interactions across organs to enable scaling to whole plant function and mortality (Hood *et al.*, 2018; Michaletz, 2018; Kleynhans *et al.*, 2021). We need benchmark datasets of physiological mortality mechanisms across organs, species, size class, life history, geographic region, season, and under climate change scenarios (Hood *et al.*, 2018). New terrestrial lidar approaches for evaluating fuels and fire effects that are based on structure and visual-spectrum imagery may be a useful approach for determining these

benchmarks and understanding vertical heterogeneity in fire impacts on plant organs at these scales (Gallagher *et al.*, 2021; Pokswinski *et al.*, 2021).

Fire model implementation needs to address the nonlinear biophysical-processes of whole-plant heat transfer and resulting fire behavior and effects based on dynamic physiology, including refined fire-effects predictions stemming from an improved understanding of mechanisms (Kleynhans *et al.*, 2021). Advances in machine learning can provide estimations of unknown process and enhance computational efficiency but require us to understand underlying processes and diagnose cases of overfitting. Directly computing many of these dynamics may be increasingly tractable as computation progresses. We additionally need to understand how the interaction among these dynamics affects fire and tree mortality at scales relevant to human decision-making. Using the inherent advantage of each scale of fire models, nested model design can work to incorporate new understanding at multiple scales (for example, plant physiology, stand management of plant density, landscape fire spread and suppression, and global carbon balance). Developing and validating nested model designs will be crucial to understand how each scale of organization influences the larger scale of organization.

Advancements in model implementation require finer spatial and temporal resolution observations of important processes to fire behavior and effects. Concerning remotely sensed drivers, we need to disentangle the numerous contributions to foliar reflectance signatures, along with advanced techniques for detection of subcanopy vegetation (Gale *et al.*, 2021). Improved spatial and spectral resolution will reduce uncertainty in characterization of water and carbon status across regions and seasons, and better statistical methods will make outcomes more robust across larger areas and disparate biomes (Yebra *et al.*, 2013). Advancements in data reduction and/or model ingestion will be needed to allow effective use of this higher resolution data. Ground-based experiments and observations can be used to better describe vegetation–fire interactions, and every prescribed burn provides an opportunity for data collection and model validation.

Nelson (2001) suggested that ‘the complexity of the task may have precluded all attempts to develop a reasonably complete physics- and physiology-based model’ of live fuel moisture. With an increasing wealth of drought physiology research, the advent of next-generation models, and new spaceborne sensor deployments on the horizon, we are finally poised to tackle the problem of providing a dynamic and mechanistic description of fire behavior and effects through vegetation processes. Doing so will better equip us and the ecosystems we depend on to survive and thrive in a future made uncertain by global change.

## Acknowledgements

We would like to thank three anonymous reviewers for their time and effort in providing valuable feedback which greatly improved the quality of this manuscript. We also acknowledge all participants of Los Alamos National Laboratory’s January 2021 Workshop for their contributions to this effort. LTD, AJ, RRL and SS were

supported by the Los Alamos National Laboratory (LANL) through its Center for Space and Earth Science (CSES). Center for Space and Earth Science is funded by LANL’s Laboratory Directed Research and Development (LDRD) program under project no. 20210528CR. AJ and ZJR received additional funding from LANL LDRD under project no. 20210689ECR. RPF and STM were supported by SERDP project RC18-1346 and an NSERC Discovery Grant. AB acknowledges funding from the Austrian Science Fund (FWF, project P32203) and from the University of Innsbruck (Early-Stage Funding, grant W-171705). MY receives funding from the Australian Research Council, the Australian Research Data Commons, The SmartSat Cooperative Research Centre and Singtel Optus Pty Limited. JKS was supported by the National Center for Atmospheric Research, a major facility sponsored by the National Science Foundation (NSF) under Cooperative Agreement no. 1852977, with additional support from NASA Arctic Boreal Vulnerability Experiment Grant 80NSSC19M0107. JKS, SPS and CX were also supported as part of the Next-Generation Ecosystem Experiments – Tropics, funded by the US Department of Energy, Office of Science, Office of Biological and Environmental Research. SPS was also partially supported by the NASA Surface Biology and Geology Mission Study (NNG20OB24A) and through the United States Department of Energy contract no. DE-SC0012704 to Brookhaven National Laboratory. CMH acknowledges US Department of Defense (DoD) Strategic Environmental Research and Development Program (SERDP) Project RC19-1119. IA declares support from NSF WIFIRE Commons under grants 2040676 and 2134904. VRD acknowledges funding from MICINN projects RTI2018-094691-B-C31; EU H2020 (grant agreements 101003890). RAP acknowledges support from US Department of Defense Strategic Environmental Research and Development Program’s Closing Gaps Project RC20-1025. USDA Forest Service personnel were supported by annual Forest Service appropriations. This document has been approved for unlimited release under LA-UR-22-20430.

## Competing interests

None declared.

## Author contributions

This manuscript was the outcome of a three-day workshop hosted by Los Alamos National Laboratory in January 2021. LTD, AKJ and RRL planned and designed the workshop. ADC facilitated the workshop. LTD, AKJ, ALA, MRG, JKH, CMH, SMH, ELL, WMJ, RHN, JJO, RAP, FP, JR, SPS, SS, JKS, NSS, DRW, CX and NY gave presentations at the workshop. J-LD, VRD, and MY contributed to presentations but were unable to attend. LTD, AKJ, and ADC moderated Q&A sessions. LTD, AKJ, RRL, ALA, JKH, WMJ, ELL, JJO and SPS moderated breakout sessions. LTD, AKJ, RRL, IA, ALA, ADC, MRG, JKH, CMH, SMH, MDH, WMJ, AJ, ELL, WM, STM, RHN, JJO, RAP, RP-F, FP, JR, KAS, ES-F, SPS, SS, JKS, CHS, NSS, DRW, MW, CX and NY participated in the workshop. LTD and AKJ led manuscript

development and writing. AB and ZJR were consulted for subject matter expertise on the manuscript. All authors contributed to manuscript writing and editing.

