Jolly *et al. Fire Ecology* (2025) 21:19
https://doi.org/10.1186/s42408-025-00361-8

Fire Ecology

ORIGINAL RESEARCH

Open Access

Combining ecophysiology and combustion traits to predict conifer live fuel moisture content: a pyro-ecophysiological approach

W. Matt Jolly[1*], Elliott T. Conrad[1], Tegan P. Brown[1,2] and Samuel C. Hillman[1,2]

Abstract

Background Fuel moisture content is a key driver of fuel flammability and subsequent fire activity and behavior worldwide. Dead fuels passively exchange moisture with the atmosphere while live fuel moisture is confounded by a mixture of seasonal carbon and water cycle dynamics. Despite the significance of live fuel moisture content (LFMC) on wildland fire potential, attempts to model its variations seasonally and between species are often inconclusive or unsuccessful.

Results Here we present a mechanistic LFMC model that uses easily measured live fuel physiological and morphological traits that are rooted in either plant ecophysiology or combustion science. These traits serve as proxies for important components of the seasonal water and carbon cycle or they capture inter-species plant morphology variations. The model decomposes LFMC based into leaf mass area (LMA), relative water content (RWC), surface-area-to-volume ratio (SAV), and the volumetric saturated water holding capacity (κ). We test 10 simplifications or variations of the mechanistic model using combinations of fixed and time-varying inputs of the four variables. A simplified mechanistic model version that uses the time-varying RWC and LMA with foliage age class-specific SAV and κ medians accounted for most of the seasonal variation in Douglas fir LFMC across two growing seasons ($r^2 = 0.91$, MAE = 12.9%). Further, this same model applied to 11 Intermountain Western US conifers adequately captured the seasonality and inter-species differences in live fuel moisture dynamics across an entire growing season and foliage age classes ($r^2 = 0.89$, MAE = 12.5%).

Conclusions This pyroecophysiology-based approach to live fuel moisture content modeling provides a more robust way to characterize seasonal variations in both fuel availability and water stress while building on decades of plant ecophysiology and combustion research. The model can be used to more appropriately represent live fuels in process-based models, it can be used to better parameterize multi-dimensional fire behavior models to represent the combined effects of biomass and moisture variations on live fuel flammability, and it can improve our ability to more accurately monitor live fuel variations with remote sensing. This new model harmonizes decades of disparate live fuel moisture research and lays a foundation for more fruitful live fuel dynamics explorations worldwide.

Keywords Live fuel moisture content, Mechanistic, Model, Specific leaf area, Relative water content, Surface-area-to-volume ratio

*Correspondence:
W. Matt Jolly
william.jolly@usda.gov
Full list of author information is available at the end of the article

Resumen

Antecedentes El contenido de humedad de los combustibles vegetales es un componente clave en la inflamabilidad y en la subsecuente actividad y comportamiento del fuego en todo el mundo. Los combustibles muertos intercambian humedad con la atmósfera de manera pasiva, mientras que en los combustibles vivos este intercambio está entremezclado por la combinación entre la dinámica estacional del carbono y el ciclo del agua. A pesar del significado que tiene el contenido de humedad de los combustibles vivos (LFMC) en el potencial de los fuegos de vegetación, los intentos de modelar sus variaciones estacionales y entre especies son muchas veces inconcluyentes o poco exitosos.

