Received: 15 October 2024 | Accepted: 7 February 2025

DOI: 10.1002/ajb2.70040

American Journal of Botany

SPECIAL ISSUE ARTICLE

From plant traits to fire behavior: Scaling issues in flammability studies

Dylan W. Schwilk[1] | Md. Azharul Alam[2] | Nathan Gill[3] | Brad R. Murray[4] | Rachael H. Nolan[5] | Stefania Ondei[6] | George L. W. Perry[7] | Alistair M. S. Smith[8] | David M. J. S. Bowman[6] | Alessandra Fidelis[9] | Pedro Jaureguiberry[10] | Imma Oliveras Menor[11,12] | Bruno H. P. Rosado[13] | Helena Roland[14] | Marta Yebra[15] | Stephanie G. Yelenik[16] | Timothy J. Curran[2]

[1]Department of Biological Sciences, Texas Tech University, Lubbock, TX, USA

[2]Department of Pest-management and Conservation, Lincoln University, Lincoln 7647, New Zealand

[3]Department of Natural Resources Management, Texas Tech University, Lubbock, TX, USA

[4]School of Life Sciences, University of Technology Sydney, NSW 2007, Australia

[5]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, New South Wales, Australia

[6]Fire Centre, School of Natural Sciences, Private Bag 55, University of Tasmania, Hobart, Tasmania 7001, Australia

[7]School of Environment, University of Auckland, Auckland 1010, New Zealand

[8]Department of Earth and Spatial Sciences, College of Science, University of Idaho, Moscow, ID 83844, USA

[9]Instituto de Biociências, Lab of Vegetation Ecology, Universidade Estadual Paulista (UNESP), Rio Claro, Brazil

[10]Instituto Multidisciplinario de Biología Vegetal (CONICET-Universidad Nacional de Córdoba) and FCEFyN, Córdoba, Argentina

[11]AMAP (Botanique et Modélisation de l'Architecture des Plantes et des Végétations), CIRAD, CNRS, INRA, IRD, Université de Montpellier, Montpellier, France

[12]Environmental Change Institute, School of Geography and the Environment, The University of Oxford, Oxford, UK

[13]Department of Ecology, State University of Rio de Janeiro (UERJ), Rio de Janeiro, Brazil

[14]National School of Tropical Botany of Rio de Janeiro, Botanical Garden Research Institute, R. Pacheco Leão, 2040 Horto, Rio de Janeiro, RJ 22470-180, Brazil

[15]Fenner School of Environment and Society, The Australian National University, Canberra ACT 2601, Australia

[16]USDA Forest Service, Rocky Mountain Research Station, 100 Valley Road, Reno, NV 89511, USA

Correspondence
Dylan W. Schwilk, Department of Biological Sciences, Texas Tech University, 2901 Main St, Lubbock, TX 79409, USA.
Email: dylan.schwilk@ttu.edu

This article is part of the American Journal of Botany special issue: "Understanding novel fire regimes using plant trait-based approaches."

Abstract

Despite fire being one of the oldest and most important ecological disturbance processes on Earth, many aspects of fire–vegetation feedbacks are poorly understood, limiting their accurate representation in predictive models. Translating plant flammability traits to fire behavior and fire effects on ecosystems has proven a challenge with different disciplines approaching the problem at widely different scales. One approach has been a top-down assessment of ecosystem-level effects of vegetation structural characteristics and plant physiology on fuel properties such as fuel moisture. This approach has had some success, but is often forced to collapse species-specific variation into a small number of functional types and, as a practical necessity, usually focuses on highly plastic traits (e.g., moisture content) that can be modeled across an ecosystem without the need to characterize species-specific characteristics. The other approach grew out of trait-centric comparative ecology and focused on how traits might influence individual plant flammability. However, the degree to which such lab-based flammability trials reflect real species-specific differences maintained during wildland fires has been questioned. We review the history of these approaches, discuss where each has succeeded, and identify areas of research aimed at closing the apparent gap in scale.

KEYWORDS
combustibility, consumability, fire behavior, fire regime, flammability, fuel architecture, fuel load, fuel moisture, ignitibility, plant traits

Fire has been a key component of the Earth system for hundreds of millions of years (Glasspool et al., 2004) and may have been used by hominids as early as 1.5 million years ago (Brain and Sillent, 1988). In addition to atmospheric oxygen and background ignitions, such as lightning, wildland fuels (e.g., living plants and their associated litter and debris) are a fundamental determinant of fire occurrence and behavior. Although fire regimes have an intrinsic range of natural variation, rapid changes in climate and land use are leading to unprecedented extreme fire events (French et al., 2015; Cunningham et al., 2024). In many regions, fire seasons are lengthening and are associated with elevated risks of extreme fire behavior and occurrence of fire events (Jolly et al., 2015). These effects are not only amplifying fire activity in fire-prone landscapes; some ecosystems where fire has historically been extremely rare are also predicted to experience increased fire activity (e.g., Aoteaora New Zealand, Melia et al., 2022; Arctic tundra, French et al., 2015; Amazonia, Brando et al., 2020). Furthermore, some ecosystems maintained by fire may have less fire activity as the systems move below critical biomass thresholds (Krawchuk and Moritz, 2011; McWethy et al., 2013) or the community composition and subsequent fuel abundance may change (e.g., "mesophication", Nowacki and Abrams, 2008). Highly flammable dead plant matter, especially leaf litter and dry graminoid cover, shaped by plant traits and phenology patterns, has been the traditional focus of fire hazard and fuel load assessments with fuel models used to characterize ecosystems in terms of plant functional groups and structure (Anderson, 1982). Plant characteristics, especially the characteristics of live plants, are important controls of landscape flammability (Anderson, 1970), and fire behavior models have been successfully grounded in the categorization of fuel types. However, parametrization of plant flammability in terms of traits important to ecological strategies remains challenging. Consequently, critical uncertainties regarding how climate change will impact plant community composition, and hence the relative flammability of fuel assemblages, limit our ability to predict future changes in fire regimes.

In an era of extreme fires, much attention has been paid to the direct effects of climate change on fire weather and fuel dryness (Ellis et al., 2022) with less consideration of the abundance of different fuel types. Living and dead fuels link fire science and plant ecology; therefore, plant traits provide an important conceptual framework for fire ecology. They provide a way to predict how individual plants and their components will ignite, burn, and influence fire behavior, broadly captured by the concept of plant "flammability" (Table 1) (Cornelissen et al., 2017; Pausas et al., 2017). For example, the quantitative description of traits such as leaf mass per area, maximum moisture content, and concentration of volatile organic compounds can inform our understanding of fine-scale fire dynamics (Murray et al., 2013; Alam et al., 2020; Burton et al., 2021; Popović et al., 2021). However, scaling from individual plants to stand-level characteristics is challenging because the interplay between plant traits and fire behavior is also shaped by environmental conditions and interactions with pathogens, herbivores, and non-fire disturbances (Younes et al., 2024). This spatiotemporal context dependence limits the ability to scale up assessments of flammability conducted on plant components (Fernandes and Cruz, 2012; Pausas and Moreira, 2012).

The multiscale nature of flammability (Figure 1) and the tremendous multiscale trait diversity in plant communities resulting from variation in species composition, individual age and size, and phenotypic plasticity presents a challenge when integrating functional ecology with fire science (Grootemaat et al., 2017a; Ganteaume, 2018; Tumino et al., 2019). Different vegetation types in the same climate experience different fire regimes (van Wilgen et al., 1990; Odion et al., 2010; Archibald et al., 2018), indicating that emergent properties of living plants can shape fire. Furthermore, several biogeographical conundrums point to a possible role for lineage-specific species traits as influencing fire regimes (Rogers et al., 2015; Archibald et al., 2018; Simpson et al., 2022). Scaling from plant traits to fire behavior at landscape scales remains challenging, with fire behavior models sometimes performing poorly when used outside of the ecosystem(s) or climatic conditions for which they were developed (Sullivan et al., 2009a, 2009b, 2009c). Moreover, there is little overlap in traits considered between the fuel modeling of fire scientists and the functional trait measurements of ecologists.

There are two contrasting, but complementary approaches to understanding the role of plant traits in influencing fire hazard and fire behavior. One approach focuses on gross plant or fuel characteristics that are amenable to landscape-scale remote sensing or modeling from vegetation maps (Abdollahi and Yebra, 2023), what we call the top-down approach. The second approach is assessing species-specific flammability traits in laboratory trials, or the bottom-up approach. A barrier to establishing general flammability relationships is that individual studies usually focus on a single fuel type such as surface fuels measured by fire spread through artificial fuel beds, crown fuels measured on shoots of woody plants, or graminoid fuels with flammability

TABLE 1 Terms and definitions.

Term	Definition	How is it measured?
Bottom-up approach	Assessment of species-specific flammability traits	Laboratory trials
Combustibility	Component of flammability that accounts for the intensity of burning	Measured variously as the highest temperature measured during burning, flame height, flame spread rate, and mass loss rate
Consumability	Component of flammability that accounts for how much of a plant is burned by fire	Measured as the percentage of burnt biomass once combustion has finished
Fire behavior	How a fire reacts to the environment, including its spread, intensity, and how it consumes fuel	In flammability trials: as individual components described here; in wildfire: from direct observations, remote sensing, and post-fire estimation of severity metrics
Fire propagation	Spread of fire across a landscape	Measured as rate of spread in laboratory or field (see also measures of post-fire heterogeneity and fire perimeters)
Fire regime	General pattern of fire occurrence in an area	Defined by the patterns of fire frequency, fire intensity, fire size, and type of fuel consumed
Flammability	Ability of a material to burn that includes how easy it is to ignite, the intensity at which it burns, the length of time it burns, and the percentage of material consumed by fire	Measured in terms of combustability, consumability, ignitibility and sustainability (see these measurements in the glossary)
Fuel architecture	Size, shape, volumetric arrangement, and distribution of fuel materials that burn during wildfires	Measured in the field for the broad fuel assemblage as compaction, bulk density, and ladder fuel presence; can also be species-specific (e.g., degree to which airflow is impeded by branches and leaves)
Fuel load	Total combustable material per unit area	LiDAR/remote sensing, as well as field survey methods
Fuel moisture	Amount of water content in plant material, affecting its likelihood of igniting and burning	Commonly quantified in small branches for live fuels, or from litter samples
Ignitibility	Component of flammability that accounts for ease with which a plant begins to burn when exposed to an ignition source	Measured as either the time to first burning from exposure or the frequency of ignition events among a set of samples
Plant traits	Measurable characteristic (e.g., architectural, morphological, phenological, physiological, chemical) to describe components of flammability	Variously (e.g., Cornelissen et al., 2003)
Sustainability	Component of flammability that accounts for how long a plant continues to burn after ignition, with or without an external heat source	Measured as the duration of combustion and can include durations of incandescence, flaming, and smoldering
Top-down approach	Treats plants as broad vegetation types or fuel types and focuses on those plant or fuel characteristics	Remote sensing tools often used

measured at the whole-plant scale. Different plant traits appear to affect different dimensions of flammability among these fuel types (Schwilk, 2015). The top-down and bottom-up approaches consider sharply contrasting spatial grains and extents with limited overlap (but see exceptions, e.g., Prior et al., 2017), which has inhibited the development of cross-scale integrated approaches to quantifying plant flammability. Additionally, it is important to note that this dichotomization breaks down under more extreme fire behavior and extreme fuel drying, where fuel characteristics may cease to be important because all biomass becomes available to burn (Cruz et al., 2022). For instance, extreme fires can burn tropical rainforests that are typically considered pyrophobic communities.

