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Combining ecophysiology and combustion traits: a pyro-ecophysiological approach to live fuel moisture prediction in common shrubs

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Abstract

Background Quantifying fuel moisture content accurately is critical for understanding global vegetation flammability. While models representing changes in dead fuel moisture are relatively advanced, the mechanisms driving fluctuations in live fuel moisture content (LFMC) have been difficult to capture. Living plants make up a large proportion of the fuel complex for wildfires, yet linking plant and combustion science to advance our understanding of wildfire risk has, to date, been limiting. Developing mechanistic approaches to link these two disciplines will confer greater understanding and capacity to model landscape fire risk in vegetated areas across the globe.

Results Here, we present a mechanistic model that combines ecophysiology and combustion traits to determine LFMC. We evaluate model performance for seasonal fluctuations in LFMC for six shrubs common to the intermountain west USA. Finally, we demonstrate how these measurements can be used to parameterize a physics-based coupled fire model (QUIC-fire) and used to assess how shrube seasonal dynamics impact modeled fire behavior and subsequent fuel consumption.

We collected 860 foliage samples across 2022 and 2023 to test the performance of the mechanistic model. The model decomposes LFMC into leaf mass area (LMA), relative water content (RWC), surface-area-to-volume ratio (SAV), and the volumetric saturated water holding capacity (κ). We tested ten model variants using combinations of fixed and time-varying inputs to understand model performance using summarized inputs. The best performing model included time-varying LMA and RWC, and seasonally fixed inputs for SAV and κ ($r^2 = 0.89$, MAE = 11.38%) across all shrub species. Physical and chemical model inputs from a single species across a season were then input to QUIC-fire, where fuel consumption changed from 2.37% early in the season (May) to 97.33% toward the end of summer in late August.

Conclusions Mechanistic calculations of LFMC from the same physical and chemical variables used to parameterize the physics-based fire model represents a step forward in our capacity to link ecophysiology and combustion science. These linkages will enable us to bridge decades of plant physiology and combustion science using fire models and simulators and it will improve our ability to interpret field measurements of LFMC across plant functional types.

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Resumen

Antecedentes La cuantificación de la humedad de los combustibles vegetales es crítica para entender la inflamabilidad de la vegetación a nivel global. Mientras que los modelos que representan cambios en la humedad del combustible muerto están bastante avanzados, los mecanismos que llevan a las fluctuaciones en el contenido de humedad de los combustibles vivos (LFMC), permanecen como difíciles de determinar. Las plantas vivas representan una gran proporción de los complejos de combustibles en incendios de vegetación, lo que hace que el vínculo entre la ciencia de las plantas y de la combustión sea limitado para avanzar en nuestro conocimiento sobre el riesgo de estos incendios. El desarrollo de aproximaciones mecanísticas para entrelazar estas dos disciplinas puede conferir una mayor comprensión y capacidad para modelar el riesgo de incendios a nivel de paisaje en áreas vegetadas de todo el mundo.

Resultados Presentamos aquí un modelo mecanístico que combina la ecofisiología de las plantas y las características de su combustión para determinar el contenido de humedad del combustible vegetal vivo (LFMC). Evaluamos la performance del modelo para determinar las fluctuaciones estacionales del LFMC para seis arbustos comunes de en la región inter-montana del oeste de los EEUU. Finalmente, demostramos cómo esas mediciones pueden ser usadas para parametrizar un modelo físico acoplado de fuego (QUIC-fire) y usado luego para determinar cómo la dinámica estacional de los arbustos impacta en el comportamiento modelado del fuego y en el subsecuente consumo del combustible. Colectamos 860 muestras de follaje entre 2022 y 2023 para probar la performance del modelo mecanístico. El modelo descompone el LFMC en: la masa del área de la hoja (LMA), el contenido relativo de agua (RWC), la relación entre el área de superficie de la hoja y el volumen (SAV), y la capacidad de retención del agua volumétrica saturada (k). Probamos diez variantes del modelo usando combinaciones de datos de ingreso fijos y variables en el tiempo para entender la performance del modelo usando resúmenes de los datos de ingreso. La performance del mejor modelo incluyó el LAM en tiempo variable, y RWC, y datos estacionales fijos para SAV y k (r^2=0.89, MAE=11.38%) para todas las especies de arbustos. Los datos de ingreso físicos y químicos del modelo para una especie a lo largo de una estación fue entonces el dato de ingreso para QUIC-fire, en el cual lel consumo del combustible cambió desde un 2,37% al inicio de la temporada (Mayo) al 97% hacia fines del verano en agosto tardío.

Conclusiones Los cálculos mecanísticos del LFMC de las mismas variables físicas y químicas usadas para parametrizar el modelo físico de fuego, representa un paso hacia adelante en nuestra capacidad para unir la ecofisiología con la ciencia de la combustión. Estas uniones nos permitirán reducir la brecha de décadas entre la fisiología vegetal y la ciencia de la combustión usando modelos de simulación en fuegos y mejorará nuestra habilidad para interpretar la LFMC entre plantas de distintos tipos funcionales.

Introduction

Across the globe fire is a common disturbance process that influences the distribution and composition of vegetation—including dominant tree species and understorey shrub communities (Pausas et al. 2017). Although fire can often promote ecosystem functioning (Bond and Keeley 2005), it can negatively impact people, infrastructure and the environment (Kelly et al. 2020; Bowman et al. 2017). As wildfire activity intensifies under climate warming in many parts of the world, land and fire managers are increasingly asked to provide fire risk estimates and forecasts to communities (Miller and Ager 2012). However, to fully resolve potential fire risk, we must understand the physical processes that underpin fire ignition and behavior across landscapes, particularly for understorey plant communities, where fires commonly ignite and spread (Finney et al. 2013).

Fuel moisture content (FMC) is a key determinant of fire activity and is commonly monitored or modeled by managers to estimate landscape fire risk and potential fire behavior (Rothermel et al. 1986; Burgan 1979; McArthur 1967). FMC describes the amount of water relative to oven dry weight, and it is important for fire behavior because some or all of the water must be removed from the fuel for efficient combustion to occur (Matthews et al. 2010). Therefore, high FMC reduces fire rate of spread and lowers overall consumption (Masinda et al. 2021; Rossa et al. 2016). Wildland fires typically burn through a mixture of live and dead fuels and while understanding FMC variability in both is important, the processes that govern water transport in and out of these fuels are fundamentally different (Jolly and Johnson 2018).

While dead fuel moisture dynamics have been studied for decades (Byram and Jemison 1943; Viney and Hatton 1990), studies investigating live fuels are comparatively recent (Viegas et al. 2001; Wagner 1977). Estimating live fuel moisture content (LFMC) is challenging because both water content and dry mass change at daily (Balaguer-Romano et al. 2022), seasonal (Pellizzaro et al. 2007; Nolan et al. 2018) and inter-annual scales (Vinodkumar et al. 2021). Approaches focused on estimating LFMC through changes to water content alone, either through drought indices and meteorological conditions (McCaw et al. 2018; Ruffault et al. 2018), or remote sensing (Qi et al. 2012; Caccamo et al. 2012), have reported mixed results and while many still provide useful products (e.g., Yebra et al. (2018); Keetch and Byram (1968)), to date we have been unable to account for all the factors driving variability in LFMC.