## ORCID

Ilkay Altintas  <https://orcid.org/0000-0002-2196-0305>  
 Adam L. Atchley  <https://orcid.org/0000-0003-2203-1994>  
 Andreas Bär  <https://orcid.org/0000-0002-0059-3964>  
 Adam D. Collins  <https://orcid.org/0000-0001-9554-5190>  
 L. Turin Dickman  <https://orcid.org/0000-0003-3876-7058>  
 Jean-Luc Dupuy  <https://orcid.org/0000-0002-2192-8057>  
 Michael R. Gallagher  <https://orcid.org/0000-0003-0175-558X>  
 J. Kevin Hiers  <https://orcid.org/0000-0002-6813-8941>  
 Chad M. Hoffman  <https://orcid.org/0000-0001-8715-937X>  
 Sharon M. Hood  <https://orcid.org/0000-0002-9544-8208>  
 Matthew D. Hurteau  <https://orcid.org/0000-0001-8457-8974>  
 W. Matt Jolly  <https://orcid.org/0000-0002-0457-6563>  
 Alexandra K. Jonko  <https://orcid.org/0000-0001-6026-5527>  
 Alexander Josephson  <https://orcid.org/0000-0001-7079-5302>  
 Rodman R. Linn  <https://orcid.org/0000-0002-5746-4880>  
 E. Louise Loudermilk  <https://orcid.org/0000-0001-8191-8670>  
 Wu Ma  <https://orcid.org/0000-0003-2656-339X>  
 Sean T. Michaletz  <https://orcid.org/0000-0003-2158-6525>  
 Rachael H. Nolan  <https://orcid.org/0000-0001-9277-5142>  
 Joseph J. O'Brien  <https://orcid.org/0000-0003-3446-6063>  
 Russell A. Parsons  <https://orcid.org/0000-0001-5091-8993>  
 Raquel Partelli-Feltrin  <https://orcid.org/0000-0002-5076-8515>  
 François Pimont  <https://orcid.org/0000-0002-9842-6207>  
 Víctor Resco de Dios  <https://orcid.org/0000-0002-5721-1656>  
 Joseph Restaino  <https://orcid.org/0000-0001-7923-638X>  
 Zachary J. Robbins  <https://orcid.org/0000-0001-5839-4127>  
 Karla A. Sartor  <https://orcid.org/0000-0002-0459-1990>  
 Emily Schultz-Fellenz  <https://orcid.org/0000-0002-8181-5003>  
 Shawn P. Serbin  <https://orcid.org/0000-0003-4136-8971>  
 Sanna Sevanto  <https://orcid.org/0000-0001-9127-5285>  
 Jacquelyn K. Shuman  <https://orcid.org/0000-0003-2588-2161>  
 Nicholas S. Skowronski  <https://orcid.org/0000-0002-5801-5614>  
 David R. Weise  <https://orcid.org/0000-0002-9671-7203>  
 Chonggang Xu  <https://orcid.org/0000-0002-0937-5744>  
 Marta Yebra  <https://orcid.org/0000-0002-4049-9315>  
 Nicolas Younes  <https://orcid.org/0000-0001-5331-6138>

## References

- Ackerly D. 2004. Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecological Monographs* 74: 25–44.
- Alam MA, Wyse SV, Buckley HL, Perry GLW, Sullivan JJ, Mason NWH, Buxton R, Richardson SJ, Curran TJ. 2020. Shoot flammability is decoupled from leaf flammability, but controlled by leaf functional traits. *Journal of Ecology* 108: 641–653.
- Albini FA. 1976. *Estimating wildfire behavior and effects*. General technical report, INT-30. Ogden, UT, USA: USDA Forest Service, Intermountain Forest and Range Experiment Station.
- Anderson MC, Yang Y, Xue J, Knipper KR, Yang Y, Gao F, Hain CR, Kustas WP, Cawse-Nicholson K, Hulley G *et al.* 2021. Interoperability of ECOSTRESS and Landsat for mapping evapotranspiration time series at sub-field scales. *Remote Sensing of Environment* 252: 112189.
- Andrews PL. 2013. Current status and future needs of the BehavePlus Fire Modeling System. *International Journal of Wildland Fire* 23: 21–33.
- ANU Institute for Space. 2021. *OzFuel pre-phase A study: Australian forest fuel monitoring from space*. [WWW document] URL [inspace.anu.edu.au/activity/missions/ozfuel](https://inspace.anu.edu.au/activity/missions/ozfuel) [accessed 13 January 2022].
- Atchley AL, Linn R, Jonko A, Hoffman C, Hyman JD, Pimont F, Sieg C, Middleton RS. 2021. Effects of fuel spatial distribution on wildland fire behaviour. *International Journal of Wildland Fire* 30: 179.
- Baffoin R, Charrier G, Bouchardon A-E, Bonhomme M, Améglio T, Lacoïnte A. 2021. Seasonal changes in carbohydrates and water content predict dynamics of frost hardiness in various temperate tree species. *Tree Physiology* 41: 1583–1600.
- Balaguer-Romano R, Díaz-Sierra R, Madrigal J, Voltas J, Resco de Dios V. 2020. Needle senescence affects fire behavior in Aleppo Pine (*Pinus halepensis* Mill.) stands: a simulation study. *Forests* 11: 1054.
- Banerjee T, Heilman W, Goodrick S, Hiers JK, Linn R. 2020. Effects of canopy midstory management and fuel moisture on wildfire behavior. *Scientific Reports* 10: 17312.
- Bär A, Michaletz ST, Mayr S. 2019. Fire effects on tree physiology. *New Phytologist* 223: 1728–1741.
- Bär A, Nardini A, Mayr S. 2018. Post-fire effects in xylem hydraulics of *Picea abies*, *Pinus sylvestris* and *Fagus sylvatica*. *New Phytologist* 217: 1484–1493.
- Bär A, Schröter DM, Mayr S. 2021. When the heat is on: high temperature resistance of buds from European tree species. *Plant, Cell & Environment* 44: 2593–2603.
- Barker Plotkin A, Blumstein M, Lafflower D, Pasquarella VJ, Chandler JL, Elkinton JS, Thompson JR. 2021. Defoliated trees die below a critical threshold of stored carbon. *Functional Ecology* 35: 2156–2167.
- Berenguer E, Lennox GD, Ferreira J, Malhi Y, Aragão LEOC, Barreto JR, Del Bon Espírito-Santo F, Figueiredo AES, França F, Gardner TA *et al.* 2021. Tracking the impacts of El Niño drought and fire in human-modified Amazonian forests. *Proceedings of the National Academy of Sciences, USA* 118: e2019377118.
- Bianchi LO, Oddi FJ, Muñoz M, Defossé GE. 2019. Comparison of leaf moisture content and ignition characteristics among native species and exotic conifers in northwestern Patagonia, Argentina. *Forest Science* 65: 375–386.
- Boardman CR, Diatenberger MA, Weise DR. 2021. Specific heat capacity of wildland foliar fuels to 434°C. *Fuel* 292: 120396.
- Bond WJ. 2021. Out of the shadows: ecology of open ecosystems. *Plant Ecology & Diversity* 14: 205–222.
- Bond WJ, Keeley JE. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution* 20: 387–394.
- Bond WJ, van Wilgen BW. 1996. *Fire and plants*. London, UK: Chapman & Hall.
- Bowman DMJS, Balch JK, Artaxo P, Bond WJ, Carlson JM, Cochrane MA, D'Antonio CM, DeFries RS, Doyle JC, Harrison SP *et al.* 2009. Fire in the Earth system. *Science* 324: 481–484.
- Bowman WD, Roberts SW. 1985. Seasonal and diurnal water relations adjustments in three evergreen chaparral shrubs. *Ecology* 66: 738–742.
- Bowyer P, Danson FM. 2004. Sensitivity of spectral reflectance to variation in live fuel moisture content at leaf and canopy level. *Remote Sensing of Environment* 92: 297–308.
- Burnett AC, Anderson J, Davidson KJ, Ely KS, Lamour J, Li Q, Morrison BD, Yang D, Rogers A, Serbin SP. 2021. A best-practice guide to predicting plant traits from leaf-level hyperspectral data using partial least squares regression. *Journal of Experimental Botany* 72: 6175–6189.
- Butler BW, Dickinson MB. 2010. Tree injury and mortality in fires: developing process-based models. *Fire Ecology* 6: 55–79.
- Byram GM. 1959. Combustion of forest fuels. In: Davis KP, ed. *Forest fire: control and use*. New York, NY, USA: McGraw-Hill, 61–89.
- Cawse-Nicholson K, Townsend PA, Schimel D, Assiri AM, Blake PL, Buongiorno MF, Campbell P, Carmon N, Casey KA, Correa-Pabón RE *et al.* 2021. NASA's surface biology and geology designated observable: a perspective on surface imaging algorithms. *Remote Sensing of Environment* 257: 112349.