The top-down assessment of fuels, often using remote sensing or vegetation mapping, aims to assess ecosystem level effects of plant characteristics on stand, community, and landscape fuel properties (Figure 1). This approach is well integrated with fire behavior models and forms the basis of tools used by fire incident teams during active fires (e.g., LANDFIRE, Rollins et al., 2017). These assessments generally require collapsing species-specific variation into functional types (Anderson, 1982; Scott and Burgan, 2005). The fuel model approach has underpinned fire hazard and behavior prediction particularly in the United States and Europe (Cruz et al., 2025) where such fuel models combining plant traits of dominant species and ecosystem level vegetation structural characteristics are widely used. More recently, there has been increasing interest in including physiological traits in the assessment of flammability (Jolly and Johnson, 2018) and in examining traits such as those regulating plant water-use and carbon dynamics that can be

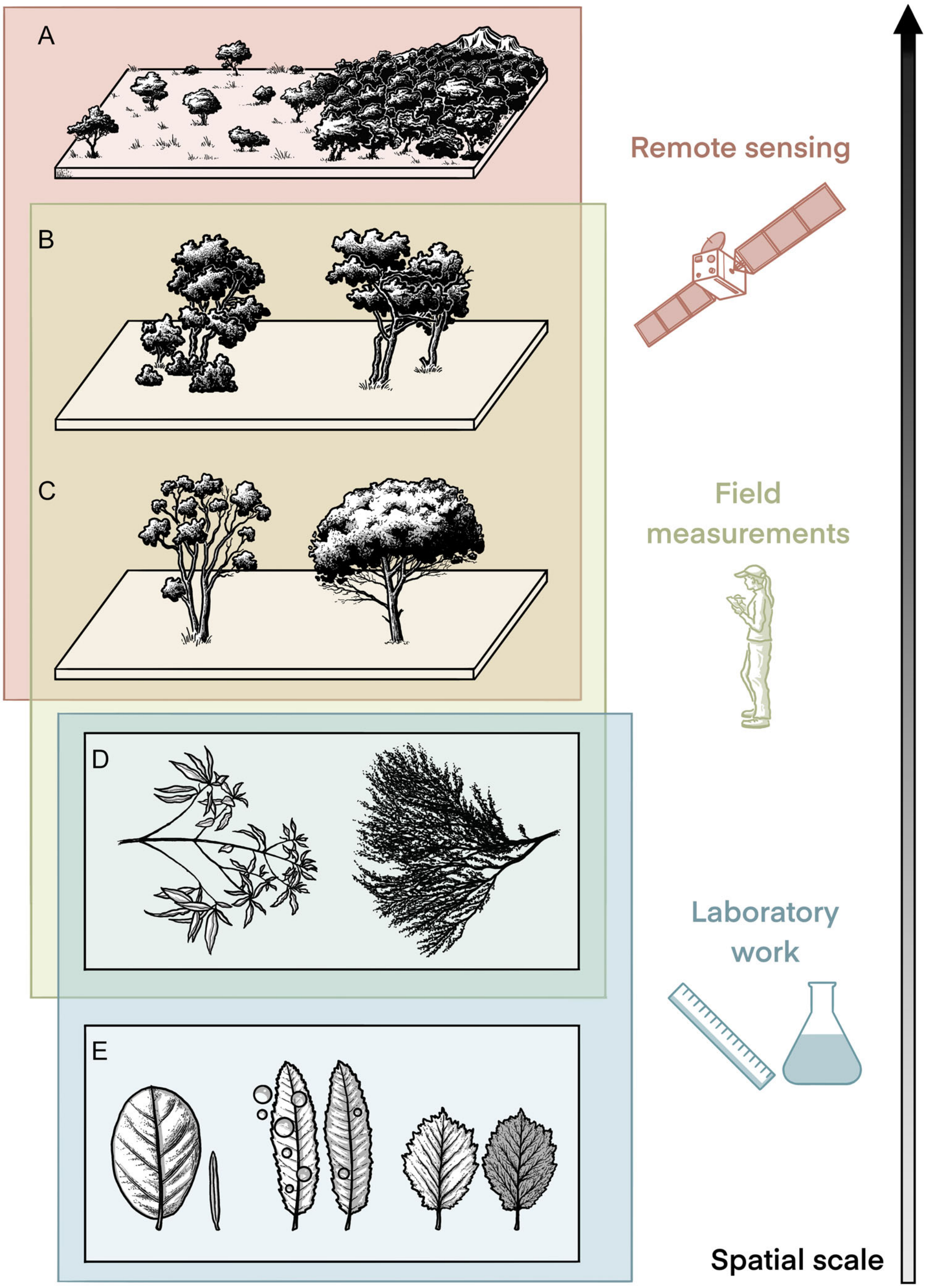

FIGURE 1 Illustration of methods used to assess fuel characteristics (moisture, architecture, chemistry, and mass) across a range of scales from communities and landscapes to individual plant organs or excised parts (A–E). Remote sensing, field measurements, and laboratory work are each suitable for assessing fuel characteristics at different but overlapping portions of this range, thereby creating opportunities to synthesize the "top-down" and "bottom-up" approaches to understanding flammability.

modeled across an ecosystem (e.g., Drucker et al., 2023). In ecosystems dominated by one or a few species, this approach is essentially species-specific, as in chamise-dominated California chaparral where the moisture content of live fuel has been shown to predict fire hazard (Park et al., 2022).

The bottom-up approach has involved laboratory experiments and has been integrated into wildland fire science for decades especially in the vast literature on measuring and modeling fuels (e.g., Anderson, 1970; Rothermel, 1986). However, such work was rarely explicitly linked with plant morphological or physiological traits. A trait-based bottom-up approach has the potential to link well-studied ecological strategies of plants with fire and vegetation feedback processes. However, it is uncertain how well individual-level measures of plant flammability predict fire behavior in wildland fires or how these effects vary with fire weather conditions. The results of lab-based flammability trials of leaves, litter, and detached branches have demonstrated extensive variation in multiple dimensions of flammability (Varner et al., 2015; Cui et al., 2020; Popović et al., 2021). However, there is a gap between these flammability parameters usually measured at the organ or partial plant level and the emergent flammability of actual plant communities. In litter fuels, plant traits can have both additive and non-additive effects that extrapolate well to local fire behavior (Schwilk and Caprio, 2011; de Magalhães and Schwilk, 2012; van Altena et al., 2012; Kane et al., 2021). There remains debate about how trait variation influences wildfire relative to climate, weather, and topography, especially for crown fire. Nevertheless, traits have been used successively in fire behavior assessment (Cardoso et al., 2018), modeling (Zylstra et al., 2016), and hazard prediction (Balaguer-Romano et al., 2022). This scaling challenge is not unique to fire ecology and is an example of a broader debate in functional ecology regarding how well plant traits predict ecosystem-level processes (van der Plas et al., 2020; Gornish et al., 2023; Hagan et al., 2023).

In this review, we examine the efficacy of trait-based bottom-up approaches and top-down landscape flammability assessment across four important fuel characteristics (fuel moisture, fuel chemistry, fuel architecture, and fuel load). We address two main questions: (1) How well do traits measured at the organism-level match fuel characteristics measured at broader scales? (2) How well do species-specific traits predict fire behavior? Finally, we identify approaches that can advance the field of plant flammability from plant to landscape scales.

FLAMMABILITY IS MULTIDIMENSIONAL

The dimensions of intrinsic plant flammability

Whole-plant flammability is a compound functional trait (Jaureguiberry et al., 2011) and can be assessed using different variables of measurement (Pérez-Harguindeguy et al., 2013), across a range of scales of organization from plant tissues and excised parts to organs, shoots, and entire individuals (White and Zipperer, 2010; Younes et al., 2024), and for live, dry, or dead fuel (Melnik et al., 2021; Boving et al., 2023). Common to these multiple dimensions, scales, and fuel types is the measurement of intrinsic plant flammability, a multivariate concept that represents the inherent burning properties of plants as determined by their physicochemical traits (Varner et al., 2015). Anderson (1970) established three intrinsic flammability variables that are widely used in fire ecology research: ignitibility, sustainability, and combustibility (Table 1).

Ignitibility is the ease with which a plant begins to burn when exposed to an ignition source (Gill and Moore, 1996), most frequently measured as either the time to ignition (Murray et al., 2013) or the frequency of ignition events among a set of samples exposed to an ignition source (Wyse et al., 2016). *Sustainability* is how long a plant burns after ignition, with or without an external heat source (White and Zipperer, 2010; Jaureguiberry et al., 2011). Sustainability is most frequently measured as the duration of combustion and can include durations of incandescence, flaming, and smoldering (Ormeño et al., 2020). *Combustibility* refers to the intensity of burning, measured variously as the highest temperature measured during burning (Alam et al., 2020), flame height (de Magalhães and Schwilk, 2012), flame spread rate (Ganteaume et al., 2011b), and mass loss rate (Simpson et al., 2016). Martin et al. (1993) considered consumability as a fourth dimension of intrinsic plant flammability, representing how much of a plant is consumed by fire. *Consumability* is commonly measured as the percentage of burnt biomass once combustion has finished (Burger and Bond, 2015; Zanzarini et al., 2022).

Relationships among dimensions of flammability

Comparative flammability studies have explored interspecific relationships between the four intrinsic flammability dimensions (i.e., ignitibility, sustainability, combustibility, and consumability). A key goal of such investigations has been to determine whether there are species for which all four flammability variables are aligned (Murray et al., 2023). In this context, some evidence exists for correlations between intrinsic flammability variables. Previous work has shown that leaf ignitibility and sustainability are negatively correlated, such that species with leaves that take a long time to ignite also possess leaves that burn for a long time (Krix et al., 2019; but see Grootemaat et al., 2015). Cawson et al. (2023) showed that shoot sustainability is positively correlated with shoot combustibility. Further evidence that some flammability variables are correlated is provided by studies requiring the use of dimensionality reduction methods (e.g., principal component analysis) to consider collinearity among ignitibility, sustainability, combustibility, and consumability (Prior et al., 2017; Wyse et al., 2018).

Relationships among variables differ when measured on different fuel types. Flammability studies of surface fuels (leaf and twig litter) tend to show two relatively equal and orthogonal axes of variation, with one axis representing flame duration and/or total heat released and another axis associated with ignitability and spread rate (de Magalhães and Schwilk, 2012; Engber et al., 2012; Prior et al., 2018). In well-aerated fuels such as grasses, on the other hand, flammability measures are often more strongly correlated, suggesting a single major axis of variation (Simpson et al., 2016; Gao and Schwilk, 2018; Padullés Cubino et al., 2018). In addition to differences across fuel types, another possible explanation for differing results is differences in how flammability is measured (Younes et al., 2024). There is a need to develop globally consistent methodologies of assessment and analysis of intrinsic plant flammability (Ocampo-Zuleta et al., 2024) to enable robust conclusions about the nature of inter-relationships among flammability variables.

Relationships between plant flammability variables and fire behavior descriptors

Theoretical frameworks suggest that each dimension of a plant's intrinsic flammability corresponds to a specific aspect of fire behavior and ecosystem processes (Table 1). For example, Gill and Zylstra (2005) proposed that ignitability, combustibility, and sustainability at the individual plant level are linked to the rate of fire spread, flame length, and fire residence time, respectively. Conversely, Pausas et al. (2017) argued that the rate of fire spread is more closely related to combustibility. The consumability axis is theoretically aligned with fire severity at the ecosystem level and often measured by the amount of above- and below-ground organic matter consumed by fire (Gill and Zylstra, 2005; Keeley, 2009). There are few empirical test theoretical models of landscape flammability, with one study from the Australian monsoon tropics supporting two axes: total heat release and rate of spread (Prior et al., 2018).

Researchers have also attempted to connect these dimensions of flammability with flammability metrics at different scales to better predict fire behavior. For instance, Grootemaat et al. (2017b) investigated the relationship between individual leaf flammability and fuel-bed flammability, finding that the time to ignition of individual leaves was correlated with several flammability parameters in fuel beds, including the rate of fire spread. Consequently, fire spread can be understood as a sequence of ignition events, where the ease of ignition of individual leaves accelerates the spread of fire from one leaf to another (Grootemaat et al., 2017b).

Plant traits to fuel characteristics across scales

Given the multidimensionality of flammability, predicting fire behavior at community and ecosystem scales based on bottom-up approaches is extraordinarily difficult (Loudermilk et al., 2022). To examine flammability across scales, we consider four major categories of fuel characteristics likely to be influenced by plant traits: fuel moisture, fuel architecture, fuel chemistry, and fuel load (Table 1). These are not independent; for example, architecture can influence moisture dynamics and fuel load, and leaf chemistry interacts with leaf moisture. Each of these categories also encompasses mixtures of live and dead fuel components and how they interact with the fuel complex. Below we discuss how different plant traits in each category impact flammability across ecological scales and identify the challenges in bridging scales and their causes.

Fuel moisture across scales

Fuel moisture content, whether of dead or live fuels, has long been recognized to affect time to ignition (Rothermel, 1972). Water acts as a heat sink; thus, a high moisture content requires more energy to evaporate water before ignition can occur, and the amount of water in the fuel impacts the effective heat of combustion, and the rate and form of heat released (Smith et al., 2013; Campos-Ruiz et al., 2022). The relationship between fuel moisture and flammability has been extensively studied in the laboratory, and there is strong evidence that this association is negative (Bowman et al., 2014; Popović et al., 2021). Fuel moisture content is negatively correlated with ignitibility at a range of fuel scales, including leaf (Murray et al., 2013; Grootemaat et al., 2015; Simpson et al., 2016; Krix et al., 2019; Younes et al., 2024), litter (Plucinski and Anderson, 2008; Blauw et al., 2015; Burton et al., 2023), shoot (Wyse et al., 2018; Murray et al., 2023), and the whole plant (shrubs, Weise et al., 2005; grasses, Simpson et al., 2016; forbs and shrubs, Zanzarini et al., 2022). However, the relationships between moisture content and sustainability (negative, positive, and neutral) and consumability (negative and neutral) are ambiguous (Popović et al., 2021; Younes et al., 2024). Associations with fuel moisture content are the best studied of all trait–flammability relationships, and the effect of moisture content may outweigh that of other traits, such as phytochemistry (Alessio et al., 2008). Moisture thresholds can delineate flammable and nonflammable vegetation. Thresholds for dead fuels (moisture of extinction values) depend upon fuel type and wind speed (Matthews, 2013), but often range from 15% to 40% (Scott and Burgan. 2005; Smith et al., 2013). Recent research has also identified thresholds for live fuels (Sultana, 2022; Boving et al., 2023).