More recent live fuel dynamics work has focused on understanding the contribution of physiological plant traits in controlling fluctuations in both the water mass (numerator) and dry mass (denominator) of the LFMC equation (Pivovaroff et al. 2019; Nolan et al. 2020; Scarff et al. 2021; Boving et al. 2023). Water content fluctuations have been linked to relative water content (RWC), which quantifies the amount of water in a sample relative to saturation and is a more direct metric of water stress in plants than LFMC. Jolly et al. (2014) demonstrated that RWC is strongly related to changes in LFMC, and (Nolan et al. 2020) mechanistically linked these using pressure volume curves derived from leaf water potential measurements. Other authors have demonstrated the utility of normalized dry matter metrics such as leaf mass area (LMA), or its inverse, specific leaf area (SLA) for estimating seasonal fluctuations in LFMC for overstorey trees (Brown et al. 2022; Nolan et al. 2020). Griebel et al. (2023) report that SLA was the single most important variable for predicting LFMC fluctuations in Australian *Eucalyptus* woodlands in a biophysical model that accounted for up to 89% of the variability in LFMC. Recently, Jolly et al. (2025) described a physiology-based mechanistic model that fully resolves LFMC from four physio-chemical variables: RWC, LMA, surface-area-to-volume ratio (SAV), and a species specific scalar that describes foliage volumetric maximum water holding capacity (κ). The authors demonstrate the strong performance of this model for mature conifer tree foliage. However, the capacity of the mechanistic LFMC model to characterize seasonal fluctuations in shrub foliage has not been evaluated to date.

Understanding seasonal fluctuations in LFMC is important for modeling fire behavior and fire risk to communities (Pimont et al. 2019). The inputs to the (Jolly et al. 2025) mechanistic LFMC model (RWC, LMA, SAV and κ) have direct relationships with flammability, thus including these in LFMC modeling will aid bridging the gap between plant physiology and fire behavior. For example, fuel dry matter (represented in the model through LMA) is comprised primarily of structural compounds, starches, sugars and crude fat. In addition to being important for plant function, these variables facilitate flaming combustion by creating pyrolyzates when heated and providing the solid fuel for combustion (Boardman et al. 2021). The role of SAV in flammability is well established (Brown 1970; Burton et al. 2021), as fuels with higher surface area per unit mass acclimate more quickly to changes in temperature, and so are more responsive to radiative and convective heat transfer (Rothermel and Anderson 1966). In turn, this can promote faster ignition time (Santoni et al. 2014) if fuel complex bulk density is sufficient. The direct relationship between these physio-chemical variables and combustion means that many fire behavior models use similar physio-chemical inputs. High-fidelity fire spread simulators, such as QUIC-fire (Linn et al. 2020), have been developed to capture complex wildland and prescribed fire dynamics in 3D and require a suite of inputs to describe fuel conditions and structure. The benefit of calculating LFMC mechanistically from the physio-chemical variables referenced here is that these same variables, or direct derivatives of, can be used in the fire behavior model as inputs for predicting fire behavior. Consequently, the characterization of fuel condition and fire spread can be drawn from the same set of consistent inputs. This may be particularly important in ecosystems with a high proportion of shrubby understorey fuels, as the condition of these fuels partially determines whether fires that ignite at ground level are able to transition to crown fires (Chuvieco et al. 2009; Jolly 2007).

Here we present a study that aims to evaluate the performance of a recently developed (Jolly et al. 2025) physiology-based mechanistic LFMC model for six common understorey shrubs in the inter-mountain west USA. We demonstrate how plant physical and chemical characteristics vary seasonally within a species, and across different species, and how this interacts with LFMC. Finally, we input a season of measured data for a single species into QUIC-fire, a physics-based coupled fire-atmospheric model, to assess the impact of seasonal shrub dynamics on modeled fire behavior.

Methods

Study area

We collected foliage samples from six shrubs common to the inter-mountain west USA (Janish and Thorne 1972) during the 2022 and 2023 fire seasons. In 2022, *Physocarpus malvaceus* (Greene) Kuntze (mallow ninebark, PHYMAL) foliage was sampled intensively at weekly intervals between May and September. In 2023, we collected foliage from *Amelanchier alnifolia* (Nutt.) Nutt. (western service berry, AMEALN), *Ceanothus velutinus* Douglas ex Hook. (snowbrush, CEAVEL), *Mahonia repens* (Lindl.) G. Don (Oregon-grape, MAHREP), *Spiraea betulifolia* Pall. (white spirea, SPIBET), *Symphoricarpos albus* (L.) S.F. Blake (common snowberry, SYMALB), and PHYMAL four times between June and August.

We sampled at two locations: Blue Mountain National Recreation Area (PHYMAL) and TV Mountain (AMEALN, CEAVEL, MAHREP, SPIBET, SYMALB). Blue Mountain (latitude: 46.82918, longitude: −114.11812) is approximately 10 km south-west of Missoula, Montana, USA, while TV Mountain (latitude: 47.00239, longitude: −114.03398) is approximately 14 km to the north. The area has a warm humid continental climate (Köppen-Geiger Dfb), which is characterized by warm summers and cold winters (Peel et al. 2007). July is typically the warmest month (monthly temperature normal (T) = 20.2 °C), and December the coldest (monthly T normal = −4.2 °C), with an annual precipitation normal of 425.7 mm (data for Missoula, MT, 1991–2020) (NOAA 2021). The sampling areas are both open mixed stands of Douglas-fir (*Pseudotsuga menziesii*) and Ponderosa Pine (*Pinus ponderosa*) forest.

Field data collection

Foliage samples were collected in two cohorts across 2022 and 2023. In 2022, we collected twenty-four PHYMAL foliage samples on a weekly basis between May and September. In 2023, we collected twenty foliage samples for all six shrub species four times between June and August. Across both years, field sampling was conducted in the morning to ensure enough time to process all samples on the same day, consequently, LFMC may not reflect a daily minima (peak flammability), but is consistent across the dataset. Across the two seasons, the timing of collection was targeted to the fire season in the inter-mountain west USA, although the months of collection differ due to seasonal differences in foliage green-up and senescence. Individual foliage samples were gathered from randomly selected plants within a designated 100 m × 100 m area. We collected the samples by cutting sun-exposed terminal branches that had a bud and/or were actively flowering (if applicable) and transported to the laboratory in a sealed plastic bag in a cooler.

Laboratory analysis

We processed the samples in the laboratory on the afternoon of collection. Twenty-four (in 2022) or 20 (in 2023) individual terminal leaves were excised from the sampled branchlets using a razor blade and the fresh mass (FM) recorded to the nearest 0.1 mg. Fresh volume (FV) was determined using a balance density kit (Model EX224, Ohaus, Parsippany, NJ, USA). Each sample was patted dry, placed on a piece of white paper with a measurement reference, flattened with a piece of clear perspex and photographed. To estimate one-sided projected surface area (SA), the photographs were processed using ImageJ software following (Ferreira and Rasband 2012). The leaves were then placed into vials with the petiole of each leaf submerged in de-ionized water (Arndt et al. 2015). Sealed vials were left to re-hydrate overnight at 4 °C. Twenty-four hours later, we extracted the samples, patted them dry with paper towel and reweighed to determine a turgid mass (TM). Leaves were then placed in a labeled muffin pan, dried in a convection oven for 48 h at 70 °C and re-weighed to determine the dry mass (DM).