- Chapin FSI, Schulze E-D, Mooney HA. 1990. The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics* 2: 423–447.
- Chatziefstratiou EK, Bohrer G, Bova AS, Subramanian R, Frasson RPM, Scherzer A, Butler BW, Dickinson MB. 2013. FireStem2D – a two-dimensional heat transfer model for simulating tree stem injury in fires. *PLoS ONE* 8: e70110.
- Chlus A, Kruger EL, Townsend PA. 2020. Mapping three-dimensional variation in leaf mass per area with imaging spectroscopy and lidar in a temperate broadleaf forest. *Remote Sensing of Environment* 250: 112043.
- Christoffersen BO, Gloor M, Fauset S, Fyllas NM, Galbraith DR, Baker TR, Kruijt B, Rowland L, Fisher RA, Binks OJ *et al.* 2016. Linking hydraulic traits to tropical forest function in a size-structured and trait-driven model (TFS v.1-Hydro). *Geoscientific Model Development* 9: 4227–4255.
- Cochard H, Pimont F, Ruffault J, Martin-StPaul N. 2021. SURÉAU: a mechanistic model of plant water relations under extreme drought. *Annals of Forest Science* 78: 55.
- Countryman CM. 1966. The concept of the fire environment. *Fire Control Notes* 27: 8–10.
- Cruz MG, Alexander ME, Fernandes PM. 2022. Evidence for lack of a fuel effect on forest and shrubland fire rates of spread under elevated fire danger conditions: implications for modelling and management. *International Journal of Wildland Fire* 31: 471–479.
- Cruz MG, Gould JS, Kidnie S, Bessell R, Nichols D, Slijepcevic A, Cruz MG, Gould JS, Kidnie S, Bessell R *et al.* 2015. Effects of curing on grassfires: II. Effect of grass senescence on the rate of fire spread. *International Journal of Wildland Fire* 24: 838–848.
- Curran PJ. 1989. Remote sensing of foliar chemistry. *Remote Sensing of Environment* 30: 271–278.
- Dahlin KM, Asner GP, Field CB. 2013. Environmental and community controls on plant canopy chemistry in a Mediterranean-type ecosystem. *Proceedings of the National Academy of Sciences, USA* 110: 6895–6900.
- D'Antonio CM, Vitousek PM. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23: 63–87.
- Davis SD, Mooney HA. 1986. Water use patterns of four co-occurring chaparral shrubs. *Oecologia* 7: 172–177.
- Deeming JE, Cohen JD, Burgan RE. 1977. *The National fire-danger rating system – 1978*. General technical report, INT-GTR-39. Ogden, UT, USA: US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station.
- Dennison PE, Moritz MA. 2009. Critical live fuel moisture in chaparral ecosystems: a threshold for fire activity and its relationship to antecedent precipitation. *International Journal of Wildland Fire* 18: 1021–1027.
- Dietenberger MA, Boardman CR, Shotorban B, Mell W, Weise DR. 2020. Thermal degradation modeling of live vegetation for fire dynamic simulator. In: *Proceedings, 2020 Spring technical meeting, Central States Section of the Combustion Institute*, 1–20.
- Ely KS, Burnett AC, Lieberman-Cribbin W, Serbin SP, Rogers A. 2019. Spectroscopy can predict key leaf traits associated with source–sink balance and carbon–nitrogen status. *Journal of Experimental Botany* 70: 1789–1799.
- Fan L, Wigneron J-P, Xiao Q, Al-Yaari A, Wen J, Martin-StPaul N, Dupuy J-L, Pimont F, Al Bitar A, Fernandez-Moran R *et al.* 2018. Evaluation of microwave remote sensing for monitoring live fuel moisture content in the Mediterranean region. *Remote Sensing of Environment* 205: 210–223.
- Feret J-B, François C, Asner GP, Gitelson AA, Martin RE, Bidet LPR, Ustin SL, le Maire G, Jacquemoud S. 2008. PROSPECT-4 and 5: advances in the leaf optical properties model separating photosynthetic pigments. *Remote Sensing of Environment* 112: 3030–3043.
- Fettig CJ, Runyon JB, Homicz CS, James PMA, Ulyshen MD. 2022. Fire and insect interactions in North American forests. *Current Forestry Reports* 8: 301–316.
- Finney MA. 1998. *FARSITE: fire area simulator-model development and evaluation*. Res. Pap. RMRS-RP-4, Revised 2004. Ogden, UT, USA: US Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Finnigan J. 2000. Turbulence in plant canopies. *Annual Review of Fluid Mechanics* 32: 519–571.
- Fletcher TH, Pickett BM, Smith SG, Spittle GS, Woodhouse MM, Haake E, Weise DR. 2007. Effects of moisture on ignition behavior of moist California chaparral and Utah leaves. *Combustion Science and Technology* 179: 1183–1203.
- Franco AC, Rossatto DR, de Carvalho Ramos Silva L, da Silva Ferreira C. 2014. Cerrado vegetation and global change: the role of functional types, resource availability and disturbance in regulating plant community responses to rising CO<sub>2</sub> levels and climate warming. *Theoretical and Experimental Plant Physiology* 26: 19–38.
- Furniss TJ, Hessburg PF, Povak NA, Salter RB, Wigmosta MS. 2022. Predicting future patterns, processes, and their interactions: benchmark calibration and validation procedures for forest landscape models. *Ecological Modelling* 473: 110099.
- Gale MG, Cary GJ, Van Dijk AIJM, Yebra M. 2021. Forest fire fuel through the lens of remote sensing: review of approaches, challenges and future directions in the remote sensing of biotic determinants of fire behaviour. *Remote Sensing of Environment* 255: 112282.
- Gallagher MR, Maxwell AE, Guillén LA, Everland A, Loudermilk EL, Skowronski NS. 2021. Estimation of plot-level burn severity using terrestrial laser scanning. *Remote Sensing* 13: 4168.
- Gettelman A, Geer AJ, Forbes RM, Carmichael GR, Feingold G, Posselt DJ, Stephens GL, van den Heever SC, Varble AC, Zuidema P. 2022. The future of Earth system prediction: advances in model-data fusion. *Science Advances* 8: eabn3488.
- Giglio L, Randerson JT, van der Werf GR. 2013. Analysis of daily, monthly, and annual burned area using the fourth-generation global fire emissions database (GFED4). *Journal of Geophysical Research: Biogeosciences* 118: 317–328.
- Grootemaat S, Wright IJ, van Bodegom PM, Cornelissen JHC, Cornwell WK. 2015. Burn or rot: leaf traits explain why flammability and decomposability are decoupled across species. *Functional Ecology* 29: 1486–1497.
- Grossiord C, Buckley TN, Cernusak LA, Novick KA, Poulter B, Siegwolf RTW, Sperry JS, McDowell NG. 2020. Plant responses to rising vapor pressure deficit. *New Phytologist* 226: 1550–1566.
- Guanter L, Kaufmann H, Foerster S, Brotsky A, Wulf H, Bochow M, Boesche N, Brell M, Buddenbaum H, Chabrillat S *et al.* 2016. *EnMAP science plan*. Potsdam, Germany: GFZ Data Services.
- Hammond WM, Yu K, Wilson LA, Will RE, Anderegg WRL, Adams HD. 2019. Dead or dying? Quantifying the point of no return from hydraulic failure in drought-induced tree mortality. *New Phytologist* 223: 1834–1843.
- Hiers JK, O'Brien JJ, Varner JM, Butler BW, Dickinson M, Furman J, Gallagher M, Godwin D, Goodrick SL, Hood SM *et al.* 2020. Prescribed fire science: the case for a refined research agenda. *Fire Ecology* 16: 11.
- Hoffman CM, Sieg CH, Linn RR, Mell W, Parsons RA, Ziegler JP, Hiers JK. 2018. Advancing the science of wildland fire dynamics using process-based models. *Fire* 1: 32.
- Hood SM. 2021. Physiological responses to fire that drive tree mortality. *Plant, Cell & Environment* 44: 692–695.
- Hood SM, Varner JM, van Mantgem P, Cansler CA. 2018. Fire and tree death: understanding and improving modeling of fire-induced tree mortality. *Environmental Research Letters* 13: 113004.
- Hough WA, Albini FA. 1978. *Predicting fire behavior in palmetto-gallberry fuel complexes*. Research paper SE-RP-174. Asheville, NC, USA: USDA Forest Service, Southeastern Forest Experiment Station, 48 p.
- Huang M, Ray J, Hou Z, Ren H, Liu Y, Swiler L. 2016. On the applicability of surrogate-based Markov chain Monte Carlo-Bayesian inversion to the Community Land Model: case studies at flux tower sites. *Journal of Geophysical Research: Atmospheres* 121: 7548–7563.
- Ibanez T, Platt WJ, Bellingham PJ, Vieilledent G, Franklin J, Martin PH, Menkes C, Pérez-Saliciup DR, Russell-Smith J, Keppel G. 2022. Altered cyclone–fire interactions are changing ecosystems. *Trends in Plant Science* 27: 1218–1230.
- Jolly WM. 2007. Sensitivity of a surface fire spread model and associated fire behaviour fuel models to changes in live fuel moisture. *International Journal of Wildland Fire* 16: 503–509.
- Jolly WM, Hadlow AM, Huguet K, Jolly WM, Hadlow AM, Huguet K. 2014. De-coupling seasonal changes in water content and dry matter to predict live conifer foliar moisture content. *International Journal of Wildland Fire* 23: 480–489.
- Jolly WM, Hintz J, Linn RL, Kropp RC, Conrad ET, Parsons RA, Winterkamp J. 2016. Seasonal variations in red pine (*Pinus resinosa*) and jack pine (*Pinus banksiana*) foliar physio-chemistry and their potential influence on stand-scale wildland fire behavior. *Forest Ecology and Management* 373: 167–178.