Fuel moisture in dead and excised fuels

Dead fuel moisture is a strong driver of litter flammability (Varner et al., 2015; Kreye et al., 2018; de Magalhães and Schwilk, 2021). Dead fuel moisture can vary from 1% to saturated and accordingly can create fuels with low energy thresholds for ignition to levels that extinguish spreading fire and is driven by relative humidity, solar radiation, wind, and microclimate conditions, as well as by plant traits that influence surface area to volume ratios, litter packing, and bulk density (Rothermel, 1986; Kreye et al., 2018, 2023).

Dead fuel moisture is represented explicitly in U.S. fire behavior models. In these models, the moisture in dead fuel depends on precipitation and variable drying conditions driven by wind, temperature, humidity, and insolation (Rothermel, 1986; Viney, 1991; Nelson, 2000). Species-specific characteristics are included only through the fuel-type specifications. However, in systems where leaf litter drives surface fire, interspecific differences can result in differing litter flammability where part of the species effect is realized through different moisture absorption/adsorption dynamics and drying rates (Talhelm and Smith, 2018; de Magalhães and Schwilk, 2021; Kane et al., 2021; Kreye et al., 2018, 2023). Additionally, canopy cover and soil moisture influence the litter microenvironment, affecting drying rates and flammability (Kreye et al., 2020; Zhao et al., 2022).

Fuel moisture in living plants

Moisture of live fuels is much more complex to understand than moisture in dead fuels and depends on plant physiology; plants can transport water and nutrients across their tissues on short time scales (Nolan et al., 2022). Live fuel moisture content (LFMC) is the ratio of water mass (g) to dry mass (g) in fresh biomass and is commonly quantified in small branches. It is tightly correlated with other measures of plant water content such as leaf relative water content (proportion of water content relative to saturated condition) and can vary with plant water potential (Boving et al., 2023; Mahmud et al., 2025, in this issue). In laboratory studies, the relationship between LFMC and time to ignition has been described as a linear relationship or a threshold relationship (Xanthopoulos and Wakimoto, 1993; Terrah et al., 2020). Such discrepancies potentially result from the heat flux applied or the mode of heat transfer (i.e., convective versus radiative) because radiant heating will take substantially longer than convection heating to ignite small fuel pieces (Cohen and Finney, 2023), and radiant heaters can produce both types of heat flux depending on sample positioning. Despite laboratory studies demonstrating a negative relationship between LFMC and flammability, the importance of LFMC in field studies is debated (Alexander and Cruz, 2013; Rossa and Fernandes, 2018). There are multiple, not mutually exclusive, potential reasons for the discrepancy between laboratory and field studies: (1) the challenges of isolating the effect of LFMC from other variables (e.g., wind speed, solar radiation, topographic slope, dead fuel moisture) in the field; (2) the higher heat fluxes in wildfires than in laboratory studies may mask any effect of LFMC on time to ignition (Alexander and Cruz, 2013); (3) the relatively low variation in LFMC observed in field studies may be insufficient to induce an effect on time to ignition (Pimont et al., 2019); (4) the moister conditions of vegetation in field experiments, which are often conducted under mild conditions for safety reasons (Fernandes and Cruz, 2012; Alexander and Cruz, 2013; Rossa and Fernandes, 2018; Pimont et al., 2019); (5) differences in vegetation structure that may affect the relative importance of LFMC; and (6) errors in estimates of LFMC in the field (Pimont et al., 2019). Further field-based studies are required to examine the relative importance on LFMC on fire behavior.

This ongoing debate leads to differences in how LFMC is included in fire behavior models across different systems. For example, in Australia, fire behavior models for short stature or highly horizontally connected vegetation, such as grasslands and shrublands, require inputs of LFMC or proxies for LFMC, such as plant curing (Cruz et al., 2015). In contrast, fire behavior models for taller eucalypt forests do not consider LFMC (Cruz et al., 2015). Live fuel moisture is not explicitly included in U.S. fire behavior models based on the Rothermel (1972) fire behavior equations (reviewed by Sullivan, 2009a, 2009b, 2009c); however, LFMC is implicitly included in such models through dead to live fuel biomass ratios or as constants in fuel type categories (known as fuel models; Finney, 1998). It has been proposed that failures of the Rothermel (1972) equations to predict fire spread in shrub fuels may arise from how moisture effects are parameterized (Weise et al., 2016; García et al., 2020). Despite the inconsistent consideration of LFMC in models, there is growing evidence that low LFMC is associated with wildfire extent (Chuvieco et al., 2009; Dennison et al., 2008, 2009; Nolan et al., 2016; Argañaraz et al., 2018; Luo et al., 2019; Park et al., 2022; Rao et al., 2022) and increased receptivity of landscapes to lightning ignitions (Rao et al., 2023; Wickramasinghe et al., 2024).

There are multiple challenges to estimating LFMC across broad spatial scales. Top-down approaches may not characterize fine-scale spatial patterns in LFMC. Perhaps most importantly, LFMC is temporally dynamic. Remote sensing methods are used to assess hazard (e.g., Fuelcast, https://www.fuelcast.net/); however, such methods typically produce poor forecasts of temporal changes in fuel moisture (but see Miller et al., 2023). Ongoing efforts to link top-down with bottom-up approaches that use correlated plant traits to predict leaf flammability traits, including LFMC (Nolan et al., 2018; Balaguer-Romano et al., 2022). Hydraulic traits such as leaf saturated moisture content and leaf capacitance have also been used to predict fuel moisture and flammability (Scarff et al., 2021; Nolan et al., 2022). Recent studies have also reported that leaf water potential is a strong predictor of flammability (Sultana, 2022; Boving et al., 2023); however, the degree of sensitivity to water potential can vary across species and may depend not just on water content but on the rate of water loss during preheating (Mahmud et al., 2025, this issue).

Fuel architecture across scales

Fuel architecture refers to the size, shape, volumetric arrangement, and distribution of fuel materials that burn during wildfires (Table 1). Although fuel architecture is often quantified based on the volumetric arrangement of assemblages of different live and dead fuel components, with metrics such as compaction, bulk density, ladder fuel presence, among others (Kreye et al., 2014), some studies have addressed the architecture of individual plants (White and Zipperer, 2010). Fuel architecture influences flammability by affecting variables such as ignition, combustion, heat transfer, wind patterns, and the airflow across fuel scales (Papió and Trabaud, 1990; Zylstra et al., 2016). Architecture also influences the flammability of smaller fuel particles that are routinely examined in the laboratory (e.g., leaves, litter, shoots; Alam et al., 2025) and larger fuels and mixtures of fuels in the field such as surface fuels (e.g., grasses, leaves, litter), ladder fuels (e.g., shrubs, small trees), and canopy fuels (e.g., tree crown).

Fuel architecture of live plants

Fuel architecture is an important determinant of flammability at larger fuel scales such as the shoot and whole plant.

For shoots, the physical arrangement of leaves in the branches likely plays a more important role in influencing flammability than leaf size and shape (Alam et al., 2020). However, some work has found that architectural traits are less important in determining flammability than leaf traits such as leaf dry matter content and leaf thickness (Alam et al., 2025). Key architectural traits at the shoot level include branch ramification, leaf and twig fraction mass, and fuel bulk density, with species with more fine branches, higher leaf fraction mass, and higher bulk density being more flammable (Santacruz-García et al., 2019; Alam et al., 2025). At the whole-plant level, especially for trees and shrubs, the spatial arrangement and density of leaves and branches on the stem, the vertical and horizontal distribution of the fine fuels, and the retention of dead fuels in the crown or around the base of the plant determine flammability (Mitsopoulos and Dimitrakopoulos, 2007). For example, manipulative field experiments demonstrated that the canopy architecture of dead fuel retention in the shrub *Adenostoma fasciculatum* is more important than total fuel load in enhancing fire intensity (Schwilk, 2003). A tree crown structure with closely connected leaves and branches is more likely to carry a fire than a crown with sparse branches due to more efficient heat transfer in the former (Saura-Mas et al., 2010; Schwilk, 2015). Also, plants with continuous vertical fuel from the ground to the crown (ladder fuels) are more likely to propagate a surface fire into the tree crown, producing crown fires, which are more intense (Graham et al., 2004; Menning and Stephens, 2007; Mitsopoulos and Dimitrakopoulos, 2007). Likewise, dense lateral branching in the crown and well-connected aerial branching between adjacent trees help spread and sustain a fire more than those with gaps in fuel continuity (Graham et al., 2004; Menning and Stephens, 2007; Mitsopoulos and Dimitrakopoulos, 2007). Fire ecologists have often assumed that architectural differences across herbaceous species are less important than are differences in biomass to fire behavior, supported by studies of grassland fuels, indicating that flammability strongly depends on fuel load (Simpson et al., 2016; Padullés Cubino et al., 2018). However, there are some indications of other architectural effects on flammability in grasses related to the positioning of biomass (Gao and Schwilk, 2018, 2022).

Fuel architecture in dead and litter fuels

Extrapolating flammability across scales is challenging (Fernandes and Cruz, 2012). A striking example of the decoupling between the flammability of individual fuel elements and their corresponding fuel beds is seen in small, thin shrub leaves. These leaves ignite easily as individual plant parts or when attached to a shoot, but when organized as litter, produce low heat release rates due to poor ventilation (Scarff and Westoby, 2006). Emergent properties of leaf-litter fuel beds, such as packing ratio and bulk density, influence airflow and can override the effects of individual leaf flammability (Grootemaat et al., 2017b). A litter layer with larger leaves and other materials facilitates ventilation and ensures more oxygen availability, resulting in fires that burn more rapidly, whereas small leaves tend to produce a compacted litter structure that can restrict airflow and so burn slowly or rarely (de Magalhães and Schwilk, 2012; Van Altena et al., 2012; Ganteaume, 2018). Consequently, litter flammability is aeration-limited, while canopy flammability, where fuels are usually well ventilated, is not (Schwilk, 2015; Varner et al., 2015).

Although leaf-level flammability measurements do not predict flammability of surface fuels composed of leaf litter, ground fuels do provide an example where extrapolating from fine to coarser scales has succeeded: Surface fire behavior in one temperate forest was predicted by the abundance-weighted leaf traits known to influence fuel aeration (Schwilk and Caprio, 2011). At the extreme of oxygen limitation, fuels in organic soils and peat bogs can be extensively consumed during smoldering combustion (Turetsky et al., 2015; Walker et al., 2019, Prior et al., 2024). In addition to natural fuel beds, forest management practices can lead to large areas of masticated (i.e., chipped or shredded) material as a part of fuel-thinning operations, a practice that has increased over time particularly in the wildland–urban interface (Reed et al., 2020). The size, shape, and chemistry of these masticated materials, as well as material depth, can affect how tightly they pack and how long they retain moisture and therefore flammability and fire spread rates. Fuel-bed characteristics in this case depend upon species composition and the machinery used to create masticated material (Kreye et al., 2014).

Elevated dead fine fuels, such as fibrous and ribbon barks, are a unique, albeit important, type of wildfire fuel. Some species, particularly many eucalypts, have a comparatively high biomass of this fuel type that is often specifically measured in hazard assessments (Pickering et al., 2023). These fuels are important in generating embers and fire brands that can spread wildfires over long (>30 km) distances through a process known as spotting (Tarifa, 1965; Manzello et al., 2007) and can depend on both plant traits that facilitate brand formation (Pickett et al., 2005; Penman et al., 2017) and the receptivity of the fuel bed to ignition by lofted brands (Ganteaume et al., 2011a). Spotting is included in simulated fire spread models such as FARSITE (Fire Area Simulator; Finney, 1998, 2004), but such models often fail to predict fire perimeters accurately under conditions favorable to spotting (Zigner et al., 2020). Further work on factors influencing the likelihood that a spot fire will lead to an ignition and subsequent fire spread is needed from both top-down and bottom-up perspectives. Spatial vegetation flammability data sets need to be developed to enable utility, municipal, and land management planners to target, remove, or reduce certain vegetation types or debris identified to have a higher probability of promoting spot-fire ignitions.