Estimating physical and chemical characteristics

LFMC was determined using two separate equations in this study. The existing approach takes the fresh mass and dry mass and expresses it as water content as a percent of oven dry weight:

$$LFMC = \frac{Fresh\ Mass - Dry\ Mass}{Dry\ Mass} \times 100 \tag{1}$$

LFMC was then calculated following Jolly et al. (2025). This equation expresses LFMC as a function of four common physiological measurements that are also included in some fire behavior models: relative water content (RWC), leaf mass area (LMA), surface-area-to-volume-ratio (SAV) and the maximum water holding capacity of the sample, labeled by the authors as kappa (κ).

$$LFMC\ (\%) = \frac{\frac{RWC}{100} \times \kappa}{LMA \times SAV} \times 100 \tag{2}$$

RWC is a standard metric used by physiologists to quantify the water content of plants (González and González-Vilar 2001) and it describes the the amount of water in a sample relative to the maximum amount that can be held at saturation (turgid mass). It is calculated as:

$$RWC\ (\%) = \frac{Fresh\ Mass - Dry\ Mass}{Turgid\ Mass - Dry\ Mass} \times 100 \tag{3}$$

Leaf mass area (LMA) represents the mass of foliage per unit area. Specific leaf area (SLA) is the inverse of LMA as is also commonly used in plant physiology studies. LMA was calculated from all-sided projected surface area (SA) and dry weight using the following equation:

$$LMA\ (kg\ m^{-2}) = \frac{Dry\ Mass}{\alpha \times Surface\ Area} \tag{4}$$

where α is a factor to scale from one-sided projected foliage surface area to all-sided surface area. Scaling may be required, as LMA and SLA are typically calculated from one-sided projected surface area (Poorter et al. 2009). However, all-sided surface area is a more relevant metric for combustion science due to its role in heat transfer, and (all-sided) surface area to volume ratio (SAV, also commonly expressed as SVR) is a key input to the

QUIC-fire simulation model. For the broadleaf shrubs in this study, α was assumed to be 2, however, α varies across foliage types. To calculate surface-area-to-volume ratio, total surface area was divided by the fresh volume of the foliage following:

$$SAV\ (m^2\ m^{-3}) = \frac{\alpha \times Surface\ Area}{Fresh\ Volume} \quad (5)$$

κ is a scaling parameter that represents the maximum amount of water that a sample can expand to hold at saturation. It was calculated in this study as:

$$\kappa\ (kg\ m^{-2}) = \frac{Turgid\ Mass - Dry\ Mass}{Fresh\ Volume} \quad (6)$$

Modeling fire behavior using the QUIC-fire simulator

Five weeks of data that represented the range of seasonal fluctuations in LMA, RWC, SAV, and κ for PHYMAL foliage were extracted from the full dataset and input to the QUIC-fire fire behavior simulator (Linn et al. 2020). Table 1 reports these data.

QUIC-fire settings

QUIC-Fire is a physics-based fire behavior model designed to capture the complex interactions between fuel, atmospheric flow, and fire dynamics (Lin et al. 2020). In this study, QUIC-fire simulations were run with a 2 × 1.5 km domain, employing a vertical grid with two cell layers to differentiate between surface and PHYMAL fuel components. The initial layer of cells was parameterized to represent a fully cured, homogeneous grass model capable of reliably carrying fire. Using fuel attributes consistent with the (Scott and Burgan 2005) grass fuel model, the surface fuel layer was assigned a fuel load of 0.5 kg m^2, a fuel bed depth of 0.5 m, a fuel moisture content of 5%, and a surface area-to-volume ratio of 4000 $m^2\ m^{-3}$ (Lin et al. 2020). The second vertical cell layer, spanning 1–2 m, represented a homogeneous layer of PHYMAL fuels, incorporating SAV, LFMC and BD from Table 1 for each of the five time periods. Furthermore, a westerly background wind was input at a height of 6.1 m, with a speed of 6 m s^{-1}. All five QUIC-fire simulations employed the same surface fuels and background winds, differing only in the representation of shrub fuels collected throughout the season. The results are reported as percent fuel consumption in the shrub fuel layer compared to the input conditions. For further detail on the QUIC-fire simulator, see Lin et al. (2020).

Estimating bulk density of PHYMAL

QUIC-fire requires an estimate of total bulk density (BD) for burnable fuels, which includes foliage and stem mass for Ninebark (PHYMAL). These data are reported in Table 1. We estimated foliage BD using reasonable assumptions for mean shrub height (H), leaf area index (LAI) and assumed leaf angle. H was input as 1.35m following (Habeck 1992), LAI was assumed to be 2 following (Keane 2008) and leaf angle assumed to be 45° for all foliage. LAI assesses foliage area per unit ground area as a flat plane, which can under-represent the total foliage area when the leaves are suspended at an angle. Therefore, we adjusted LAI for leaf angle (LAI_{angle}) by dividing LAI by the inverse cosine of the assumed leaf angle, which was input as 0.79, equal to 45° in radians (White et al., 2000). Foliage BD was calculated from LAI_{angle} using the following equation:

$$Bulk\ density\ (kg\ m^{-3}) = \frac{LMA \times LAI_{angle}}{Height} \quad (7)$$

Stem BD was estimated by building an allometric equation to relate stem mass to foliage mass. Ten PHYMAL shrubs were collected and separated into foliage and stem components. These were dried for 48 h at 70 °C and weighed. We developed a simple linear regression ($n = 10$) between foliage and stem mass with the y-intercept forced through zero, which resulted in R^2=0.96 and slope of 4.92 (Supplementary Material Table 1). Stem mass per unit foliage was therefore multiplied by 4.92. Total bulk density (Table 1) is the sum of foliage and stem BD.

Table 1 Data that were extracted from the full seasonal dataset to input to the QUIC-fire simulator. Data are presented as mean values of the week of collection

Date	LMA (kg m^{-2})	SAV ($m^2\ m^{-3}$)	RWC (%)	LFMC (%)	BD Foliage (kg m^{-3})	BD Stem (kg m^{-3})	BD Total (kg m^{-3})
2022-05-18	0.060	2936.8	70.1	258.2	0.134	0.659	0.792
2022-06-01	0.046	5257.7	90.9	269.4	0.102	0.504	0.607
2022-07-06	0.055	5785.4	79.2	147.2	0.121	0.597	0.718
2022-08-03	0.057	6592.6	56.4	94.5	0.127	0.625	0.752
2022-08-25	0.062	6896.8	41.8	56.4	0.137	0.676	0.814

Table 2 An overview of the ten model variants tested to in this study to model live fuel moisture content, describing the time-varying and fixed model input parameters evaluated. The acronyms stand for: leaf mass area (LMA), relative water content (RWC), surface-area-to-volume ratio (SAV), maximum water holding capacity (κ)

Model type	Model ID	Time-variant parameters	Fixed parameters
Single time varying input models	Model 1	LMA	RCW, SAV, κ
	Model 2	RWC	LMA, SAV, κ
	Model 3	SAV	LMA, RWC, κ
	Model 4	κ	LMA, RAC, SAV
Two time varying input models	Model 5	LMA, RWC	SAV, κ
	Model 6	SAV, RWC	LMA, κ
	Model 7	RWC, κ	LMA, SAV
	Model 8	LMA, SAV	RWC, κ
	Model 9	LMA, κ	RAC, SAV
	Model 10	SAV, κ	LMA, RWC

Data analysis

In total, we collected and processed 860 individual foliage samples throughout sampling campaigns in 2022 ($n = 384$) and 2023 ($n = 476$). The data are presented in two cohorts: 2023 data to assess the differences in physical and chemical characteristics across species, and 2022 data to assess seasonal variability within one species (PHYMAL) and model potential fire behavior. We have combined the data to evaluate the performance of the mechanistic LFMC model, however, for these analyses, data collection was restricted to the same range across 2022 and 2023, resulting in three sampling weeks from 2022 being removed. Consequently, we assessed model performance using $n = 792$ data points.