Resultados Presentamos aquí un modelo mecanístico de LFMC que usa características físicas y químicas fáciles de medir y que provienen tanto de la eco-fisiología vegetal como de la ciencia de la combustión. Estas características sirven como aproximaciones para componentes importantes del ciclo estacional del agua y del carbono o capturan variaciones morfológicas entre especies. El modelo descompone LFMC basado en la masa del área de las hojas (LMA), contenido de humedad relativo (RWC), la relación entre el área de la superficie de la hoja y su volumen (SAV), y la capacidad volumétrica de las hojas de contener el agua a saturación (k). Probamos 10 simplificaciones o variaciones del modelo mecanístico usando combinaciones de ingresos (*inputs*) variables en el tiempo de cuatro variables. Una versión del modelo mecanístico simple que usa las variables en el tiempo de RWC y LMA con las medianas de clases de follaje específicas SAV y k fueron las que mostraron la mayor variación en el LFMC en pino Oregón a lo largo de dos estaciones de crecimiento ($r^2 = 0.91$, MAE=12.9%). Además, el mismo modelo aplicado a 11 coníferas del Oeste inter-montano de los Estado Unidos capturaron adecuadamente la estacionalidad y diferencias entre especies en la dinámica del LFMC a lo largo de una estación de crecimiento completa y entre las clases de edad del follaje ($r^2 = 0.89$, MAE=12.5%).

Conclusiones Esta aproximación modelada del LFMC basada en la Piro-eco-fisiología provee de un modo más robusto para caracterizar las variaciones estacionales tanto en la disponibilidad del combustible como en el estrés hídrico, cimentadas en décadas de investigaciones sobre eco-fisiología de plantas y combustión. El modelo puede ser usado para representar más adecuadamente el LFMC en modelos basados en procesos, puede ser usado para parametrizar mejor modelos multi-dimensionales de comportamiento para representar los efectos combinados de la biomasa, y las variaciones en la inflamabilidad de los combustibles vivos y puede mejorar nuestra habilidad para monitorear mejor las variaciones en el LFMC mediante sensores remotos. Este nuevo modelo armoniza décadas de investigaciones dispares y sienta las bases para una exploración más fructífera de la dinámica de la humedad de los combustibles vivos en todo el mundo.

Background

Wildland fires are a common ecological disturbance that globally burn between 360 and 380 million hectares each year (Chuvieco et al. 2016). Some fires fill help maintain healthy ecosystems but other fires can heavily impact people, property, and infrastructure (Bowman et al. 2009). In an effort to promote a well-founded relationship with fire, we must understand the physical process that dictate how they will ignite and spread across diverse landscapes. This information would enable us to make proactive decisions about how we co-exist with wildfires, how we most effectively manage fire-prone landscapes, and how we respond to wildfires when they ignite.

Wildfire activity is dominated by factors such as fuel amount, arrangement and physio-chemistry, terrain orientation and steepness, and weather (Countryman 1972). Weather interacts to drive spatial and temporal variations in both fuel amount and conditions. These dynamic changes fuel condition largely dictate where and how wildfires burn. Fuel moisture content (FMC) is a common dynamic fuel condition metric that has long been shown to influence fire potential (Gisborne 1936; Byram 1943; Fons 1950). FMC describes the amount of water in the fuel expressed as a ratio of its oven-dried mass and it can be used to characterize both living and dead vegetation. Live and dead FMC are commonly used as inputs to predictive models of wildland fire danger or fire behavior (Rothermel 1972; Perry 1998). These fire models are used for a variety of purposes such as mapping wildfire risk (Finney et al. 2011), monitoring current wildfire potential (Bradshaw et al. 1984; Stocks et al. 1989), or responding to wildfires (Jolly et al. 2019). Ultimately, fuel moisture dynamics are integral to both our understanding of wildland fire behavior and the decision support tools we use to effectively manage wildfires.

Wildland fires commonly burn in mixtures of live and dead fuels. Dead fuel moisture dynamics and flammability have been studied for decades (Fons 1950; Viney 1991). However, live fuel dynamics have received relatively less exploration. Live fuel moisture content is confounded by the fact that both water content and dry matter vary simultaneously throughout the season (Ackley 1954; Kozlowski and Clausen 1965; Jolly et al. 2014). Efforts to model seasonal variation solely from water balance variations have been met with mixed success and these studies generally cannot explain all of the live fuel moisture content variations despite being trained on a limited group of species (Pellizzaro et al. 2007; Ruffault et al. 2018).