Fuel chemistry across scales

Plant tissues contain numerous chemical elements and compounds, many of which have been linked to plant flammability across fuel scales. The most important of these is water (see section Fuel moisture across scales), although plant water content is traditionally (as it is herein) considered separately from plant chemistry (Younes et al., 2024). Some of the earliest research into plant traits associated with flammability focused on chemistry such as mineral ash content (Broido and Nelson, 1964; Mutch and Philpot, 1970; Philpot, 1970). Phytochemicals that affect flammability fall into three main groups: essential elements (e.g., C, N, K, P, Ca, Ma, S; Salisbury and Ross, 1992); primary metabolites that are essential for growth, development, and reproduction (e.g., carbohydrates, amino acids, fatty acids, and vitamins; Schlaeppi et al., 2021), and secondary metabolites that have no direct role in primary functions but are useful in other ways such as plant defense against herbivores (Neilson et al., 2013). While the term "secondary metabolites" is widely used in the literature, and we have retained it here for consistency with previous work, we prefer the term "specialized metabolites" because they are derived from primary metabolism to fulfill specific functions, essentially adaptations that enhance survival. "Specialized" avoids the connotations of "secondary" as being less important.

The relationship between certain essential elements and flammability has received some attention. For instance, there is evidence for a negative relationship between P and leaf and litter flammability (Scarff and Westoby, 2008; Grootemaat et al., 2015), although this relationship is not universal across fuel scales (Mason et al., 2016; Grootemaat et al., 2017b; Alam et al., 2020), and P may influence flammability less than traits such as moisture content and leaf morphology (Turner, 1994; Scarff et al., 2012). Nitrogen is another essential element that has been linked to flammability, although again results have been mixed across fuel scales (Mason et al., 2016; Grootemaat et al., 2015, 2017b; Gowda et al., 2022). Other essential elements such as K, Ca, and Mg have rarely been investigated in relation to their impact on flammability (Popović et al., 2021; Rahman et al., 2023), although Budha-Magar et al. (2024) reported negative relationships between shoot flammability and various leaf nutrients (Mg, K, S, Ca, but not P). While essential elements may be correlated with flammability, these relationships are often weaker than those between flammability and other traits (e.g., leaf moisture content, twig dry matter content, and retained dead material; Budha-Magar et al., 2024).

Primary metabolites, such as carbohydrates and fatty acids, may be positively correlated with different flammability traits at the leaf, litter, and bark scales (Mason et al., 2016; Grootemaat et al., 2017b), likely due to their low relative molecular mass and high volatility (Page et al., 2012). Nonstructural carbohydrates such as sugars and starches enhanced the sustainability of living needles of *Pinus banksiana*, and foliar chemistry had a greater influence on flammability than moisture content (Campos-Ruiz et al., 2022). Further research into primary metabolite–flammability relationships should prove fruitful.

Secondary metabolites are the most extensively studied group of chemicals in relation to their influence on flammability across fuel scales and include volatile organic compounds such as phenolics and terpenes, lignins, and tannins (Owens et al., 1998; Pausas et al., 2016; Ormeño et al., 2020; Ganteaume et al., 2021; Guerrero et al., 2024). Of these chemical groups, terpenes have received the most attention at the leaf and litter scales for trees (Popović et al., 2021) and are considered in more detail below. The relationships between secondary metabolites and flammability are complex and can be idiosyncratic, depending on the type of fuel examined, the level at which chemical compounds are studied (e.g., at broad group, subgroup, or molecular levels), and the diversity of compounds examined. As with other chemical traits, the effect of secondary compounds on flammability may be less important than that of water content (Alessio et al., 2008).

Terpenes are unsaturated hydrocarbons composed of isoprene units (C_5) and are known to be flammable due to their high heating value and low flash point (Ormeño et al., 2020). While terpene content is by far the most frequently studied chemical trait on both live leaves and litter for trees, its relationship with flammability is inconsistent across studies (Popović et al., 2021). For instance, for combustibility, eight of 10 studies reported a positive relationship with leaf terpene content, and one study each reported a neutral and a negative relationship. For ignitibility and leaf terpenes, five studies reported positive relationships, three reported neutral, and one positive, while for sustainability five of six studies reported a negative relationship, with the other a positive relationship (Popović et al., 2021). While general patterns between terpene content and flammability may be lacking, there is evidence to suggest that terpenes drive flammability in particular species and groups. For instance, in *Rosmarinus officinalis*, high terpene content increased ignitability, and genetic differences between individuals hinted that such differences in flammability were heritable (Pausas et al., 2016). Furthermore, in the genus *Pinus*, in which flammability (He et al., 2012; Varner et al., 2022) and terpenes (Mitić et al., 2017) have been shown to be phylogenetically conserved and terpenes drive differences in the flammability of leaf litter (Ormeño et al., 2020), differences in terpene content have been suggested to be behind unexplained variations in litter flammability (Varner et al., 2022).

There is a paucity of research on the effect of chemistry on fire at community and landscape scales, although the widely used Rothermel fire spread equations include a mineral content damping coefficient, which can be set to vary across fuel types (Rothermel, 1972). Fuel chemistry likely influences flammability at landscape scales through interactions between soil chemistry and plant traits and herbivory-induced defenses. Plants from low-fertility ecosystems tend to have traits (e.g., small sclerophyllous leaves, high leaf dry matter content) that make them more flammable (Ojeda et al., 2010; Gibson et al., 2015; Paula et al., 2024). In Australian mallee ecosystems with a Mediterranean-type climate, soil fertility had a strong influence on the probability of fire estimated based on fire interval data, although this relationship was dependent on vegetation type, and the effect of rainfall was stronger (Gibson et al., 2015). In a continental-wide examination of fire activity in Australia, there was a negative relationship between soil P and both area burned and fire radiative power, after controlling for climate (Prior et al., 2017). Unexpectedly, there was a weak positive relationship between soil P and flame rate of spread in grass and litter fuels, which was attributed to the influence of soil P on flammability being less than that of leaf moisture content (Scarff et al., 2012; Prior et al., 2017). In a global study of drivers of fire activity in Mediterranean-type climate regions, low-fertility soils (lower pH and higher concentration of exchangeable aluminum) were positively associated with higher fire activity, although other measures of soil fertility (P, N, C:N) were not related to fire activity (Paula et al., 2024). Intriguingly, these relationships between low soil fertility and higher fire activity may be maintained via positive feedbacks mediated by high-flammability plant species: Low soil fertility selects species with traits (small leaves, high leaf dry matter content) that promote high flammability, and these species burn readily, resulting in frequent fires that deplete soil nutrient pools, favoring species with traits associated with high flammability (Wood and Bowman, 2012; Hinojosa et al., 2021; Paula et al., 2024). While more work is needed to disentangle how soil chemistry influences flammability, these studies show the value of incorporating soil fertility in models predicting future fire regimes.

Fuel load across scales

Fuel load, the total combustible material, is usually defined as mass/area and is often estimated through top-down approaches. Interactions between fuel load and fuel structure across multiple scales make it difficult to isolate the effects of each driver. At the finest scales, fuel load is determined by the density of plant biomass. Leaf dry matter content (LDMC) is related to the amount of carbon in a leaf available for combustion and is calculated as the ratio of dry mass to water-saturated fresh mass (Pérez-Harguindeguy et al., 2013), so is related to live fuel moisture content. At the individual leaf level, higher LDMC has shown a negative relationship with different flammability axes. For instance, Rahman et al. (2023) reported that leaves with higher LDMC required higher ignition temperatures. Similarly, Mason et al. (2016) reported a negative correlation between the rate of temperature increase and LDMC, indicating that higher LDMC is associated with lower combustibility. In contrast, at the shoot level, higher LDMC is associated with increased flammability, demonstrating a decoupling of flammability between leaf and shoot levels (Alam et al., 2020). Alam et al. (2020) and Potts et al. (2022) further demonstrated that LDMC significantly influenced shoot flammability measures connected to all axes of flammability (ignition percentage, burnt biomass, burn time, and maximum temperature) across growth forms and families. Ortiz et al. (2023) corroborated these findings, showing that LDMC positively influenced burn time and maximum temperature. Importantly in the context of isolating fuel load versus fuel structural effects, Alam et al. (2025) demonstrated that LDMC was a better predictor of shoot flammability than various architectural traits. Finally, at the global scale, patterns in LDMC have been linked to fire activity, especially among plants with postfire regeneration abilities (resprouting or reseeding), that have higher LDMC (Dai et al., 2025).

As the scale of analysis expands to include not only shoot characteristics but also individual crowns, fuel density is another important predictor of flammability. At fine scales, fuel load is often measured as mass per unit volume, and at the broadest scales, as mass per unit area. As fuel density increases, fire spread rate tends to decrease while burning time increases (Grootemaat et al., 2017a; Prior et al., 2017). However, an important point of distinction regarding fuel-bed density (or litter-bed density) is that it may have starkly different influences on flammability/fire behavior in canopies versus litter (see section Fuel architecture across scales). Furthermore, herbivores and fire interact (Bond, 2005), and the flammability of vegetation on nutrient-poor soils may in part result from relatively lower herbivory pressure (Archibald and Hempson, 2016).

A central element of predicting fire behavior at broad scales is how to characterize the crown size of individual trees and shrubs. In fire behavior models, crown size is often represented by canopy bulk density and canopy height (height from canopy base to top of canopy). Both are seen as essential predictors of wildland fire behavior (Affleck et al., 2012), with greater canopy sizes leading to increased fire intensity in the presence of vertical fuel continuity (Agee, 1996). Keyser and Smith (2010) demonstrated that these metrics of canopy size were insufficient without including the context of vertical structure; even after accounting for vertical structure, the relationship between fuel load and fire behavior is complex and dynamic across stand to landscape scales. Vegetation cover affects fuel loads, thereby reducing fire spread rate, heat release, and area burned as the distance between the crowns of neighboring individuals increases. However, horizontal variability in fuel load can lead to increased spread rate, heat release, and area burned (Atchley et al., 2021). Light detecting and ranging (LiDAR) technology facilitates efficient assessment of fuel architecture with great precision across broad scales (e.g., Price and Gordon, 2016), and methods such as structure from motion imaging may continue to make this possible at lower cost (Reilly et al., 2024).

Within a fuel of similar architecture such as grass fuels, biomass strongly influences fire behavior, and grassland fire occurrence often depends on previous-season growth conditions that influence fire season fuel loads. For example, invasive *Bromus tectorum* in the Great Basin of the western United States, which has altered fire regimes, exhibits multiyear effects of past precipitation on current season fire extent (Pilliod et al., 2017). Biomass and net primary productivity have often been used as proxies for fuel density to predict landscape flammability (Bradstock et al., 2010; Pausas et al., 2017). Both these metrics can be estimated across very broad extents through remote sensing or modeling. Distinctions between separate categories of biomass can be important to retain even at the broadest scales; for example, Newberry et al. (2020) found grass biomass to be the primary driver of landscape flammability across savanna–forest transition zones in Brazil, although Cardoso et al. (2018) found grass species flammability to be more important than biomass in such ecosystem boundaries in Gabon.

Interactions across fuel characteristics and non-additive effects

When considering the scaling of flammability from the leaf to organism to community scale, it is important to consider how interactions between adjacent fuel components influence whether fire will propagate from one fuel element to another (Finney et al., 2012). If the first fuel element ignites, the probability of the adjacent elements also igniting will depend on intrinsic properties such as fuel moisture and chemical composition. Additionally, this probability is influenced by extrinsic properties, both inherently non-static—such as the distance between elements, which affects the degree of pre-heating and airflow (e.g., wind, air entrainment) that can supply oxygen or cool the elements through convection (Sullivan, 2009a)—and static, such as topography (Finney et al., 2012). Under non-extreme fire conditions, even in the presence of significant pre-heating, element to element propagation generally occurs after direct flame contact, with factors such as slope and wind increasing this degree of flame contact (Finney et al., 2012). Under extreme fire conditions (i.e., forest fire danger index > 50), fire propagation and spread becomes independent of fuel conditions (Cruz et al., 2022), and there is evidence from a range of vegetation types (forests, shrublands) that the relevance of species-level fuel characteristics on fire behavior in the field decreases directly as a function of the forest fire danger index (Bessie and Johnson, 1995; Cruz et al., 2022). However, further work to determine thresholds where trait-based differences in fuels are relevant is warranted, especially in light of models that highlight the importance of convection for fire propagation (Cohen and Finney, 2023).