- Jolly WM, Johnson DM. 2018. Pyro-ecophysiology: shifting the paradigm of live wildland fuel research. *Fire* 1: 8.
- Kamoske AG, Dahlin KM, Serbin SP, Stark SC. 2021. Leaf traits and canopy structure together explain canopy functional diversity: an airborne remote sensing approach. *Ecological Applications* 31: e02230.
- Karavani A, Boer MM, Baudena M, Colinas C, Díaz-Sierra R, Pemán J, de Luis M, Enríquez-de-Salamanca Á, Resco de Dios V. 2018. Fire-induced deforestation in drought-prone Mediterranean forests: drivers and unknowns from leaves to communities. *Ecological Monographs* 88: 141–169.
- Karp AT, Faith JT, Marlon JR, Staver AC. 2021. Global response of fire activity to late Quaternary grazer extinctions. *Science* 374: 1145–1148.
- Keane RE, Cary GJ, Davies ID, Flannigan MD, Gardner RH, Lavorel S, Lenihan JM, Li C, Rupp TS. 2004. A classification of landscape fire succession models: spatial simulations of fire and vegetation dynamics. *Ecological Modelling* 179: 3–27.
- Keane RE, Loehman RA, Holsinger LM. 2011. *The FIREBGCv2 landscape fire and succession model: a research simulation platform for exploring fire and vegetation dynamics*. Gen. Tech. Rep. RMRS-GTR-255. Fort Collins, CO, USA: US Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Keeley JE. 1998. Coupling demography, physiology and evolution in chaparral shrubs. In: Rundel PW, Montenegro G, Jaksic FM, eds. *Ecological studies. Landscape disturbance and biodiversity in Mediterranean-type ecosystems*. Berlin, Heidelberg, Germany: Springer, 257–264.
- Kilzer FJ, Broido A. 1965. Speculations on the nature of cellulose pyrolysis. *Pyrodynamics* 2: 151–163.
- Kleynhans EJ, Atchley AL, Michaletz ST. 2021. Chapter Eleven – Modeling fire effects on plants: from organs to ecosystems. In: Johnson EA, Miyanishi K, eds. *Plant disturbance ecology, 2<sup>nd</sup> edn*. San Diego, CA, USA: Academic Press, 383–421.
- Knapp AK. 1985. Effect of fire and drought on the ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie. *Ecology* 66: 1309–1320.
- Knapp AK, Fahnestock JT, Hamburg SP, Statland LB, Seastedt TR, Schimel DS. 1993. Landscape patterns in soil–plant water relations and primary production in tallgrass prairie. *Ecology* 74: 549–560.
- Knapp EE, Estes BL, Skinner CN. 2009. *Ecological effects of prescribed fire season: a literature review and synthesis for managers*. Gen. Tech. Rep. PSW-GTR-224. Albany, CA, USA: US Department of Agriculture, Forest Service, Pacific Southwest Research Station.
- Krawchuk MA, Haire SL, Coop J, Parisien M-A, Whitman E, Chong G, Miller C. 2016. Topographic and fire weather controls of fire refugia in forested ecosystems of northwestern North America. *Ecosphere* 7: e01632.
- Lee EH, Beedlow PA, Brooks JR, Tingey DT, Wickham C, Rugh W. 2022. Physiological responses of Douglas-fir to climate and forest disturbances as detected by cellulose carbon and oxygen isotope ratios. *Tree Physiology* 42: 5–25.
- Li F, Lawrence DM. 2017. Role of fire in the global land water budget during the twentieth century due to changing ecosystems. *Journal of Climate* 30: 1893–1908.
- Linn R, Reiser J, Colman J, Winterkamp J. 2002. Studying wildfire behavior using FIRETEC. *International Journal of Wildland Fire* 11: 233–246.
- Louarn G, Song Y. 2020. Two decades of functional–structural plant modelling: now addressing fundamental questions in systems biology and predictive ecology. *Annals of Botany* 126: 501–509.
- Lu D, Ricciuto D. 2019. Efficient surrogate modeling methods for large-scale Earth system models based on machine-learning techniques. *Geoscientific Model Development* 12: 1791–1807.
- Ma W, Zhai L, Pivovarov A, Shuman J, Buotte P, Ding J, Christoffersen B, Knox R, Moritz M, Fisher RA *et al.* 2021. Assessing climate change impacts on live fuel moisture and wildfire risk using a hydrodynamic vegetation model. *Biogeosciences* 18: 4005–4020.
- Macías Fauria M, Michaletz ST, Johnson EA. 2011. Predicting climate change effects on wildfires requires linking processes across scales. *WIREs Climate Change* 2: 99–112.
- de Magalhães RMQ, Schwilk DW. 2012. Leaf traits and litter flammability: evidence for non-additive mixture effects in a temperate forest. *Journal of Ecology* 100: 1153–1163.
- de Magalhães RQ, Schwilk DW. 2021. Moisture absorption and drying alter nonadditive litter flammability in a mixed conifer forest. *Journal of Ecology* 109: 234–245.
- van Mantgem PJ, Falk DA, Williams EC, Das AJ, Stephenson NL. 2018. Pre-fire drought and competition mediate post-fire conifer mortality in western U.S. National Parks. *Ecological Applications* 28: 1730–1739.
- Marino E, Yebra M, Guillén-Climent M, Algeet N, Tomé JL, Madrigal J, Guijarro M, Hernando C. 2020. Investigating live fuel moisture content estimation in fire-prone shrubland from remote sensing using empirical modelling and RTM simulations. *Remote Sensing* 12: 2251.
- Martínez-Vilalta J, Sala A, Asensio D, Galiano L, Hoch G, Palacio S, Piper FI, Lloret F. 2016. Dynamics of non-structural carbohydrates in terrestrial plants: a global synthesis. *Ecological Monographs* 86: 495–516.
- Martin-StPaul N, Ruffault J, Pimont F, Dupuy J-L. 2018. Live fuel moisture content: variability, predictability and impact on fire behavior and activity. In: Viegas DX, ed. *Advances in forest fire research*. Coimbra, Portugal: Imprensa da Universidade de Coimbra, 246–253.
- Matt FJ, Dietsberger MA, Weise DR. 2020. Summative and ultimate analysis of live leaves from Southern U.S. forest plants for use in fire modeling. *Energy & Fuels* 34: 4703–4720.
- McAllister S, Weise DR. 2017. Effects of season on ignition of live wildland fuels using the forced ignition and flame spread test apparatus. *Combustion Science and Technology* 189: 231–247.
- Mell W, Maranghides A, McDermott R, Manzano SL. 2009. Numerical simulation and experiments of burning Douglas fir trees. *Combustion and Flame* 156: 2023–2041.
- Michaletz ST. 2018. Xylem dysfunction in fires: towards a hydraulic theory of plant responses to multiple disturbance stressors. *New Phytologist* 217: 1391–1393.
- Michaletz ST, Johnson EA. 2006. Foliage influences forced convection heat transfer in conifer branches and buds. *New Phytologist* 170: 87–98.
- Michaletz ST, Johnson EA. 2007. How forest fires kill trees: a review of the fundamental biophysical processes. *Scandinavian Journal of Forest Research* 22: 500–515.
- Michaletz ST, Johnson EA. 2008. A biophysical process model of tree mortality in surface fires. *Canadian Journal of Forest Research* 38: 2013–2029.
- Michaletz ST, Johnson EA, Mell WE, Greene DF. 2013. Timing of fire relative to seed development may enable non-serotinous species to recolonize from the aerial seed banks of fire-killed trees. *Biogeosciences* 10: 5061–5078.
- Michaletz ST, Johnson EA, Tyree MT. 2012. Moving beyond the cambium necrosis hypothesis of post-fire tree mortality: cavitation and deformation of xylem in forest fires. *New Phytologist* 194: 254–263.
- Midgley JJ, Kruger LM, Skelton R. 2011. How do fires kill plants? The hydraulic death hypothesis and Cape Proteaceae ‘fire-resisters’. *South African Journal of Botany* 77: 381–386.
- Milla R, Palacio S, Maestro-Martínez M, Montserrat-Martí G. 2007. Leaf exchange in a Mediterranean shrub: water, nutrient, non-structural carbohydrate and osmolyte dynamics. *Tree Physiology* 27: 951–960.
- Mitchell SR, Harmon ME, O’Connell KEB. 2009. Forest fuel reduction alters fire severity and long-term carbon storage in three Pacific Northwest ecosystems. *Ecological Applications* 19: 643–655.
- Moesinger L, Dorigo W, de Jeu R, van der Schalie R, Scanlon T, Teubner I, Forkel M. 2020. The global long-term microwave vegetation optical depth climate archive (VODCA). *Earth System Science Data* 12: 177–196.
- Neilson RP, Pitelka LF, Solomon AM, Nathan R, Midgley GF, Fragoso JMV, Lischke H, Thompson K. 2005. Forecasting regional to global plant migration in response to climate change. *Bioscience* 55: 749–759.
- Nelson RM. 2001. Chapter 4 – Water relations of forest fuels. In: Johnson EA, Miyanishi K, eds. *Forest fires*. San Diego, CA, USA: Academic Press, 79–149.
- Nolan RH, Blackman CJ, de Dios VR, Choat B, Medlyn BE, Li X, Bradstock RA, Boer MM. 2020. Linking forest flammability and plant vulnerability to drought. *Forests* 11: 779.
- Nolan RH, Boer MM, Resco de Dios V, Caccamo G, Bradstock RA. 2016. Large-scale, dynamic transformations in fuel moisture drive wildfire activity across southeastern Australia. *Geophysical Research Letters* 43: 4229–4238.
- Nolan RH, Collins L, Leigh A, Ooi MKJ, Curran TJ, Fairman TA, Resco de Dios V, Bradstock R. 2021. Limits to post-fire vegetation recovery under climate change. *Plant, Cell & Environment* 44: 3471–3489.
- Nolan RH, Hedo J, Arteaga C, Sugai T, Resco de Dios V. 2018. Physiological drought responses improve predictions of live fuel moisture dynamics in a Mediterranean forest. *Agricultural and Forest Meteorology* 263: 417–427.