To understand variability in model inputs across species for LFMC, RWC, LMA, SAV, and κ, and evaluate the mechanistic models, we produced simple boxplots, and tables of median and standard deviation. We tested ten candidate models (Table 2) using different combinations of time-varying (median per sample data) and fixed (seasonal median) input parameters to model LFMC. Correlation coefficients, mean absolute error (MAE) and Nash-Sutcliffe efficiency (NSE) (Nash and Sutcliffe 1970) for these ten models are presented. We plotted the best performing model using the *ggplot* package (Wickham 2016).

To understand seasonal variability of model inputs in a single species, and understand effects on fire behavior, we produced simple boxplots and input seasonal data (blue boxplots) to the QUIC-fire model. Foliage senescence meant that samples collected on 2022-09-01 were mostly dead, and these samples could not be re-hydrated, nor could the foliage be laid flat to determine a projected surface area, consequently, we have removed foliage samples collected on 2022-09-01 (1 September 2022) from subsequent analyses. Data analyses were performed using the R statistical software, version 4.1.3 (R Core Team 2022), or the QUIC-fire tool.

Results

The data are presented in two cohorts: 2023 data to assess the differences in physical and chemical characteristics across species, and 2022 data to assess seasonal variability within one species (PHYMAL) and model potential fire behavior.

Variation in physical and chemical characteristics across species

We collected 476 individual foliage samples from six common intermountain west shrubs throughout 2023.

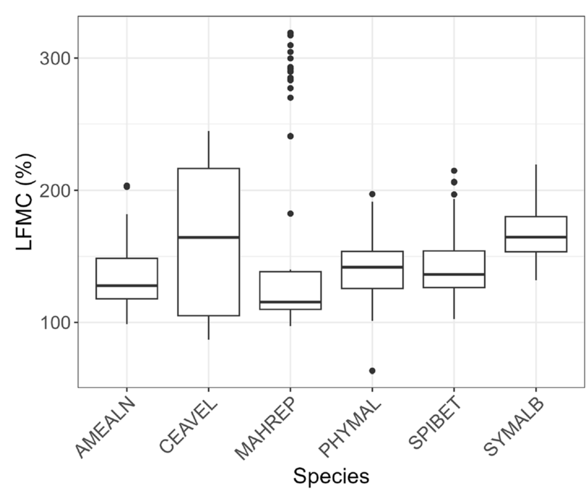

Fig. 1 A boxplot depicting variability in live fuel moisture content (LFMC) across the six shrub species observed in this study in 2023, $n = 476$. The box depicts the interquartile range, while the whiskers illustrate the top and bottom 25% of the data. The black data points are outliers in the dataset. The acronyms stand for PHYMAL (*P. malvaceus*), AMEALN (*A. alnifolia*), CEAVEL (*C. velutinus*), MAHREP (*M. repens*), SPIBET (*S. betulifolia*), SYMALB (*S. albus*)

Table 3 Variation in the inputs to the mechanistic live fuel moisture model across the six shrubs species sampled in 2023. The values presented are live fuel moisture content (LFMC), relative water content (RWC), leaf mass area (LMA), surface-area-to-volume ratio (SAV), and the maximum water holding capacity (κ), $n = 476$. Values in parentheses are standard deviation. The acronyms stand for PHYMAL (*P. malvaceus*), AMEALN (*A. alnifolia*), CEAVEL (*C. velutinus*), MAHREP (*M. repens*), SPIBET (*S. betulifolia*), SYMALB (*S. albus*)

Species	LFMC (%)	RWC (%) (%)	SAV ($m^2\ m^{-3}$)	LMA ($kg\ m^2$)	κ ($kg\ H_2O\ m^{-3}$)
AMEALN	127.8 (24.7)	85.7 (5.2)	9777.5 (1530.8)	0.035 (0.007)	531.5 (46.4)
CEAVEL	164.4 (57.8)	91.5 (2.4)	5438.6 (1208.1)	0.061 (0.021)	503.7 (74.5)
MAHREP	115.4 (76.4)	90.9 (4.4)	8271.1 (967.4)	0.05 (0.012)	537.1 (106.1)
PHYMAL	150.2 (52.6)	82.8 (7.2)	9423.4 (2148.6)	0.034 (0.006)	560.8 (81.0)
SPIBET	136.3 (24.8)	85.7 (3.5)	13531.2 (1588.1)	0.024 (0.004)	515.4 (44.3)
SYMALB	164.6 (20.0)	85.5 (3.9)	9611.4 (1104.0)	0.030 (0.005)	565.3 (60.5)

LFMC varied between species, ranging from seasonal median values of 115% (MAHREP) to 164% for CEAVEL and SYMALB (Fig. 1, Table 3). Maximum observed LFMC values varied to a greater extent, with the highest maximum LFMC observed for MAHREP (319%) and the lowest maximum for AMEALN (203%). The lowest minimum (driest) LFMC value observed in the 2023 dataset was for PHYMAL foliage (63%), although is an outlier in the dataset and may represent senescing foliage. The next lowest value was for CEAVAL (86.7%), while the highest minimum LFMC was 132% for SYMALB foliage (Fig. 1).

Inter-specific variation in RWC and κ was low across shrub species, while differences in LMA and SAV were comparitively high. Boxplots illustrating variation in the physical and chemical inputs to the mechanistic LFMC model are depicted in Fig. 2. Median RWC values ranged from 82.8 % (PHYMAL) to 91.5 % (CEAVEL) (Table 3). Similarly, inter-specific differences in the maximum water holding capacity (κ) were limited, varying between