Non-additive effects challenge the extrapolation of individual plant flammability to the flammability of mixed-species communities. These effects, which arise from emergent physicochemical properties in fuel mixtures, lead to outcomes that cannot be accurately predicted by simply considering the flammability of individual species. When plants of differing flammability burn together, they can exhibit one of two effects: an additive effect, where the flammability of the mixture reflects the average of the individual species; or a non-additive effect, where the most or least flammable species may dominate, resulting in a net flammability higher or lower than expected (de Magalhães and Schwilk, 2012; van Altena et al., 2012; Della Rocca et al., 2018). This phenomenon of non-additivity has been documented in several studies assessing the flammability of surface fuel beds (de Magalhães and Schwilk, 2012; van Altena et al., 2012; Varner et al., 2017; Bowman et al., 2018; Della Rocca et al., 2018) and shoots (Wyse et al., 2018, Wei et al., 2025). Non-additive effects are most common for fire spread and duration, which likely reflects flames propagating via the most flammable components of a fuel bed (van Altena et al., 2012). These non-additive effects indicate that it is challenging to predict the flammability of a plant community solely based on aggregating the flammability of its individual species, although attempts have been made to do this using community-weighted means of flammability (Padullés Cubino et al., 2018). Given the complexity introduced by non-additive effects, there is a pressing need to better understand how these interactions occur when mixtures of species are burned, particularly using leaves, shoots or whole individuals.

CONCLUSIONS

Although some tissue and organismal scale plant traits influence flammability and hence fire behavior, their effect size remains unresolved as is how their influences vary among different vegetation types and change with fire weather. Live fuel moisture is one fuel characteristic where scaling from leaf to landscapes has been most successfully established, with work from both approaches linking trait investigations with remotely sensed data (e.g., Scarff et al., 2021; Griebel et al., 2023). There is evidence that some plant traits (e.g., leaf traits that control leaf litter flammability, Schwilk and Caprio, 2011) influence patterns of local fire severity such that they drive fire behavior at landscape scales. For other fuel characteristics such as architecture, there is potential to link trait measurements with newly available three-dimensional remotely sensed information, although the mechanistic connections need better study.

There has been progress in assessing which leaf-level traits matter for shoot-level flammability, but there are still gaps in extrapolating from shoot to individual up to the community and landscape scales despite the use of broader scale methods such as wind tunnels (e.g., Marino et al., 2014). This paucity of studies linking lab-based measurements of flammability and plant traits with wildland fire has reinforced a conceptual disconnection between top-down and bottom-up approaches. Research that directly addresses the criticisms of trait-centric approaches (e.g., that flammability measured at low heat fluxes does not inform stand level fire, Fernandes and Cruz, 2012) is also sorely needed. Bridging this conceptual gap demands carefully designed multiscale studies that use comparable measures of different dimensions of flammability and consistently used terminologies to describe traits and plant and community architecture. Of prime importance are experimental tests of flammability at the species level that predict fire behavior at the stand and community levels. Putting aside the mechanistic understanding of how plant traits influence fire, evaluating whether abundance-weighted averages of species-level shoot or individual level measurements of flammability can predict fire behavior is a key contribution. Finally, a critical applied research question is identifying how different traits affect fire weather thresholds (e.g., fire weather indices) when variation in fuel characteristics is overwhelmed by climatic factors in determining fire behavior (Cruz et al., 2022).

While in this review we have highlighted many areas where there are empirical and theoretical discrepancies between top-down and bottom-up approaches to predicting flammability, we remain hopeful that these can be overcome. Indeed, having researchers using both approaches working together will help mitigate the increasing impacts of changing fire regimes on human society (Bowman et al., 2020) and global biodiversity (Kelly et al., 2020).

DECLARATION OF FUNDING

M.A.A. was funded by a Lincoln University Argyle Fund Grant. H.R. and B.R. were funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Brazil (CAPES)—Finance Code 001, and H.R. was supported by the Labex CeMEB and publicly funded through the I-SITE Excellence Program of the University of Montpellier, under the Investissements France 2030. B.R. was funded by Carlos Chagas Filho Foundation for Research Support of the State of Rio de Janeiro (CNE E-26/200.446/2023). A.M.S.S. is funded by the NASA FireSense program (80NSSC24K1305) and the National Science Foundation and the Idaho Established Program to Stimulate Competitive Research awards 2242769 and 2316126. D.M.J.S.B. is supported by an Australian Government Australian Research Council Laureate Fellowship (FL220100099). A.F. is supported by grants Conselho Nacional de Desenvolvimento Científico e Tecnológico (312689/2021-7) and Fundação de Amparo à Pesquisa do Estado de São Paulo (2023/16620-0). Funding for the creation of Figure 1 came from the Brian Mason Scientific and Technical Trust (BMT 2023_08 to T.J.C. and M.A.A.). This work was supported in part by the USDA Forest Service, Rocky Mountain Research Station. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy.

AUTHOR CONTRIBUTIONS

D.W.S. conceived the review and wrote the first outline. D.W.S., T.J.C., M.A.A., N.G., B.R.M., R.H.N., G.L.W.P., and A.M.S.S. drafted major text sections. S.O., N.G., T.J.C. and D.W.S. designed the figure, and all authors contributed text and comments to multiple drafts of the manuscript.

ACKNOWLEDGMENTS

The authors thank the Special Issue Editor and two anonymous reviewers whose comments greatly improved the manuscript. The authors also thank Jagoba Malumbres-Olarte for creating the artwork for Figure 1.

CONFLICT OF INTEREST STATEMENT

Dylan W. Schwilk is an Associate Editor of the *American Journal of Botany* and Pedro Jaureguiberry, Imma Oliveras Menor, Stephanie G. Yelenik, and Timothy J. Curran are Special Issue Editors. None of these authors took part in the peer-review and decision-making processes for this paper.

ORCID

Dylan W. Schwilk http://orcid.org/0000-0003-3833-1932
Md. Azharul Alam http://orcid.org/0000-0001-9706-9925
George L. W. Perry http://orcid.org/0000-0001-9672-9135
Alistair M. S. Smith http://orcid.org/0000-0003-0071-9958
David M. J. S. Bowman http://orcid.org/0000-0001-8075-124X
Pedro Jaureguiberry http://orcid.org/0000-0002-7392-5157
Bruno H. P. Rosado http://orcid.org/0000-0002-8924-8672
Helena Roland http://orcid.org/0000-0003-4838-7403
Stephanie G. Yelenik http://orcid.org/0000-0002-9011-0769
Timothy J. Curran http://orcid.org/0000-0001-8817-4360

REFERENCES

Abdollahi, A., and M. Yebra. 2023. Forest fuel type classification: review of remote sensing techniques, constraints and future trends. *Journal of Environmental Management* 342: 118315.

Affleck, D. L., C. R. Keyes, and J. M. Goodburn. 2012. Conifer crown fuel modeling: current limits and potential for improvement. *Western Journal of Applied Forestry* 27: 65–169.

Agee, J. K. 1996. The influence of forest structure on fire behavior. *In* Proceedings of the 17th Annual Forest Vegetation Management Conference, 52–68, 1996. Forest Vegetation Management Conference, Mt. Shasta, CA, USA. Website: https://www.fs.usda.gov/rm/pubs/rmrs_gtr292/1996_agee.pdf

Alam, M. A., S. V. Wyse, H. L. Buckley, G. L. W. Perry, X. Cui, J. J. Sullivan, D. W. Schwilk, and T. J. Curran. 2025. Fuel architecture influences interspecific variation in shoot flammability, but not as much as leaf traits. *Journal of Ecology* 113: 322–338.

Alam, M. A., S. V. Wyse, H. L. Buckley, G. L. W. Perry, J. J. Sullivan, N. W. H. Mason, R. Buxton, et al. 2020. Shoot flammability is decoupled from leaf flammability, but controlled by leaf functional traits. *Journal of Ecology* 108: 641–653.

Alessio, G. A., J. Peñuelas, J. Llusià,in R. Ogaya, M. Estiarte, and M. De Lillis. 2008. Influence of water and terpenes on flammability in some dominant Mediterranean species. *International Journal of Wildland Fire* 17: 274–286.

Alexander, M. E. and M. G. Cruz. 2013. Corrigendum to: Assessing the effect of foliar moisture on the spread rate of crown fires. *International Journal of Wildland Fire* 22: 869–870.

Anderson, H. E., 1970. Forest fuel ignitibility. *Fire Technology* 6: 312–319.

Anderson, H. E. 1982. Aids to determining fuel models for estimating fire behavior. General Technical Report INT-122. U.S. Department of

Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, USA.

Archibald, S., and G. P. Hempson. 2016. Competing consumers: contrasting the patterns and impacts of fire and mammalian herbivory in Africa. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371: 20150309.

Archibald, S., C. E. Lehmann, C. M. Belcher, W. J. Bond, R. A. Bradstock, A. L. Daniau, K. G. Dexter, et al. 2018. Biological and geophysical feedbacks with fire in the Earth system. *Environmental Research Letters* 13: 033003.

Argañaraz, J. P., M. A. Landi, C. M. Scavuzzo, and L. M. Bellis. 2018. Determining fuel moisture thresholds to assess wildfire hazard: A contribution to an operational early warning system. *PLoS One* 13: e0204889.

Atchley, A. L., R. Linn, A. Jonko, C. Hoffman, J. D. Hyman, F. Pimont, C. Sieg, and R. S. Middleton. 2021. Effects of fuel spatial distribution on wildland fire behaviour. *International Journal of Wildland Fire* 30: 179–189.

Balaguer-Romano, R., R. Díaz-Sierra, M. De Cáceres, À. Cunill-Camprubí, R. H. Nolan, M. M. Boer, J. Voltas, and V. R. de Dios. 2022. A semi-mechanistic model for predicting daily variations in species-level live fuel moisture content. *Agricultural and Forest Meteorology* 323: 109022.

Bessie, W. C., and E. A. Johnson. 1995. The relative importance of fuels and weather on fire behavior in subalpine forests. *Ecology* 76: 747–762.

Blauw, L. G., N. Wensink, L. Bakker, R. S. P. Van Logtestijn, R. Aerts, N. A. Soudzilovskaia, and J. H. C. Cornelissen. 2015. Fuel moisture content enhances nonadditive effects of plant mixtures on flammability and fire behavior. *Ecology and Evolution* 5: 3830–3841.

Bond, W. J. 2005. Large parts of the world are brown or black: a different view on the 'Green World' hypothesis. *Journal of Vegetation Science* 16: 261–266.

Boving, I., J. Celebrezze, R. Salladay, A. Ramirez, L. D. Anderegg, and M. Moritz. 2023. Live fuel moisture and water potential exhibit differing relationships with leaf-level flammability thresholds. *Functional Ecology* 37: 2770–2785.

Bowman, D. M. J. S., B. J. French, and L. D. Prior. 2014. Have plants evolved to self-immolate? *Frontiers in Plant Science* 5: 590.

Bowman, D. M. J. S., C. Haverkamp, K. D. Rann, and L. D. Prior. 2018. Differential demographic filtering by surface fires: How fuel type and fuel load affect sapling mortality of an obligate seeder savanna tree. *Journal of Ecology* 106: 1010–1022.

Bowman, D. M., C. A. Kolden, J. T. Abatzoglou, F. H. Johnston, G. R. van der Werf, and M. Flannigan. 2020. Vegetation fires in the Anthropocene. *Nature Reviews Earth & Environment* 1: 500–515.

Bradstock, R. A. 2010. A biogeographic model of fire regimes in Australia: current and future implications. *Global Ecology and Biogeography* 19: 145–158.

Brain, C. K., and A. Sillent. 1988. Evidence from the Swartkrans cave for the earliest use of fire. *Nature* 336: 464–466.

Brando, P., M. Macedo, D. Silvério, L. Rattis, L. Paolucci, A. Alencar, M. Coe, and C. Amorim. 2020. Amazon wildfires: Scenes from a foreseeable disaster. *Flora* 268: p.151609.

Broido, A., and M. A. Nelson. 1964. Ash content: its effect on combustion of corn plants. *Science* 46: 652–663.

Budha-Magar S., N. J. Day, H. L. Buckley, O. R. Burge, S. J. Richardson, D. W. Schwilk, R. R. Ross, and T. J. Curran. 2024. Plant morphological traits and leaf nutrient concentration are associated with flammability and phylogenetic relationships in sub-alpine vegetation, New Zealand. *International Journal of Wildland Fire* 33: WF24038.

Burger, N., and W. Bond. 2015. Flammability traits of Cape shrubland species with different post-fire recruitment strategies. *South African Journal of Botany* 101: 40–48.