- O'Brien JJ, Hiers JK, Varner JM, Hoffman CM, Dickinson MB, Michaletz ST, Loudermilk EL, Butler BW. 2018. Advances in mechanistic approaches to quantifying biophysical fire effects. *Current Forestry Reports* 4: 161–177.
- O'Brien JJ, Kevin Hiers J, Mitchell RJ, Varner JM, Mordecai K. 2010. Acute physiological stress and mortality following fire in a long-unburned longleaf pine ecosystem. *Fire Ecology* 6: 1–12.
- O'Brien JJ, Loudermilk EL, Hiers JK, Pokswinski SM, Hornsby B, Hudak AT, Strother D, Rowell E, Bright BC. 2016. Canopy-derived fuels drive patterns of in-fire energy release and understory plant mortality in a longleaf pine (*Pinus palustris*) sandhill in Northwest Florida, USA. *Canadian Journal of Remote Sensing* 42: 489–500.
- Ollinger SV. 2011. Sources of variability in canopy reflectance and the convergent properties of plants. *New Phytologist* 189: 375–394.
- Parsons RA, Mell WE, McCauley P. 2011. Linking 3D spatial models of fuels and fire: effects of spatial heterogeneity on fire behavior. *Ecological Modelling* 222: 679–691.
- Parsons RA, Pimont F, Wells L, Cohn G, Jolly WM, de Coligny F, Rigolot E, Dupuy J-L, Mell W, Linn RR. 2018. Modeling thinning effects on fire behavior with STANDFIRE. *Annals of Forest Science* 75: 7.
- Parsons RA, Wells L, Linn R, Hiers K, Marcozzi A, Rosales D. 2020. *FASTFUELS: 3D fuels for next generation fire models*. Missoula Fire Sciences Laboratory, MT, USA. [WWW document] URL <https://www.firelab.org/project/fastfuels-3d-fuels-next-generation-fire-models> [accessed 16 January 2022].
- Partelli-Feltrin R, Johnson DM, Sparks AM, Adams HD, Kolden CA, Nelson AS, Smith AMS. 2020. Drought increases vulnerability of *Pinus ponderosa* saplings to fire-induced mortality. *Fire* 3: 56.
- Partelli-Feltrin R, Smith AMS, Adams HD, Kolden CA, Johnson DM. 2021. Short- and long-term effects of fire on stem hydraulics in *Pinus ponderosa* saplings. *Plant, Cell & Environment* 44: 696–705.
- Pausas JG, Moreira B. 2012. Flammability as a biological concept. *New Phytologist* 194: 610–613.
- Pimont F, Parsons R, Rigolot E, de Coligny F, Dupuy J-L, Dreyfus P, Linn RR. 2016. Modeling fuels and fire effects in 3D: model description and applications. *Environmental Modelling & Software* 80: 225–244.
- Pimont F, Ruffault J, Martin-StPaul NK, Dupuy J-L, Pimont F, Ruffault J, Martin-StPaul NK, Dupuy J-L. 2019a. Why is the effect of live fuel moisture content on fire rate of spread underestimated in field experiments in shrublands? *International Journal of Wildland Fire* 28: 127–137.
- Pimont F, Ruffault J, Martin-StPaul NK, Dupuy J-L, Pimont F, Ruffault J, Martin-StPaul NK, Dupuy J-L. 2019b. A cautionary note regarding the use of cumulative burnt areas for the determination of fire danger index breakpoints. *International Journal of Wildland Fire* 28: 254–258.
- Pokswinski S, Gallagher MR, Skowronski NS, Loudermilk EL, Hawley C, Wallace D, Everland A, Wallace J, Hiers JK. 2021. A simplified and affordable approach to forest monitoring using single terrestrial laser scans and transect sampling. *MethodsX* 8: 101484.
- Poorter H, Niinemets Ü, Poorter L, Wright IJ, Villar R. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist* 182: 565–588.
- Pratt RB, Jacobsen A, Jacobs S, Esler K. 2012. Xylem transport safety and efficiency differ among fynbos shrub life history types and between two sites differing in mean rainfall. *International Journal of Plant Sciences* 173: 474–483.
- Pratt RB, Jacobsen AL, Ramirez AR, Helms AM, Traugh CA, Tobin MF, Heffner MS, Davis SD. 2014. Mortality of resprouting chaparral shrubs after a fire and during a record drought: physiological mechanisms and demographic consequences. *Global Change Biology* 20: 893–907.
- Quan X, Yebra M, Riaño D, He B, Lai G, Liu X. 2021. Global fuel moisture content mapping from MODIS. *International Journal of Applied Earth Observation and Geoinformation* 101: 102354.
- Quintiere JG. 2006. *Fundamentals of fire phenomena*. Chichester, UK: Wiley.
- Rabin SS, Melton JR, Lasslop G, Bachelet D, Forrest M, Hantson S, Kaplan JO, Li F, Manganon S, Ward DS *et al.* 2017. The Fire Modeling Intercomparison Project (FireMIP), phase 1: Experimental and analytical protocols with detailed model descriptions. *Geoscientific Model Development* 10: 1175–1197.
- Rambal S. 1993. The differential role of mechanisms for drought resistance in a Mediterranean evergreen shrub: a simulation approach. *Plant, Cell & Environment* 16: 35–44.