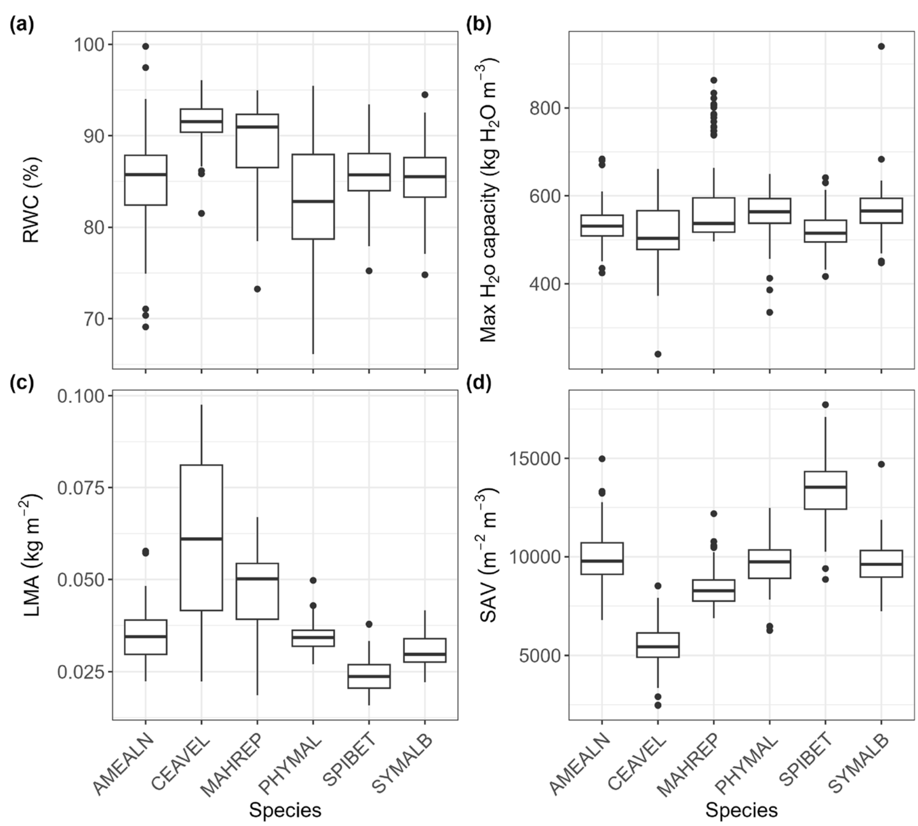

Fig. 2 Boxplots depicting variation across six common shrubs species for **a** relative water content (RWC), **b** maximum water holding capacity (κ), **c** leaf mass area (LMA), and **d** surface-area-to-volume ratio (SAV). For each panel, $n = 476$. The acronyms stand for PHYMAL (*P. malvaceus*), AMEALN (*A. alnifolia*), CEAVEL (*C. velutinus*), MAHREP (*M. repens*), SPIBET (*S. betulifolia*), SYMALB (*S. albus*)

Table 4 Performance metrics for ten model variants of the mechanistic live fuel moisture model. The acronyms stand for: leaf mass area (LMA), relative water content (RWC), surface-area-to-volume ratio (SAV), maximum water holding capacity (κ)

Model ID	Time-variant parameters	Fixed parameters	r^2	MAE	NSE
Model 1	LMA	RCW, SAV, κ	0.73	19.27	0.66
Model 2	RWC	LMA, SAV, κ	0.30	23.58	0.22
Model 3	SAV	LMA, RWC, κ	0.06	28.99	0.03
Model 4	κ	LMA, RAC, SAV	0.25	30.79	0.17
Model 5	LMA, RWC	SAV, κ	0.89	11.38	0.84
Model 6	SAV, RWC	LMA, κ	0.26	23.97	0.20
Model 7	RWC, κ	LMA, SAV	0.64	22.19	0.46
Model 8	LMA, SAV	RWC, κ	0.86	14.85	0.76
Model 9	LMA, κ	RAC, SAV	0.68	18.86	0.67
Model 10	SAV, κ	LMA, RWC	0.36	27.03	0.27

species medians of 503.7 kg H_2O m^{-3} (CEAVEL) and 565.3 kg H_2O m^{-3} (SYMABL), a percentage change of 12.2% across species. In contrast, substantial differences were observed across species for LMA and SAV. The highest population median LMA was for CEAVEL (0.061 kg m^{-2}), and lowest for SPIBET (0.024 kg m^{-2}), constituting a 154.2% difference between the lowest and highest median LMA values. SAV also varied substantially (148.8%) between the lowest and highest species median values, from 5438.6 m^{-2} m^{-3} to 13531.2 $m^{-2}m^{-3}$ for CEAVEL and SPIBET, respectively (Table 3). Plots depicting seasonal variation within each shrub species are provided in Supplementary Material (Figs. S1–S5).

Performance of the mechanistic live fuel moisture model

The model resolves all variability in LFMC when measured input data are used. To explore model performance using summarized inputs, which are more realistic in a management context, week of collection and seasonal median values were then input to Eq. 2. Table 4 describes model performance across ten model variants. Model 5, which included time-varying LMA and RWC, and seasonally fixed inputs for SAV and κ, was the strongest model. This variant explained 89% of LFMC variability, had the lowest mean absolute error across all variants (MAE = 11.38 %) and the highest fidelity to the 1:1 line (NSE = 0.84) (Fig. 3, Table 4). Partial dependence plots (Supplementary Material Fig. S6) depict the marginal effect of each input on modeled LFMC. RWC and κ display positive relationships, while biomass-based metrics (LMA and SAV) have negative relationships with modeled LFMC.

Impact of seasonal variation in foliage characteristics on modeled fire behavior

Patterns of seasonal variation in PHYMAL foliage varied across the different inputs between May and September (Fig. 4). Within this time frame, LFMC (calculated using Eq. 1) ranged from a median value of 262% in the first week of sampling in May to 52% in late August. Once PHYMAL foliage started to senesce in September, LFMC declined to a median value of 22% (Fig. 4a). Seasonal dynamics of RWC diverged from LFMC dynamics, following a humped shape relationship compared to the gradual decline of LFMC. RWC

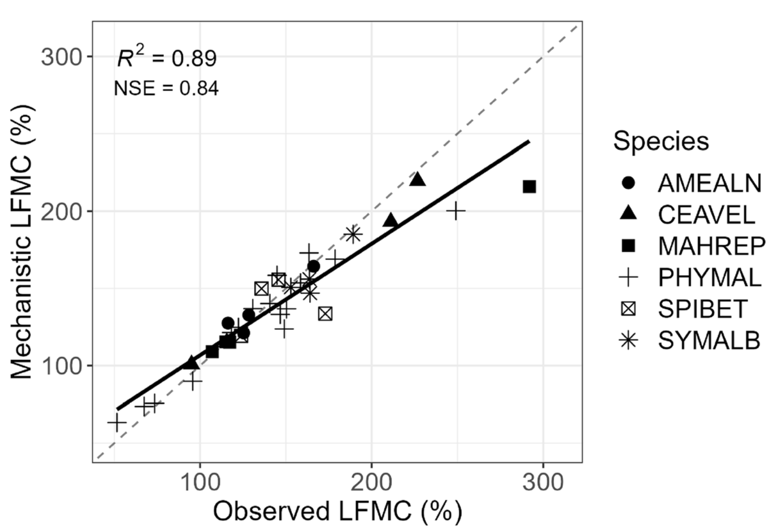

Fig. 3 Observed median live fuel moisture content (*x*-axis) and mechanistic LFMC derived using Model 5 (Table 4) and median data inputs (*y*-axis). The shrubs are grouped by species (shape), with a trend line, r^2 and NSE value printed for all data combined. The acronyms stand for PHYMAL (*P. malvaceus*), AMEALN (*A. alnifolia*), CEAVEL (*C. velutinus*), MAHREP (*M. repens*), SPIBET (*S. betulifolia*), SYMALB (*S. albus*)