Burton, J. E., J. G. Cawson, A. I. Filkov, and T. D. Penman. 2021. Leaf traits predict global patterns in the structure and flammability of forest litter beds. *Journal of Ecology* 109: 1344–1355.

Burton, J. E., T. D. Penman, A. I. Filkov, and J. G. Cawson. 2023. Multi-scale investigation of factors influencing moisture thresholds for litter bed flammability. *Agricultural and Forest Meteorology* 337: 109514.

Campos-Ruiz, R., M. A. Parisien, and M. D. Flannigan. 2022. Physico-chemical characteristics controlling the flammability of live *Pinus banksiana* needles in central Alberta, Canada. *International Journal of Wildland Fire* 31: 857–870.

Cardoso, A. W., I. Oliveras, K. A. Abernethy, K. J. Jeffery, D. Lehmann, J. Edzang Ndong, I. McGregor, et al. 2018. Grass species flammability, not biomass, drives changes in fire behavior at tropical forest-savanna transitions. *Frontiers in Forests and Global Change* 1: 14.

Cawson, J. G., J. E. Burton, B. J. Pickering, V. Demetriou, and A. I. Filkov. 2023. Quantifying the flammability of living plants at the branch scale: which metrics to use? *International Journal of Wildland Fire* 32: 1404–1421.

Chuvieco, E., I. González, F. Verdú, I. Aguado, and M. Yebra. 2009. Prediction of fire occurrence from live fuel moisture content measurements in a Mediterranean ecosystem. *International Journal of Wildland Fire* 18: 430–441.

Cohen, J., and M. Finney. 2023. Fuel particle heat transfer part 2: radiation and convection during spreading laboratory fires. *Combustion Science and Technology* 195: 3122–3147.

Cornelissen, J. H. C., S. Grootemaat, L. M. Verheijen, W. K. Cornwell, P. M. Van Bodegom, R. Van Der Wal, and R. Aerts. 2017. Are litter decomposition and fire linked through plant species traits? *New Phytologist* 216: 653–669.

Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Díaz, N. Buchmann, D. E. Gurvich, P. B. Reich, et al. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335–380.

Cruz, M. G., M. E. Alexander, and P. M. Fernandes. 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, M. G., J. S. Gould, M. E. Alexander, A. L. Sullivan, W. L. McCaw, and S. Matthews. 2015. Empirical-based models for predicting head-fire rate of spread in Australian fuel types. *Australian Forestry* 78: 118–158.

Cruz, M. G., C. M. Hoffman, and P. M. Fernandes. 2025. Global synthesis of quantification of fire behaviour characteristics in forests and shrublands: recent progress. *Current Forestry Reports* 11: 8.

Cui, X., A. P. Paterson, S. V. Wyse, M. A. Alam, K. Maurin, R. Pieper, J. Padullés Cubino, et al. 2020. Shoot flammability of vascular plants is phylogenetically conserved and related to habitat fire-proneness and growth form. *Nature Plants* 6: 355–359

Cunningham, C. X., G. J. Williamson, R. H. Nolan, L. Teckentrup, M. M. Boer, and D. M. Bowman. 2024. Pyrogeography in flux: reorganization of Australian fire regimes in a hotter world. *Global Change Biology* 30: e17130.

Dai, D., D. Yu, W. Gao, G. L. W. Perry, A. M. Paterson, C. You, S. Zhou, et al. 2025. Leaf dry matter content is phylogenetically conserved and related to environmental conditions, especially wildfire activity. *Ecology Letters* 28: e70056.

de Magalhães, R. M. Q., and D. W. Schwilk. 2012. Leaf traits and litter flammability: evidence for non-additive mixture effects in a temperate forest. *Journal of Ecology* 100: 1153–1163.

de Magalhães, R. Q. and D. W. Schwilk. 2021. Moisture absorption and drying alter nonadditive litter flammability in a mixed conifer forest. *Journal of Ecology* 109: 234–245.

Della Rocca, G., R. Danti, C. Hernando, M. Guijarro, and J. Madrigal. 2018. Flammability of two Mediterranean mixed forests: study of the non-additive effect of fuel mixtures in laboratory. *Frontiers in Plant Science* 9: 825.

Dennison, P. E., and M. A. Moritz. 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.

Dennison, P. E., M. A. Moritz, and R. S. Taylor. 2008. Evaluating predictive models of critical live fuel moisture in the Santa Monica Mountains, California. *International Journal of Wildland Fire* 17: 18–27.

Drucker, J. R., A. Farguell, C. B. Clements, and A. K. Kochanski. 2023. A live fuel moisture climatology in California. *Frontiers in Forests and Global Change* 6: 1203536.

Ellis, T. M., D. M. Bowman, P. Jain, M. D. Flannigan, and G. J. Williamson. 2022. Global increase in wildfire risk due to climate-driven declines in fuel moisture. *Global Change Biology* 28: 1544–1559.

Engber, E. A., and J. M. Varner III. 2012. Patterns of flammability of the California oaks: the role of leaf traits. *Canadian Journal of Forest Research* 42: 1965–1975.

Fernandes, P. M. and M. G. Cruz. 2012. Plant flammability experiments offer limited insight into vegetation–fire dynamics interactions. *New Phytologist* 194: 606–609.

Finney, M. A. 1998. *FARSITE*: Fire area simulator—model development and evaluation. Research Paper RMRS-RP-4. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, CO, USA.

Finney, M. A., J. D. Cohen, S. S. McAllister, and W. M. Jolly. 2012. On the need for a theory of wildland fire spread. *International Journal of Wildland Fire* 22: 25–36.

French, N. H. F., L. K. Jenkins, T. V. Loboda, M. Flannigan, R. Jandt, L. L. Bourgeau-Chavez, and M. Whitley. 2015. Fire in arctic tundra of Alaska: past fire activity, future fire potential, and significance for land management and ecology. *International Journal of Wildland Fire* 24: 1045–1061.

Ganteaume, A. 2018. Does plant flammability differ between leaf and litter bed scale? Role of fuel characteristics and consequences for flammability assessment. *International Journal of Wildland Fire* 27: 342–352.

Ganteaume, A., M. Guijarro, M. Jappiot, C. Hernando, C. Lampin-Maillet, P. Pérez-Gorostiaga, and J. A. Vega. 2011a. Laboratory characterization of firebrands involved in spot fires. *Annals of Forest Science* 68: 531–541.

Ganteaume, A., J. Marielle, L.-M. Corinne, C. Thomas, and B. Laurent. 2011b. Effects of vegetation type and fire regime on flammability of undisturbed litter in Southeastern France. *Forest Ecology and Management* 261: 2223–2231.

Ganteaume, A., B. Romero, C. Fernandez, E. Ormeño, and C. Lecareux. 2021. Volatile and semi-volatile terpenes impact leaf flammability: differences according to the level of terpene identification. *Chemoecology* 31: 259–275.

Gao, X., and D. W. Schwilk. 2018. Grass canopy architecture influences temperature exposure at soil surface. *Fire* 1: 35.

Gao, X., and D. W. Schwilk. 2022. Burn hot or tolerate trees: flammability decreases with shade tolerance in grasses. *Oikos* 2022: e08930.

García, M., D. Riaño, M. Yebra, J. Salas, A. Cardil, S. Monedero, J. Ramirez, et al. 2020. A live fuel moisture content product from Landsat TM satellite time series for implementation in fire behavior models. *Remote Sensing* 12: 1714.

Gibson, R. K., R. A. Bradstock, T. Penman, D. A. Keith, and D. A. Driscoll. 2015. Climatic, vegetation and edaphic influences on the probability of fire across mediterranean woodlands of south-eastern Australia. *Journal of Biogeography* 42: 1750–1760.

Gill, A. M., and P. H. Moore. 1996. Ignitibility of leaves of Australian plants (Vol. 34). CSIRO Plant Industry, Canberra, Australia.

Gill, A. M. and P. Zylstra. 2005. Flammability of Australian forests. *Australian Forestry* 68: 87–93.

Glasspool, I. J., D. Edwards, and L. Axe. 2004. Charcoal in the Silurian as evidence for the earliest wildfire. *Geology* 32: 381–383.

Gornish, E. S., C. Campbell, L. Svejcar, S. M. Munson, K. Vaughn, M. K. Spaeth, S. G. Yelenik, et al. 2023. Functional traits are used in restoration practice: a response to Merchant et al. (2022). *Restoration Ecology* 31: e13880.

Gowda, J. H., M. Blackhall, L. Shipley, T. Kitzberger, and F. Tiribelli. 2022. Are digestibility and flammability related? Two variables shaping landscape dynamics of northwestern Patagonian forests. *Forest Ecology and Management* 503: 119810.

Graham, R. T., S. McCaffrey, and T. B. Jain. 2004. Science basis for changing forest structure to modify wildfire behavior and severity. General Technical Report RMRS-GTR-120. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, CO, USA.

Griebel, A., M. M. Boer, C. Blackman, B. Choat, D. S. Ellsworth, P. Madden, B. Medlyn, et al. 2023. Specific leaf area and vapour pressure deficit control live fuel moisture content. *Functional Ecology* 37: 719–731.

Grootemaat, S., I. J. Wright, P. M. Van Bodegom, and J. H. C. Cornelissen. 2017a. Scaling up flammability from individual leaves to fuel beds. *Oikos* 126: 1428–1438.

Grootemaat, S., I. J. Wright, P. M. Van Bodegom, J. H. C. Cornelissen, and W. K. Cornwell. 2015. Burn or rot: leaf traits explain why flammability and decomposability are decoupled across species. *Functional Ecology* 29: 1486–1497.

Grootemaat, S., I. J. Wright, P. M. Van Bodegom, J. H. C. Cornelissen, and V. Shaw. 2017b. Bark traits, decomposition and flammability of Australian forest trees. *Australian Journal of Botany* 65: 327–338.

Guerrero, F., L. Espinoza, C. Carmona, M. Blackhall, C. Quintero, K. Ocampo-Zuleta, S. Paula, et al. 2024. Unraveling the chemistry of plant flammability: exploring the role of volatile secondary metabolites beyond terpenes. *Forest Ecology and Management* 572: 122269.

Hagan, J. G., J. J. Henn, and W. H. Osterman. 2023. Plant traits alone are good predictors of ecosystem properties when used carefully. *Nature Ecology & Evolution* 7: 332–334.

He, T., J. G. Pausas, C. M. Belcher, D. W. Schwilk, and B. B. Lamont. 2012. Fire-adapted traits of *Pinus* arose in the fiery Cretaceous. *New Phytologist* 194: 751–759.

Hinojosa, M. B., E. Albert-Belda, B. Gómez-Muñoz, and J. M. Moreno. 2021. High fire frequency reduces soil fertility underneath woody plant canopies of Mediterranean ecosystems. *Science of the Total Environment* 752: 141877.

Jaureguiberry, P., G. Bertone, and S. Díaz. 2011. Device for the standard measurement of shoot flammability in the field: flammability measurement in the field. *Austral Ecology* 36: 821–829.

Jolly, W. M., M. A. Cochrane, P. H. Freeborn, Z. A. Holden, T. J. Brown, G. J. Williamson, and D. M. J. S. Bowman. 2015. Climate-induced variations in global wildfire danger from 1979 to 2013. *Nature Communications* 6(1). https://doi.org/10.1038/ncomms8537

Jolly, W. M., and D. M. Johnson. 2018. Pyro-ecophysiology: shifting the paradigm of live wildland fuel research. *Fire* 1: 8.

Kane, J. M., J. K. Kreye, R. Barajas-Ramirez, and J. M. Varner. 2021. Litter trait driven dampening of flammability following deciduous forest community shifts in eastern North America. *Forest Ecology and Management* 489: 119100.

Keeley, J. E. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire* 18: 116–126.

Kelly, L. T., K. M. Giljohann, A. Duane, N. Aquilué, S. Archibald, E. Batllori, A. F. Bennett, et al. 2020. Fire and biodiversity in the Anthropocene. *Science* 370: eabb0355.

Keyser, T., and F. W. Smith. 2010. Influence of crown biomass estimators and distribution on canopy fuel characteristics in ponderosa pine stands of the Black Hills. *Forest Science* 56: 156–165.

Krawchuk, M. A., and M. A. Moritz. 2011. Constraints on global fire activity vary across a resource gradient. *Ecology* 92: 21–132.

Kreye, J. K., N. W. Brewer, P. Morgan, J. M. Varner, A. M. S. Smith, C. M. Hoffman, and R. D. Ottmar. 2014. Fire behavior in masticated fuels: a review. *Forest Ecology and Management* 314: 193–207.

Kreye, J. K., J. K. Hiers, J. M. Varner, B. Hornsby, S. Drukker, and J. J. O'Brien. 2018. Effects of solar heating on the moisture dynamics of forest floor litter in humid environments: composition, structure, and position matter. *Canadian Journal of Forest Research* 48: 1331–1342.