- Rao K, Williams AP, Diffenbaugh NS, Yebra M, Konings AG. 2022. Plant–water sensitivity regulates wildfire vulnerability. *Nature Ecology & Evolution* 6: 332–339.
- Rao K, Williams AP, Flefil JF, Konings AG. 2020. SAR-enhanced mapping of live fuel moisture content. *Remote Sensing of Environment* 245: 111797.
- Reinhardt E, Crookston NL. 2003. *The fire and fuels extension to the forest vegetation simulator*. Gen. Tech. Rep. RMRS-GTR-116. Ogden, UT, USA: US Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Resco de Dios V. 2020. *Plant–fire interactions: applying ecophysiology to wildfire management*. Cham, Switzerland: Springer.
- Resco de Dios V, Arteaga C, Hedo J, Gil-Pelegrín E, Voltas J. 2018. A trade-off between embolism resistance and bark thickness in conifers: are drought and fire adaptations antagonistic? *Plant Ecology & Diversity* 11: 253–258.
- Resco de Dios V, Arteaga C, Peguero-Pina JJ, Sancho-Knapik D, Qin H, Zveusch OK, Sun W, Williams DG, Boer MM, Voltas J *et al.* 2020. Hydraulic and photosynthetic limitations prevail over root non-structural carbohydrate reserves as drivers of resprouting in two Mediterranean oaks. *Plant, Cell & Environment* 43: 1944–1957.
- Resco de Dios V, Hedo J, Cunill Camprubí À, Thapa P, Martínez del Castillo E, Martínez de Aragón J, Bonet JA, Balaguer-Romano R, Díaz-Sierra R, Yebra M *et al.* 2021. Climate change induced declines in fuel moisture may turn currently fire-free Pyrenean mountain forests into fire-prone ecosystems. *Science of the Total Environment* 797: 149104.
- Riano D, Vaughan P, Chuvieco E, Zarco-Tejada PJ, Ustin SL. 2005. Estimation of fuel moisture content by inversion of radiative transfer models to simulate equivalent water thickness and dry matter content: analysis at leaf and canopy level. *IEEE Transactions on Geoscience and Remote Sensing* 43: 819–826.
- Rishmawi K, Huang C, Zhan X. 2021. Monitoring key forest structure attributes across the conterminous United States by integrating GEDI LiDAR measurements and VIIRS data. *Remote Sensing* 13: 442.
- Rohatgi A. 2021. WebPlotDigitizer, Pacifica, CA, USA, v.4.5. [WWW document] URL <https://automeris.io/WebPlotDigitizer> [accessed 29 August 2021].
- Rothermel RC. 1972. *A mathematical model for predicting fire spread in wildland fuels*. Res. Pap. INT-115. Ogden, UT, USA: US Department of Agriculture, Intermountain Forest and Range Experiment Station.
- Rothermel RC, Philpot CW. 1973. Predicting changes in chaparral flammability. *Journal of Forestry* 71: 640–643.
- Rouet-Leduc J, Pe'er G, Moreira F, Bonn A, Helmer W, Shahsavani Zadeh SAA, Zizka A, van der Plas F. 2021. Effects of large herbivores on fire regimes and wildfire mitigation. *Journal of Applied Ecology* 58: 2690–2702.
- Ruckman EM, Schwinning S, Lyons KG. 2012. Effects of phenology at burn time on post-fire recovery in an invasive *C<sub>4</sub>* grass. *Restoration Ecology* 20: 756–763.
- Ruffault J, Limousin J-M, Pimont F, Dupuy J-L, De Cáceres M, Cochard H, Mouillot F, Blackman CJ, Torres-Ruiz JM, Parsons RA *et al.* 2022a. Plant hydraulic modelling of leaf and canopy fuel moisture content reveals increasing vulnerability of a Mediterranean forest to wildfires under extreme drought. *New Phytologist* 237: 1256–1269.
- Ruffault J, Martin-StPaul N, Pimont F, Dupuy J-L. 2018. How well do meteorological drought indices predict live fuel moisture content (LFMC)? An assessment for wildfire research and operations in Mediterranean ecosystems. *Agricultural and Forest Meteorology* 262: 391–401.
- Ruffault J, Pimont F, Cochard H, Dupuy J-L, Martin-StPaul N. 2022b. SUR-EAU-ECOS v.2.0: a trait-based plant hydraulics model for simulations of plant water status and drought-induced mortality at the ecosystem level. *Geoscientific Model Development* 15: 5593–5626.
- Ruswick SK, O'Brien JJ, Aubrey DP. 2021. Carbon starvation is absent regardless of season of burn in *Liquidambar styraciflua* L. *Forest Ecology and Management* 479: 118588.
- Sánchez-Costa E, Poyatos R, Sabaté S. 2015. Contrasting growth and water use strategies in four co-occurring Mediterranean tree species revealed by concurrent measurements of sap flow and stem diameter variations. *Agricultural and Forest Meteorology* 207: 24–37.
- Sayer MAS, Tyree MC, Kuehler EA, Jackson JK, Dillaway DN. 2020. Physiological mechanisms of foliage recovery after spring or fall crown scorch in young longleaf pine (*Pinus palustris* Mill.). *Forests* 11: 208.