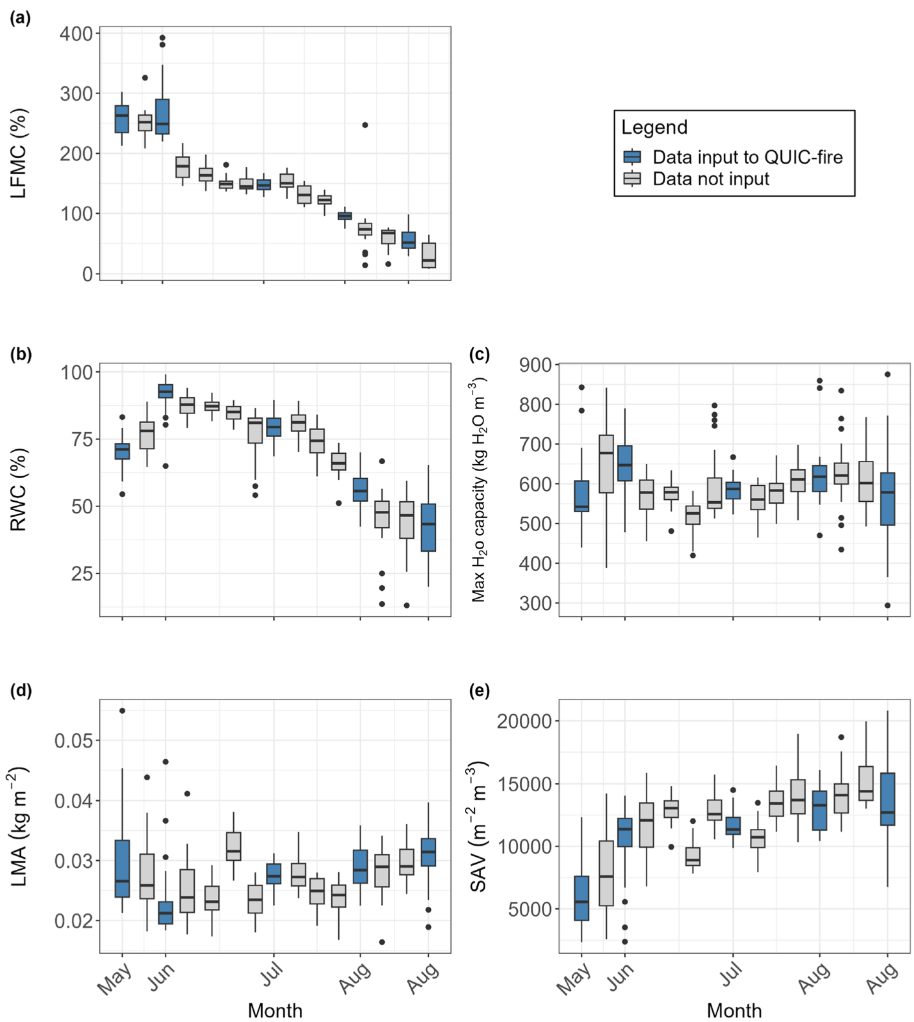

Fig. 4 Summary data figures depicting seasonal variation in Ninebark foliage sampled in this study, including **a** live foliar moisture content (LFMC) measured on a dry weight basis, **b** relative water content (RWC), **c** maximum water holding capacity (κ), **d** leaf mass area (LMA), and **e** surface-area-to-volume ratio (SAV). The blue boxes denote the sampling weeks that correspond to the QUIC-fire model simulations, gray boxes were not input to the simulator. In plot a, $n = 383$, for plots b–e, $n = 359$

started at a weekly median value of 71%, increasing to 93% in June and then declining to a season low of 43% later in the season (Fig. 4b). The standard deviation of RWC doubled throughout the season, ranging from 6.1% in May to 12% in late August. Seasonal variability in the leaf mass per unit area was comparatively low. The lowest weekly median LMA value was observed on June 1 (0.021 kg m−2), and the highest on June 23 (0.032 kg m−2). Although LMA tended to oscillate rather than trend in any single direction, weekly increases in LMA were observed in the last five weeks of monitoring (Fig. 4c). Substantial variation in surface area and foliage volume (Fig. 4d, e) resulted in an increase of 160% in SAV between the first week of sampling and the SAV peak in late August. Following the peak, SAV remained stable and finally declined slightly in late August. The maximum water holding capacity κ fluctuated within a relatively small envelope of variability (Fig. 4f), ranging between weekly median values of 526 to 677 kg H_2O m^{-3}.

Seasonal decline in LFMC, and increases in bulk density and SAV (Table 1) resulted in substantial increases in fuel consumption using the QUIC-fire fire behavior simulator across the season (Fig. 5, Table 5). Conditions in May and June resulted in limited fuel consumption in the shrub fuel layer, with only 2.37% and 17.68% fuel consumed at 1200 s following ignition (Table 5), respectively. In contrast, fire carried readily in the PHYMAL