Kreye, J. K., J. M. Kane, and J. M. Varner. 2023. Multivariate roles of litter traits on moisture and flammability of temperate northeastern North American tree species. *Fire Ecology* 19: 21.

Kreye, J. K., J. M. Kane, J. M. Varner, and J. K. Hiers. 2020. Radiant heating rapidly increases litter flammability through impacts on fuel moisture. *Fire Ecology* 16: 8.

Krix, D. W., M. L. Phillips, and B. R. Murray. 2019. Relationships among leaf flammability attributes and identifying low-leaf-flammability species at the wildland–urban interface. *International Journal of Wildland Fire* 28: 295–307.

Loudermilk, E. L., J. J. O'Brien, S. L. Goodrick, R. R. Linn, N. S. Skowronski, and J. K. Hiers. 2022. Vegetation's influence on fire behavior goes beyond just being fuel. *Fire Ecology* 18: 9.

Luo, K., X. Quan, B. He, and M. Yebra. 2019. Effects of live fuel moisture content on wildfire occurrence in fire-prone regions over Southwest China. *Forests* 10: 887.

Mahmud, A., N. Aktepe, and D. W. Schwilk. 2025. Moisture loss rate drives the species-specific sensitivity of shoot flammability to water status. *American Journal of Botany*, In press.

Manzello, S. L., A. Maranghides, and W. E. Mell. 2007. Firebrand generation from burning vegetation. *International Journal of Wildland Fire* 16: 458–462.

Marino, E., C. Hernando, J. Madrigal, and M. Guijarro. 2014. Short-term effect of fuel treatments on fire behaviour in a mixed heathland: a comparative assessment in an outdoor wind tunnel. *International Journal of Wildland Fire* 23: 1097–1107.

Martin R. E., D. A. Gordon, M.E. Gutierrez, D. S. Lee, D. M. Molina, R. A. Schroeder, D. B. Sapsis, et al. 1993. Assessing the flammability of domestic and wildland vegetation. *In* Proceedings of the 12th Conference on Fire and Forest Meteorology, 130–137, 1993, Jekyll Island, GA, USA. Society of American Foresters Publication 94–02, Bethesda, MD, USA.

Mason, N. W. H., C. Frazao, R. P. Buxton, and S. J. Richardson. 2016. Fire form and function: evidence for exaptive flammability in the New Zealand flora. *Plant Ecology* 217: 645–659.

Matthews, S., 2013. Dead fuel moisture research: 1991–2012. *International Journal of Wildland Fire* 23: 78–92.

McWethy, D. B., P. E. Higuera, C. Whitlock, T. T. Veblen, D. M. J. S. Bowman, G. J. Cary, S. G. Haberle, et al. 2013. A conceptual framework for predicting temperate ecosystem sensitivity to human impacts on fire regimes. *Global Ecology and Biogeography* 22: 900–912.

Melia, N., S. Dean, H. G. Pearce, L. Harrington, D. J. Frame, and T. Strand. 2022. Aotearoa New Zealand's 21st-century wildfire climate. *Earth's Future* 10: e2022EF002853.

Melnik, O. M., S. A. Paskaluk, M. Y. Ackerman, K. O. Melnik, D. K. Thompson, S. S. McAllister, and M. D. Flannigan. 2021. New in-flame flammability testing method applied to monitor seasonal changes in live fuel. *Fire* 5: 1.

Menning, K. M., and S. L. Stephens. 2007. Fire climbing in the forest: a semiqualitative, semiquantitative approach to assessing ladder fuel hazards. *Western Journal of Applied Forestry* 22: 88–93.

Miller, L., L. Zhu, M. Yebra, C. Rüdiger, and G. I. Webb. 2023. Projecting live fuel moisture content via deep learning. *International Journal of Wildland Fire* 32: 709–727.

Mitić, Z. S., S. Č. Jovanović, B. K. Zlatković, B. M. Nikolić, G. S. Stojanović, and P. D. Marin. 2017. Needle terpenes as chemotaxonomic markers in *Pinus*: Subsections Pinus and Pinaster. *Chemistry & Biodiversity* 14: e1600453.

Mitsopoulos, I. D., and A. P. Dimitrakopoulos. 2007. Canopy fuel characteristics and potential crown fire behavior in Aleppo pine (*Pinus halepensis* Mill.) forests. *Annals of Forest Science* 64: 287–299.

Murray, B. R., L. K. Hardstaff, and M. L. Phillips. 2013. Differences in leaf flammability, leaf traits and flammability-trait relationships between native and exotic plant species of dry sclerophyll forest. *PLoS One* 8: e79205.

Murray B. R., T. Hawthorne, T. J. Curran, D. W. Krix, M. I. Wallace, K. Young, M. L. Murray, et al. 2023. Shoot flammability patterns among plant species of the wildland–urban interface in the fire-prone Greater Blue Mountains World Heritage Area. *International Journal of Wildland Fire* 32: 1119–1134.

Mutch, R. W. and C. W. Philpot. 1970. Relation of silica content to flammability in grasses. *Forest Science* 16: 64–65.

Neilson, E. H., J. Q. D. Goodger, I. E. Woodrow, and B. L. Møller. 2013. Plant chemical defense: At what cost? *Trends in Plant Science* 18: 250–258.

Nelson, Jr., R. M.. 2000. Prediction of diurnal change in 10-h fuel stick moisture content. *Canadian Journal of Forest Research* 30: 1071–1087.

Newberry, B. M., C. R. Power, R. C. Abreu, G. Durigan, D. R. Rossatto, and W. A. Hoffmann. 2020. Flammability thresholds or flammability gradients? Determinants of fire across savanna–forest transitions. *New Phytologist* 228: 910–921.

Nolan, R. H., M. M. Boer, V. Resco De Dios, G. Caccamo, and R. A. Bradstock. 2016. Large-scale, dynamic transformations in fuel moisture drive wildfire activity across southeastern Australia. *Geophysical Research Letters* 43: 4229–4238.

Nolan, R. H., B. Foster, A. Griebel, B. Choat, B. E. Medlyn, M. Yebra, N. Younes, and M. M. Boer. 2022. Drought-related leaf functional traits control spatial and temporal dynamics of live fuel moisture content. *Agricultural and Forest Meteorology* 319: 108941.

Nolan, R. H., J. Hedo, C. Arteaga, T. Sugai, and V. Resco De Dios. 2018. Physiological drought responses improve predictions of live fuel moisture dynamics in a Mediterranean forest. *Agricultural and Forest Meteorology* 263: 417–427.

Nowacki, G. J., and M. D. Abrams. 2008. The demise of fire and "mesophication" of forests in the eastern United States. *BioScience* 58: 123–138.

Ocampo-Zuleta, K., J. G. Pausas, and S. Paula. 2024. FLAMITS: A global database of plant flammability traits. *Global Ecology and Biogeography* 33: 412–425.

Odion, D. C., M. A. Moritz, and D. A. DellaSala. 2010. Alternative community states maintained by fire in the Klamath Mountains, USA. *Journal of Ecology* 98: 96–105.

Ojeda, F., J. G. Pausas, and M. Verdú. 2010. Soil shapes community structure through fire. *Oecologia* 163: 729–735.

Ormeño, E., J. Ruffault, C. Gutigny, J. Madrigal, M. Guijarro, C. Hernando, and C. Ballini. 2020. Increasing cuticular wax concentrations in a drier climate promote litter flammability. *Forest Ecology and Management* 473: 118242.

Ortiz, A., H. M. Marinace, J. J. Fisk, L. Hankenson, A. S. Pacheco, H. D. Goodman, E. Potts, et al. 2023. Shoot flammability differences between forest and savanna trees are driven by leaf dry matter content. *Flora* 307: 152370.

Owens, M. K., C. D. Lin, C. A. Taylor, and S. G. Whisenant. 1998. Seasonal patterns of plant flammability and monoterpenoid content in *Juniperus ashei*. *Journal of Chemical Ecology* 24: 2115–2129.

Padullés Cubino, J., H. L. Buckley, N. J. Day, R. Pieper, and T. J. Curran. 2018. Community-level flammability declines over 25 years of plant invasion in grasslands. *Journal of Ecology* 106: 1582–1594.

Page, W. G., M. J. Jenkins, and J. B. Runyon. 2012. Mountain pine beetle attack alters the chemistry and flammability of lodgepole pine foliage. *Canadian Journal of Forest Research* 42: 1631–1647.

Papió, C., and L. Trabaud. 1990. Structural characteristics of fuel components of five Meditarranean shrubs. *Forest Ecology and Management* 35: 249–259.

Park, I., K. Fauss, and M. A. Moritz. 2022. Forecasting live fuel moisture of *Adenostema fasciculatum* and its relationship to regional wildfire dynamics across Southern California shrublands. *Fire* 5: 110.

Paula, S., D. P. Ramírez, S. Estay, and J. G. Pausas. 2024. Soil fertility shapes fire activity across Mediterranean-type climate regions. *Global Ecology and Biogeography* 33: 400–411.

Pausas, J. G., G. A. Alessio, B. Moreira, and J. G. Segarra-Moragues. 2016. Secondary compounds enhance flammability in a Mediterranean plant. *Oecologia* 180: 103–110.

Pausas, J. G., J. E. Keeley, and D. W. Schwilk. 2017. Flammability as an ecological and evolutionary driver. *Journal of Ecology* 105: 289–297.

Pausas, J. G., and B. Moreira. 2012. Flammability as a biological concept. *New Phytologist* 194: 610–613.

Penman, T. E., J. G. Cawson, S. Murphy, and T. J. Duff. 2017. Messmate stringybark: bark ignitability and burning sustainability in relation to fragment dimensions, hazard score and time since fire. *International Journal of Wildland Fire* 26: 866–876.

Pérez-Harguindeguy, N., S. Díaz, E. Garnier, S. Lavorel, H. Poorter, P. Jaureguiberry, M. S. Bret-Harte, et al. 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* 61: 167–234.

Philpot C. W. 1970. Influence of mineral content on the pyrolysis of plant materials. *Forest Science*. 16: 461–471.

Pickering, B. J., L. T. Bennett, and J. G. Cawson. 2023. Extending methods for assessing fuel hazard in temperate Australia to enhance data quality and consistency. *International Journal of Wildland Fire* 32: 1422–1437.

Pickett, B. M., S. G. Smith, T. H. Fletcher, and D. R. Weise. 2005. Burning characteristics of live California chaparral and Utah leaf samples. *In* Sixth Symposium on Fire and Forest Meteorology, 25–27, 2005, Canmore, Alberta, Canada. American Meteorological Society, Boston, MA, USA.

Pilliod, D. S., J. L. Welty, and R.S. Arkle. 2017. Refining the cheatgrass–fire cycle in the Great Basin: precipitation timing and fine fuel composition predict wildfire trends. *Ecology and Evolution* 7: 8126–8151.

Pimont, F., J. Ruffault, N. K. Martin-StPaul, and J. L. Dupuy. 2019. 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.

Plucinski, M. P., and W. R. Anderson. 2008. Laboratory determination of factors influencing successful point ignition in the litter layer of shrubland vegetation. *International Journal of Wildland Fire* 17: 628–637.

Popović, Z., S. Bojović, M. Marković, and A. Cerdà. 2021. Tree species flammability based on plant traits: a synthesis. *Science of the Total Environment* 800: 149625.

Potts, E., D. Tng, D. Apgaua, T. J. Curran, J. Engert, and S. G. Laurance. 2022. Growth form and functional traits influence the shoot flammability of tropical rainforest species. *Forest Ecology and Management* 522: 120485.

Price, O. F., and C. E. Gordon. 2016. The potential for LiDAR technology to map fire fuel hazard over large areas of Australian forest. *Journal of Environmental Management* 181: 663–673.

Prior, L. D., B. P. Murphy, and D. M. Bowman. 2018. Conceptualizing ecological flammability: an experimental test of three frameworks using various types and loads of surface fuels. *Fire* 1: 14.

Prior, L. D., B. P. Murphy, G. J. Williamson, M. A. Cochrane, W. M. Jolly, and D. M. J. S. Bowman. 2017. Does inherent flammability of grass and litter fuels contribute to continental patterns of landscape fire activity? *Journal of Biogeography* 44: 1225–1238.

Prior, L. D., K. Storey, G. J. Williamson, and D. M. J. S. Bowman. 2024. When soil becomes fuel: identifying a safe window for prescribed burning of Tasmanian vegetation growing on organic soils. *International Journal of Wildland Fire* 33: WF24061.