- Scarff FR, Lenz T, Richards AE, Zanne AE, Wright IJ, Westoby M. 2021. Effects of plant hydraulic traits on the flammability of live fine canopy fuels. *Functional Ecology* 35: 835–846.
- Scheller RM, Kretchun A, Hawbaker T, Henne PD. 2019. A landscape model of variable social-ecological fire regimes. *Ecological Modelling* 401: 8593.
- Scott JH, Burgan RE. 2005. *Standard fire behavior fuel models: a comprehensive set for use with Rothermel's surface fire spread model*. Gen. Tech. Rep. RMRS-GTR-153. Fort Collins, CO, USA: US Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Serbin SP, Singh A, McNeil BE, Kingdon CC, Townsend PA. 2014. Spectroscopic determination of leaf morphological and biochemical traits for northern temperate and boreal tree species. *Ecological Applications* 24: 1651–1669.
- Serbin SP, Townsend PA. 2020. Scaling functional traits from leaves to canopies. In: Cavender-Bares J, Gamon JA, Townsend PA, eds. *Remote sensing of plant biodiversity*. Cham, Switzerland: Springer International, 43–82.
- Shuman JK, Balch JK, Barnes RT, Higuera PE, Roos CI, Schwilk DW, Stavros EN, Banerjee T, Bela MM, Bendix J *et al.* 2022. Reimagine fire science for the anthropocene. *PNAS Nexus* 1: pgac115.
- Sieg CH, Linn RR, Pimont F, Hoffman CM, McMillin JD, Winterkamp J, Baggett LS. 2017. Fires following bark beetles: factors controlling severity and disturbance interactions in ponderosa pine. *Fire Ecology* 13: 1–23.
- Silva CVJ, Araújo LEOC, Barlow J, Espírito-Santo F, Young PJ, Anderson LO, Berenguer E, Brasil I, Brown IF, Castro B *et al.* 2018. Drought-induced Amazonian wildfires instigate a decadal-scale disruption of forest carbon dynamics. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 373: 20180043.
- Simpson KJ, Ripley BS, Christin P-A, Belcher CM, Lehmann CER, Thomas GH, Osborne CP. 2016. Determinants of flammability in savanna grass species. *Journal of Ecology* 104: 138–148.
- Singh A, Serbin SP, McNeil BE, Kingdon CC, Townsend PA. 2015. Imaging spectroscopy algorithms for mapping canopy foliar chemical and morphological traits and their uncertainties. *Ecological Applications* 25: 2180–2197.
- Smith AMS, Talhelm AF, Johnson DM, Sparks AM, Kolden CA, Yedinak KM, Apostol KG, Tinkham WT, Abatzoglou JT, Lutz JA *et al.* 2017. Effects of fire radiative energy density dose on *Pinus contorta* and *Larix occidentalis* seedling physiology and mortality. *International Journal of Wildland Fire* 26: 82.
- Smith RE, Richardson DM. 1990. Comparative post-fire water relations of selected reseeded and resprouting fynbos plants in the Jonkershoek Valley, Cape Province, South Africa. *South African Journal of Botany* 56: 683–694.
- Soil Survey Staff. 2022. *Gridded National Soil Survey Geographic (GSTATSGO) database for the conterminous United States*. United States Department of Agriculture, Natural Resources Conservation Service. [WWW document] URL <https://nrcs.app.box.com/v/soils> [accessed 12 December 2022].
- Sparks AH, Forbes GA, Hijmans RJ, Garrett KA. 2011. A metamodeling framework for extending the application domain of process-based ecological models. *Ecosphere* 2: art90.
- Steady WD, Partelli Feltrin R, Johnson DM, Sparks AM, Kolden CA, Talhelm AF, Lutz JA, Boschetti L, Hudak AT, Nelson AS *et al.* 2019. The survival of *Pinus ponderosa* saplings subjected to increasing levels of fire behavior and impacts on post-fire growth. *Fire* 2: 23.
- Stocks BJ, Lawson BD, Alexander ME, Van Wagner CE, McAlpine RS, Lynham TJ, Dubé DE. 1989. The Canadian forest fire danger rating system: an overview. *Forestry Chronicle* 65: 450–457.
- Sturtevant B, Fortin M-J. 2021. Understanding and modeling forest disturbance interactions at the landscape level. *Frontiers in Ecology and Evolution* 9: 653647.
- Sturtevant BR, Scheller RM, Miranda BR, Shinneman D, Syphard A. 2009. Simulating dynamic and mixed-severity fire regimes: a process-based fire extension for LANDIS-II. *Ecological Modelling* 220: 3380–3393.
- Swann DEB, Bellingham PJ, Martin PH. 2022. Resilience of a tropical montane pine forest to fire and severe droughts. *Journal of Ecology* 111: 90–109.
- Tai X, Mackay DS, Anderegg WRL, Sperry JS, Brooks PD. 2017. Plant hydraulics improves and topography mediates prediction of aspen mortality in southwestern USA. *New Phytologist* 213: 113–127.
- Talluto MV, Boulangeat I, Ameztegui A, Aubin I, Berteaux D, Butler A, Doyon F, Drever CR, Fortin M-J, Franceschini T *et al.* 2016. Cross-scale integration of knowledge for predicting species ranges: a metamodeling framework. *Global Ecology and Biogeography* 25: 238–249.