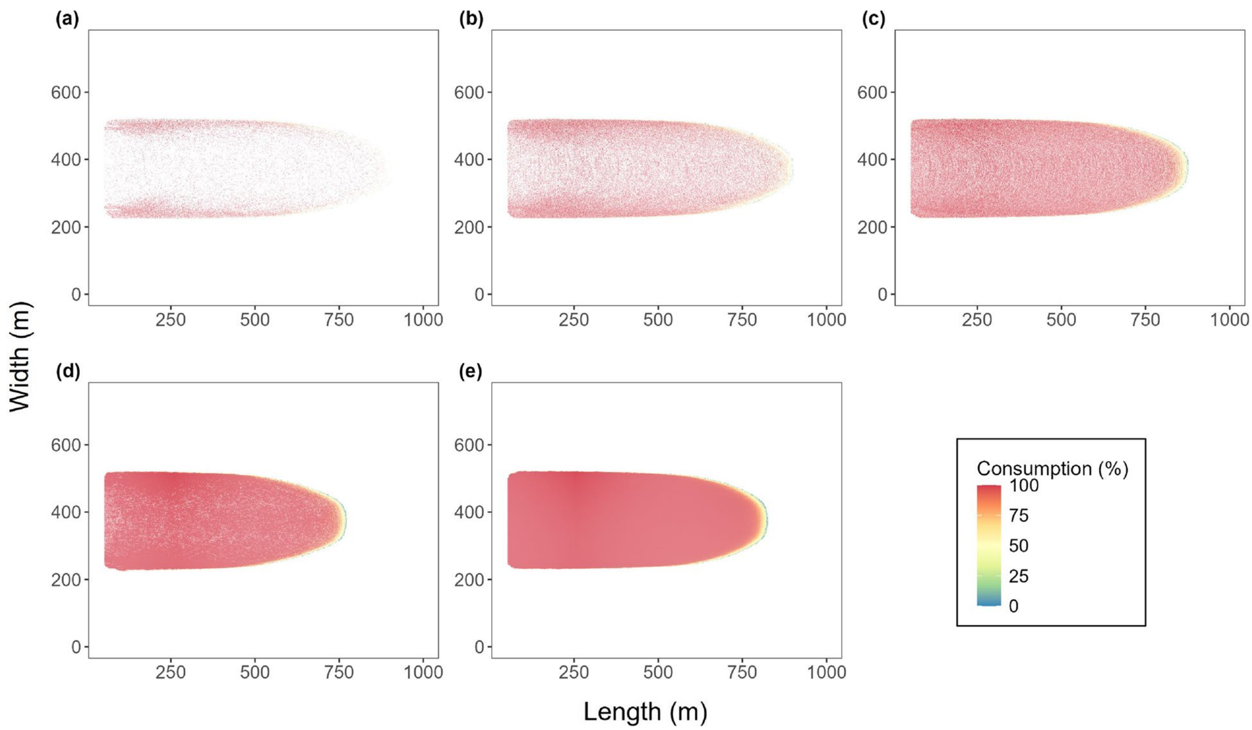

Fig. 5 Modeled fire outputs from QUIC-fire in **a** May, **b** June, **c** July, **d** early August, and **e** late August. The shading on the plot indicates fuel consumption at 1200 s after ignition. Blue areas represent limited fuel consumption, red areas represent high fuel consumption. Fuel inputs to the QUIC-fire model are described in Table 1. An ignition point was initiated on the left of the plot, with a 6 m s-1 westerly wind input at 6.1. All simulations employed the same surface fuels and background winds, differing only in the representation of shrub fuels. Further details on the QUIC-Fire settings are outlined in Section 2.5.1

shrub fuel layer under fuel conditions throughout August. At $t = 1200$ s in the QUIC-fire simulation using conditions observed on 3 August and 25 August, the model reported 84.15% and 97.33% fuel consumption, respectively (Table 5). Comparatively higher rates of consumption are evident in Fig. 5d–e, which demonstrates the spatial fuel consumption after 1200 s for all five simulations.

Table 5 Fuel consumption outputs from the QUIC-fire simulator model using the five fuel condition input scenarios described in Table 1. The data are presented as fuel consumption as a percent of the total fuel complex, and the average biomass consumed across the simulation area in absolute terms

Date	Percent total consumption (%)	Fuel consumption (kg m^{-2})
2022-05-18	2.37	0.02
2022-06-01	17.68	0.11
2022-07-06	47.71	0.34
2022-08-03	84.15	0.63
2022-08-25	97.33	0.79

Discussion

This study presents a novel mechanistic model to determine live fuel moisture content (Eq. 2) using four physio-chemical variables important for plant physiology and combustion (Jolly et al. 2025), and evaluated its performance against measured LFMC for six shrubs common to the inter-mountain west, USA. Using weekly median values for leaf mass area (LMA) and relative water content (RWC), and seasonal median values for surface-area-to-volume ratio (SAV) and maximum water holding capacity (κ), the model explained 89% of observed variability in LFMC.

Separating LFMC into four physio-chemical drivers of variability is an important step forward in bringing together the disciplines of plant physiology and combustion science. RWC, LMA, and SAV are well established metrics in the plant science literature, and the mechanistic model presented here enables fire scientists to use these data in a meaningful way to model combustion. Shrubs constitute a large proportion of available fuel in many ecosystems, and understanding LFMC dynamics in these systems is thus important for determining the fire risk that this vegetation layer poses. We have shown how mechanistic LFMC data can be input to a new generation of fire simulators, such as QUIC-fire, with important implications for modeled fire behavior across the season. While the geographic extent of our study is limited to the inter-mountain west USA, the mechanistic foundations of this model mean that it is applicable in all vegetation communities and plant functional types. Consequently, its use will enhance our understanding of, and capacity to model, seasonal fluctuations in live fuels and their effects on fire behavior and risk across the globe.

Variation in mechanistic model inputs across species and effects on LFMC

Our data show substantial variability in the four inputs to the mechanistic LFMC model across the six species sampled in 2023 (Fig. 2, Table 3). Inter-specific variability was greatest in LMA and SAV, while RWC and κ varied within a smaller envelope.

Leaf mass area

Leaf mass area (and its inverse, specific leaf area) emerged as a critical variable for predicting seasonal fluctuations in shrub LFMC. Inputting time-varying weekly median LMA, while holding all other values to a seasonal constant, explained 73% of the variability in LFMC in the mechanistic model, and when coupled with time-varying RWC was the strongest performing model variant (r^2 = 0.89) (Table 4).

LMA is a common plant physiology metric with data available for species globally in large trait databases (Kattge et al. 2020), or meta reviews (e.g., Poorter et al. (2009)). LMA is a morphological trait that integrates the complex trade-offs made by plants to optimize fitness for their environment (Poorter et al. 2009), and has been strongly linked to LFMC and other flammability metrics for both conifer- (Brown et al. 2022) and eucalypt-dominated forests (Griebel et al. 2023; Krix and Murray 2018; Murray et al. 2013). This relationship makes sense, because dry mass per unit area represents a physical upper limit on the amount of water that could be contained within the foliage element (Nolan et al. 2020). Consequently, LMA and SLA are useful scaling parameters for modeling LFMC across different types of vegetation (Scarff et al. 2021), and have been employed by other authors to model LFMC across biophysical gradients at landscape scales (Nolan et al. 2022).

Importantly, in a fire science context, mass per unit area describes the amount of fuel available for combustion within a vegetated area and we used this relationship to estimate bulk density for this study. While the range in LMA presented in our study is comparatively small, Poorter et al. (2009) found that LMA varies more than 100-fold in nature across species and landscapes. Consequently, mechanistically linking LFMC to LMA, and then extracting LMA information from plant physiology literature, could be a useful step to modeling LFMC more broadly across diverse vegetated landscapes for fire science purposes.

Relative water content

The best performing model variant included weekly median RWC, affirming the importance of capturing seasonal drought in models for LFMC. However, RWC displayed a different seasonal dry-down pattern compared to LFMC in PHYMAL foliage (Fig. 4), highlighting that it is important to use intergrated models of both water and biomass fluctuations to model seasonal changes in flammability.

Relative water content is a common measure of physiological water stress in plants (Weatherley 1950; Livingston and Brown 1912). RWC is strongly related to leaf water potential (ψ_{leaf}), which is a measure of the potential energy of water within the foliage, and is known to influence a range of physiological processes such as stomatal conduction in the leaf. RWC and ψ_{leaf} are frequently related in plant physiology literature using pressure volume curves (Tyree and Hammel 1972). In the context of modeling LFMC at landscape scales, the strong physical link between RWC and ψ_{leaf} is useful, because ψ_{leaf} is typically at equilibrium with soil water potential at dawn, and soil water potential is common product of broad scale land surface models (Rebel et al. 2012). Consequently, the depth of understanding in plant physiology literature of this metric, and physical relationship of RWC to LFMC, may facilitate mechanistic species-specific modeling of LFMC at a scale relevant for fire management planning.

Surface-area-to-volume ratio (SAV)

We observed dramatic changes in surface-area-to-volume ratio across the different species sampled (Fig. 2) and within PHYMAL across the season (Fig. 4). Despite these large differences, the best performing mechanistic LFMC model variant required only a seasonally fixed SAV input, rather than a time-varying (i.e., weekly) input (Table 4). This could be due to the correlation between SAV and LMA, or it could be related to the sensitivity of the model to SAV changes and the strength of the RWC/LMA ratio at predicting LFMC independent of the other variables. Future research capitalizing on the mechanistic model could investigate the sensitivity of LFMC to fluctuations in these inputs (e.g., Martin-StPaul et al. (2020)).