Rahman, N. E. B., S. W. Smith, W. N. Lam, K. Y. Chong, M. S. E. Chua, P. Y. Teo, D. W. J. Lee, et al. 2023. Leaf decomposition and flammability are largely decoupled across species in a tropical swamp forest despite sharing some predictive leaf functional traits. *New Phytologist* 238: 598–611.

Rao, K., A. P. Williams, N. S. Diffenbaugh, M. Yebra, C. Bryant, and A. G. Konings. 2023. Dry live fuels increase the likelihood of lightning-caused fires. *Geophysical Research Letters* 50: p.e2022GL100975.

Rao, K., A. P. Williams, N. S. Diffenbaugh, M. Yebra, and A. G. Konings. 2022. Plant-water sensitivity regulates wildfire vulnerability. *Nature Ecology & Evolution* 6: 332–339.

Reed, W. P., J. M. Varner, E. E. Knapp, and J. K. Kreye. 2020. Long-term changes in masticated woody fuelbeds in northern California and southern Oregon, USA. *International Journal of Wildland Fire* 29: 807–819.

Reilly, S., M. L. Clark, L. Loechler, J. Spillane, M. Kozanitas, P. Krause, D. Ackerly, et al. 2024. Unoccupied aerial system (UAS) Structure-from-Motion canopy fuel parameters: Multisite area-based modelling across forests in California, USA. *Remote Sensing of Environment* 312: 114310.

Rogers, B. M., A. J. Soja, M. L. Goulden, and J. T. Randerson. 2015. Influence of tree species on continental differences in boreal fires and climate feedbacks. *Nature Geoscience* 8: 228–234.

Rollins, M. G., C. Rodriguez-Franco, T. Haan, and S. Conard. 2017. Research and development wildland fire and fuels accomplishments and outcomes. FS-1086. U.S. Department of Agriculture, Forest Service, Washington, D.C., USA.

Rossa, C. G. and P. M. Fernandes. 2018. Live fuel moisture content: The 'pea under the mattress' of fire spread rate modeling? *Fire* 1: 43.

Rothermel, R. C. 1972. A mathematical model for predicting fire spread in wildland fuels. Research Paper RP-INT-15. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, USA.

Rothermel, R. C., R. A. Wilson, G. A. Morris, and S. S. Sackett. 1986. Modeling moisture content of fine dead wildland fuels: input to the BEHAVE fire prediction system. Research Paper RP-INT-359. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, USA.

Salisbury, F. B., and C. W. Ross. 1992. Plant physiology, 4th ed. Wadsworth, Belmont, CA, USA.

Santacruz-García, A. C., S. Bravo, F. del Corro, and F. Ojeda. 2019. A comparative assessment of plant flammability through a functional approach: The case of woody species from Argentine Chaco region. *Austral Ecology* 44: 1416–1429.

Saura-Mas, S., S. Paula, J. G. Pausas, and F. Lloret. 2010. Fuel loading and flammability in the Mediterranean Basin woody species with different post-fire regenerative strategies. *International Journal of Wildland Fire* 19: 783–794.

Scarff, F. R., B. F. Gray, and M. Westoby. 2012. Exploring phosphate effects on leaf flammability using a physical chemistry model. *International Journal of Wildland Fire* 21: 1042–1051.

Scarff, F. R., T. Lenz, A. E. Richards, A. E. Zanne, I. J. Wright, and M. Westoby. 2021. Effects of plant hydraulic traits on the flammability of live fine canopy fuels. *Functional Ecology* 35: 835–846.

Scarff, F. R., and M. Westoby. 2006. Leaf litter flammability in some semi-arid Australian woodlands. *Functional Ecology* 20: 745–752.

Scarff, F. R., and M. Westoby. 2008. The influence of tissue phosphate on plant flammability: a kinetic study. *Polymer Degradation and Stability* 93: 1930–1934.

Schlaeppi, K., J. J. Gross, S. Hapfelmeier, and M. Erb. 2021. Plant chemistry and food web health. *New Phytologist* 231: 957–962.

Schwilk, D. W. 2003. Flammability is a niche construction trait: canopy architecture affects fire intensity. *American Naturalist* 162: 725–733.

Schwilk, D. W. 2015. Dimensions of plant flammability. *New Phytologist* 206: 486–488.

Schwilk, D. W., and A. C. Caprio. 2011. Scaling from leaf traits to fire behaviour: community composition predicts fire severity in a temperate forest. *Journal of Ecology* 99: 970–980.

Scott, J. H., and R. E. Burgan. 2005. Standard fire behavior fuel models: a comprehensive set for use with Rothermel's surface fire spread model. General Technical Report RMRS-GTR-153. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.

Simpson, K. J., S. Archibald, and C. P. Osborne. 2022. Savanna fire regimes depend on grass trait diversity. *Trends in Ecology & Evolution* 37: 749–758.

Simpson, K. J., B. S. Ripley, P. Christin, C. M. Belcher, C. E. R. Lehmann, G. H. Thomas, and C. P. Osborne. 2016. Determinants of flammability in savanna grass species. *Journal of Ecology* 104: 138–148.

Smith, A. M. S., W. T. Tinkham, D. P. Roy, L. Boschetti, R. L. Kremens, S. S. Kumar, A. M. Sparks, and M. J. Falkowski. 2013. Quantification of fuel moisture effects on biomass consumed derived from fire radiative energy retrievals. *Geophysical Research Letters* 40: 6298–6302.

Sullivan, A. L. 2009a. Wildland surface fire spread modelling, 1990–2007. 1: Physical and quasi-physical models. *International Journal of Wildland Fire* 18: 349–368.

Sullivan, A. L. 2009b. Wildland surface fire spread modelling, 1990–2007. 2: Empirical and quasi- empirical models. *International Journal of Wildland Fire* 18: 369–386.

Sullivan, A. L. 2009c. Wildland surface fire spread modelling, 1990–2007. 3: Simulation and mathematical analogue models. *International Journal of Wildland Fire* 18: 387–403.

Sultana, N. 2022. *Traits underpinning the eco-physiological processes linking drought and flammability*. PhD. Thesis. Lincoln University, Lincoln, New Zealand.

Talhelm, A. F., and A. M. S. Smith. 2018. Litter moisture adsorption is tied to tissue structure, chemistry, and energy concentration. *Ecosphere* 9: e02198.

Tarifa, C. S., P. P. Del Notario, and F. G. Moreno. 1965. On the flight paths and lifetimes of burning particles of wood. *Symposium (International) on Combustion* 10: 1021–1037.

Terrah, S. M., F. Z. Sabi, O. Mosbah, A. Dilem, N. Hamamousse, A. Sahila, O. Harrouz, et al. 2020. Nonexistence of critical fuel moisture content for flammability. *Fire Safety Journal* 111: 102928.

Tumino, B. J., T. J. Duff, J. Q. D. Goodger, and J. G. Cawson. 2019. Plant traits linked to field-scale flammability metrics in prescribed burns in *Eucalyptus* forest. *PLoS One* 14: e0221403.

Turetsky, M. R., B. Benscoter, S. Page, G. Rein, G. R. Van Der Werf, and A. Watts. 2015. Global vulnerability of peatlands to fire and carbon loss. *Nature Geoscience* 8: 11–14.

Turner, I. M. 1994. Sclerophylly: primarily protective? *Functional Ecology* 8: 669–675.

Van Altena C., R. S. van Logtestijn, W. K. Cornwell, and J. H. Cornelissen. 2012. Species composition and fire: non-additive mixture effects on ground fuel flammability. *Frontiers in Plant Science* 3: 63.

Van Der Plas, F., T. Schröder-Georgi, A. Weigelt, K. Barry, S. Meyer, A. Alzate, R. L. Barnard, et al. 2020. Plant traits alone are poor predictors of ecosystem properties and long-term ecosystem functioning. *Nature Ecology & Evolution* 4: 1602–1611.

Van Wilgen, B. W., K. B. Higgins, and D. U. Bellstedt. 1990. The role of vegetation structure and fuel chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. *Journal of Ecology* 78: 210–222.

Varner, J. M., J. M. Kane, J. K. Kreye, and E. Engber. 2015. The flammability of forest and woodland litter: a synthesis. *Current Forestry Reports* 1: 91–99.

Varner, J. M., H. G. Kuljian and J. K. Kreye. 2017. Fires without tanoak: the effects of a non-native disease on future community flammability. *Biological Invasions* 19: 2307–2317.

Varner, J. M., T. M. Shearman, J. M. Kane, E. M. Banwell, E. S. Jules, and M. C. Stambaugh. 2022. Understanding flammability and bark thickness in the genus *Pinus* using a phylogenetic approach. *Scientific Reports* 12: 1–10.

Viney, N. 1991. A review of fine fuel moisture modelling. *International Journal of Wildland Fire* 1: 215–234.

Walker, X. J., J. L. Baltzer, S. G. Cumming, N. J. Day, C. Ebert, S. Goetz, J. F. Johnstone, et al. 2019. Increasing wildfires threaten historic carbon sink of boreal forest soils. *Nature* 572: 520–523.

Wei, P., L. Tang, Z. Xiong, B.B. Lamont, L. Chen, W. Xue, Z. Zhao, et al. 2025. Non-additive effects of leaf-litter flammability on eight subtropical tree species: implications for forest species composition and fire susceptibility. *Journal of Environmental Management* 374: 124053.

Weise, D. R., E. Koo, X. Zhou, S. Mahalingam, F. Morandini, and J.-H. Balbi. 2016. Fire spread in chaparral – a comparison of laboratory data and model predictions in burning live fuels. *International Journal of Wildland Fire* 25: 980–994.

Weise, D. R., R. H. White, F. C. Beall, and M. Etlinger. 2005. Use of the cone calorimeter to detect seasonal differences in selected combustion characteristics of ornamental vegetation. *International Journal of Wildland Fire* 14: 321–338.

White, R. H., and W. C. Zipperer. 2010. Testing and classification of individual plants for fire behaviour: plant selection for the wildland–urban interface. *International Journal of Wildland Fire* 19: 213–227.

Wickramasinghe, A. M. K., M. M. Boer, C. X. Cunningham, R. H. Nolan, D. M. J. S. Bowman, and G. J. Williamson. 2024. Modeling the probability of dry lightning-induced wildfires in Tasmania: a machine learning approach. *Geophysical Research Letters* 51: e2024GL110381.

Wood, S. W., and D. M. J. S. Bowman. 2012. Alternative stable states and the role of fire–vegetation–soil feedbacks in the temperate wilderness of southwest Tasmania. *Landscape Ecology* 27: 13–28.

Wyse, S. V., G. L. W. Perry, and T. J. Curran. 2018. Shoot-level flammability of species mixtures is driven by the most flammable species: implications for vegetation–fire feedbacks favouring invasive species. *Ecosystems* 21: 886–900.

Wyse, S. V., G. L. Perry, D. M. O'Connell, P. S. Holland, M. J. Wright, C. L. Hosted, S. L. Whitelock, et al. 2016. A quantitative assessment of shoot flammability for 60 tree and shrub species supports rankings based on expert opinion. *International Journal of Wildland Fire* 25: 466–477.

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

Younes, N., M. Yebra, M. M. Boer, A. Griebel, and R. H. Nolan. 2024. A review of leaf-level flammability traits in eucalypt trees. *Fire* 7: 183.

Zanzarini, V., A. N. Andersen, and A. Fidelis. 2022. Flammability in tropical savannas: variation among growth forms and seasons in Cerrado. *Biotropica* 54: 979–987.

Zhao, L., M. Yebra, A. I. van Dijk, G. J. Cary, and D. Hughes. 2022. Controlled field experiment clarifies the influence of soil moisture on litter moisture content. *Agricultural and Forest Meteorology* 314: 108782.

Zigner, K., L. M. V. Carvalho, S. Peterson, F. Fujioka, G.-J. Duine, C. Jones, D. Roberts, and M. Moritz. 2020. Evaluating the ability of FARSITE to simulate wildfires influenced by extreme, downslope winds in Santa Barbara, California. *Fire* 3: 29.

Zylstra, P., R. A. Bradstock, M. Bedward, T. D. Penman, M. D. Doherty, R. O. Weber, A. M. Gill, and G. J. Cary. 2016. Biophysical mechanistic modelling quantifies the effects of plant traits on fire severity: species, not surface fuel loads, determine flame dimensions in eucalypt forests. *PLoS One* 11: e0160715.

How to cite this article: Schwilk, D. W., M. A. Alam, N. Gill, B. R. Murray, R. H. Nolan, S. Ondei, G. L. W. Perry, et al. 2025. From plant traits to fire behavior: Scaling issues in flammability studies. *American Journal of Botany* 112: e70040.
https://doi.org/10.1002/ajb2.70040