- Tanase MA, Panciera R, Lowell K, Aponte C, Tanase MA, Panciera R, Lowell K, Aponte C. 2015. Monitoring live fuel moisture in semiarid environments using L-band radar data. *International Journal of Wildland Fire* 24: 560–572.
- Taylor K, Brummer T, Rew LJ, Lavin M, Maxwell BD. 2014. *Bromus tectorum* response to fire varies with climate conditions. *Ecosystems* 17: 960–973.
- Thornton PE, Thornton MM, Mayer BW, Wilhelm N, Wei Y, Devarakonda R, Cook RB. 2014. *DAYMET: daily surface weather data on a 1-km grid for North America, v.2*. Oak Ridge, TN, USA: ORNL Distributed Active Archive Center. doi: [10.3334/ORNLDAAC/1219](https://doi.org/10.3334/ORNLDAAC/1219).
- Trabaud L. 1991. Fire regimes and phytomass growth dynamics in a *Quercus coccifera* garrigue. *Journal of Vegetation Science* 2: 307–314.
- Van Wagner CE. 1973. Height of crown scorch in forest fires. *Canadian Journal of Forest Research* 3: 373–378.
- Van Wagner CE. 1977. Conditions for the start and spread of crown fire. *Canadian Journal of Forest Research* 7: 23–34.
- Varner JM, Hood SM, Doug P A, Yedinak K, Hiers JK, Jolly WM, Shearman TM, McDaniel JK, O'Brien JJ, Rowell EM. 2021. Tree crown injury from wildland fires: causes, measurement and ecological and physiological consequences. *New Phytologist* 231: 1676–1685.
- Varner JM, Putz FE, Mitchell RJ, Hiers JK, O'Brien JJ, Gordon DR. 2009. Post-fire tree stress and growth following smoldering duff fires. *Forest Ecology and Management* 258: 2467–2474.
- Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007. Let the concept of trait be functional! *Oikos* 116: 882–892.
- Vos J, Evers JB, Buck-Sorlin GH, Andrieu B, Chelle M, de Visser PHB. 2010. Functional-structural plant modelling: a new versatile tool in crop science. *Journal of Experimental Botany* 61: 2101–2115.
- de Vries J. 2021. Using evolutionary functional-structural plant modelling to understand the effect of climate change on plant communities. *in silico Plants* 3: diab029.
- Wang L, Quan X, He B, Yebra M, Xing M, Liu X. 2019. Assessment of the dual polarimetric Sentinel-1A data for forest fuel moisture content estimation. *Remote Sensing* 11: 1568.
- Weise DR, Wright CS. 2013. Wildland fire emissions, carbon and climate: characterizing wildland fuels. *Forest Ecology and Management* 317: 26–40.
- West AG, Nel JA, Bond WJ, Midgley JJ. 2016. Experimental evidence for heat plume-induced cavitation and xylem deformation as a mechanism of rapid post-fire tree mortality. *New Phytologist* 211: 828–838.
- Woolley T, Shaw DC, Ganio LM, Fitzgerald S. 2012. A review of logistic regression models used to predict post-fire tree mortality of western North American conifers. *International Journal of Wildland Fire* 21: 1–35.
- Wright HA, Bailey AW. 1982. *Fire ecology: United States and Southern Canada*. New York, NY, USA: Wiley.
- Yashwanth BL, Shotorban B, Mahalingam S, Lautenberger CW, Weise D. 2016. A numerical investigation of the influence of radiation and moisture content on pyrolysis and ignition of a leaf-like fuel element. *Combustion and Flame* 163: 301–316.
- Yebra M, Dennison PE, Chuvieco E, Riaño D, Zylstra P, Hunt ER, Danson FM, Qi Y, Jurdao S. 2013. A global review of remote sensing of live fuel moisture content for fire danger assessment: moving towards operational products. *Remote Sensing of Environment* 136: 455–468.
- Yebra M, Dijk AV, Cary G. 2018a. *Evaluation of the feasibility and benefits of operational use of alternative satellite data in the Australian Flammability Monitoring System to ensure long-term data continuity*. Bushfire & Natural Hazards CRC. [WWW document] URL [https://www.bnhrc.com.au/sites/default/files/managed/downloads/evaluation\\_fms\\_feasibility.pdf](https://www.bnhrc.com.au/sites/default/files/managed/downloads/evaluation_fms_feasibility.pdf) [accessed 16 January 2022].
- Yebra M, Quan X, Riaño D, Rozas Larraondo P, van Dijk AIJM, Cary GJ. 2018b. A fuel moisture content and flammability monitoring methodology for continental Australia based on optical remote sensing. *Remote Sensing of Environment* 212: 260–272.
- Zhou X-R, Schnepf A, Vanderborcht J, Leitner D, Lacoite A, Vereecken H, Lobet G. 2020. CPlantBox, a whole-plant modelling framework for the simulation of water- and carbon-related processes. *in silico Plants* 2: diaa001.
- Zhu W-Z, Xiang J-S, Wang S-G, Li M-H. 2012. Resprouting ability and mobile carbohydrate reserves in an oak shrubland decline with increasing elevation on the eastern edge of the Qinghai-Tibet Plateau. *Forest Ecology and Management* 278: 118–126.
- Zylstra P. 2021. Linking fire behaviour and its ecological effects to plant traits, using FRAME in R. *Methods in Ecology and Evolution* 12: 1365–1378.