SAV is a commonly measured physiological plant trait that is strongly correlated to photosynthetic rate, and the trade-offs that organisms make for light capture and water retention (Roderick et al. 2000). SAV has long been recognized as an indicator of fuel flammability (Brown 1970). The rate of heat transfer is directly proportional to the surface area of an object, thus foliage with higher surface area per unit volume will acclimate more quickly to changes in boundary conditions. In the context of combustion science, this means that foliage with high SAV will heat faster and reach ignition temperature more quickly (Schwilk 2015).

Our experiment was designed to capture inter-specific differences across species, and intra-specific differences throughout the season in a single shrub. Consequently, our study did not assess differences in SAV related to vegetation growing in different environmental conditions across spatial scales. Leaf thickness typically increases with elevation and aridity, thus SAV decreases along these gradients (Roderick et al. 2000). Although we recorded substantial variability in SAV, the small geographic range of our experiment suggests a much greater range of SAV may exist at landscape scales (Li et al. 2020). Larger scale datasets (e.g., Kattge et al. (2020)) would be useful for scaling the mechanistic model across broader landscapes and species assemblages.

Maximum water holding capacity (kappa, κ)

In testing the performance of the mechanistic model, the results demonstrate that a median κ value per species is sufficient for capturing seasonal fluctuations in LFMC (Table 4). This input has been shown to be an important metric in capturing differences in water holding capacity for new and old foliage (Jolly et al. 2025). In our study, all foliage sampled was expected to be from the year of sampling, potentially making κ a less important variable. However, to scale the LFMC model across shrubs, particularly between deciduous evergreen species, the importance of this variable is likely to increase.

Overall, the benefit of a mechanistic model is that we can decompose LFMC into components that are physiologically relevant for both moisture fluctuations and fire behavior, and separately model these inputs across species, space, and time. The discipline of pyro-ecophysiology, and the novel mechanistic live fuel moisture model presented here, provides a framework to integrate established knowledge and data across plant science disciplines into the combustion science literature. For example, the same inputs can be used to understand fluctuations in LFMC in the mechanistic model, and input to high-fidelity fire behavior models such as QUIC-fire, overall enhancing our capacity to understand changes in fuel condition across landscapes, and the impacts of those changes on potential fire activity.

Scaling live fuel moisture content from leaf to landscape scales

We have presented a mechanistic model validated at a fine scale using individual foliage elements, however, fire management decisions are typically made at much larger landscape scales. Increasingly, remote sensing is being used operationally to model seasonal fluctuations in LFMC at scales relevant to fire management decision-making, using multi-spectral (Yebra et al. 2018) or synthetic aperture radar (Rao et al. 2020) sensors. However, remote sensing approaches can at times struggle to capture dynamics under the canopy, or differentiate between different types of vegetation. Ultimately, a hybrid approach capitalizing on the scale of remote sensing and vegetation or species specific parameters such as SAV, κ, and LMA described in this research may generate the best balance for land and fire managers. Other approaches to upscaling the mechanistic LFMC model could include process-based ecosystem models such as FATES (Koven et al. 2020) or LPJ-GUESS (Smith et al. 2001), among others. Such models often include LMA or SLA to describe foliage, which could be directly related to the model described here. Alternatively, RWC could be related to leaf water potential through pressure-volume curves. These ecosystem models also commonly include a fire activity simulator, which may benefit from a mechanistic implementation of LFMC to determine vegetation flammability, and like the QUIC-fire simulator implemented here, could model flammability from an internally consistent suite of inputs.

Effects of seasonal changes in foliage using QUIC-fire simulator

Seasonal changes in RWC, LMA (input as bulk density), and SAV (Table 1) translated into substantial increases to fuel consumption using the QUIC-fire simulator (Fig. 5). Percent total fuel consumption increased from 2.37 to 97.33% between early May and late August (Table 5), with the the largest increase in modeled consumption occurring between July and early August. This aligns with a typical fire season in the inter-mountain west, USA (Riley and Loehman 2016), and the point at which seasonal RWC fluctuations transitioned from a mid-season plateau to a sharp decline prior to foliage senescence Fig. 4b), with corresponding reduction in LFMC (Fig. 4a). The substantial increase in modeled consumption suggests a threshold may exist between these inputs and fire behavior, which has also been suggested by other authors (Nolan et al. 2016).

Our application of QUIC-fire presents an increase in functionality since its original implementation, with model code adapted to allow SAV to vary throughout the different simulations. Most fire behavior models either do not explicitly include an SAV input value or do not allow it to vary dynamically. For example, while the (Rothermel 1972) model allows SAV to vary across different types of fuel classes, all live fuels are prescribed an SAV value of 1500 $ft^{-2}ft^{-3}$. Although capturing time-varying SAV did not increase the performance of the mechanistic LFMC model substantially (Table 4), capturing inter- and intra-specific variability in this metric is important for modeling fire behavior. Given the magnitude of variability in SAV across species and season (Table 3, Fig. 4d, e), and its physical relationship to combustion, varying this value within the QUIC-fire simulator represents an advancement in our capacity to model fire behavior at this scale. Given this is the first application of variable SAV within the QUIC-fire simulator, there are a range of opportunities to test the sensitivity of this model to SAV variability across species, space and time.

In addition to strong seasonal increases in rate and absolute fuel consumption, our method, and the mechanistic live fuel moisture model presented here, demonstrates the potential for future users of these types of simulators to input data from a consistent suite of inputs that are physiologically relevant for the fuels that are burning. Most fire behavior models require an input of LFMC, while many also need physical parameters of SAV, particle density, or fuel loading. The benefit of calculating LFMC from the same data is that inputs for both LFMC and fire behavior models can be internally consistent and balanced. As we have shown, these data can also be combined to generate necessary fire behavior model inputs. For example, LMA and simple leaf area index (LAI) data can be used to generate fuel loading, while particle density is simply the product of SAV and LMA.

Conclusion

Our research demonstrates that a novel, physically-based live fuel moisture model successfully predicts LFMC across different shrub species common to the intermountain west, USA. While this work was based in a single ecosystem, the mechanistic nature of this model means it can be applied in any vegetated ecosystem to enhance our understanding of inter- and intra-specific variation in LFMC. We have demonstrated how three of the model inputs (RWC, LMA, and SAV), which are commonly measured eco-physiological characteristics, can be input to a physical-based fire simulator in an internally consistent manner, to model potential changes in fire behavior across a season. This modeling approach represents a step forward in our capacity to link plant and fire science disciplines, and its mechanistic approach means it can be used to model shrub flammability across global ecosystems.

Supplementary Information

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Supplementary Material 1.

Authors' contributions

W.M.J., T.P.B., and E.T.C. designed the study; W.M.J. developed the mechanistic model; T.P.B., E.T.C., and S.C.H. collected and processed data; Z.C. completed fire simulations; T.P.B. analyzed data and created figures with assistance from M.W.J., E.T.C., and S.C.H.; T.P.B. wrote the first draft of the manuscript, all authors contributed to editing the manuscript.

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Data availability

The datasets used and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Competing interests

The authors declare no competing interests.

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