Recent live fuel dynamics research has focused on linking live fuel moisture variations to plant physiological traits such as leaf water potential (Nolan et al. 2018) and also on decoupling the water and dry matter variations of the plant to better explain the seasonal LFMC dynamics (Jolly et al. 2014; Brown et al. 2022; Griebel et al. 2023). This emerging field of pyro-ecophysiology (Jolly and Johnson 2018; Resco de Dios 2020; Dickman et al. 2023) attempts to link critical components of the plant water, carbon, and nutrient cycles to better capture the patterns and process of live fuels over space and time. Common physiological measurements of plant water stress such as leaf water potential (Nolan et al. 2018; Balaguer-Romano et al. 2022) or relative water content (Jolly et al. 2014; Ruffault et al. 2023) show promise in capturing water content variations while metrics such as leaf density, specific leaf area, or its inverse, leaf mass area, can potentially control for dry matter variations that link to the carbon and nutrient dynamics (Jolly et al. 2016; Griebel et al. 2023; Nolan et al. 2022). These studies are critical to advancing our understanding of live fuel dynamics but they are only exploring partial relationships between physiological metrics and LFMC.

Ultimately, a mechanistic model derived from live fuel physiological and morphological traits is needed (Ruffault et al. 2018). Such a model is critical to advancing our understanding of live fuel flammability and their influence on wildland fire behavior in complex fuelbeds. It is needed to allow us to better understand variations in flammability across species and time and it is also critical to our ability to model and map those seasonal variations over time with both ground-based and satellite-based assets and to more appropriately incorporate live fuel characteristics into next-generation ecosystem process and fire behavior models (Dickman et al. 2023).

Here we introduce a novel, mechanistic live fuel moisture content model that integrates established metrics from both ecophysiology and combustion science to predict LFMC variations across time and between species. We apply the model to a single species across multiple growing seasons to demonstrate its effectiveness in capturing LFMC intra-species, seasonal variations and we further extend the model to investigate LFMC variations across 11 Intermountain Western US tree species. This simple model holds potential for global application, offering improved explanation, monitoring, mapping, and modeling of conifer live fuel variations in diverse ecosystems.

Methods

Sample collection

We collected the current year ("new" foliage) and previous year's growth ("old" foliage) from live Douglas-fir (*Pseudotsuga menzeseii*) from the beginning of March to the end of October in 2021 and 2022 at the Blue Mountain National Recreation Area on the Lolo National Forest, approximately 5 miles southwest of Missoula, MT, USA. The sampling site was a large open mixed stand of mature Douglas-fir and ponderosa pine (*Pinus ponderosa*) on a gentle north aspect slope. Samples were collected weekly or twice weekly from green-up to needle hardening, late April to late June, and biweekly for the rest of the season. Eight branch tips from eight randomly selected trees were clipped each sampling date. From those, 12 new and 12 old needles were randomly drawn for foliage measurements, and the same number again for surface-area-to-volume (SAV). Trees were randomly selected from one sampling date to another, so the measurements are meant to be representative of the stand at that location and not of an individual tree or trees within the stand. Intact terminal shoots were collected from sunlit portions of randomly selected mature trees within the stand, then stored in sealed bags in a cooler for transport to the laboratory. Samples were initially processed within 4 h of collection. In 2022, new and old foliage from ten additional coniferous tree species was collected four times during the growing season from five sites in Western Montana and Idaho using the same protocol as above (Table 1).

Foliage physical and physiological characteristics

In the laboratory, 12 old needles and 12 new needles (after new foliage emergence) were randomly selected from the shoots and weighed to the nearest 0.01 mg. Volume was determined using a balance density kit (Ohaus density kit). Weighed needles were then taped flat to a white piece of paper that included a surface area measurement reference and photographed. Photographs were processed using ImageJ software (Schneider et al. 2012) to measure projected surface area. Needles were gently unpeeled from the paper, placed into vials of de-ionized water, and left to rehydrate overnight at 4 °C. Rehydrated needles were weighed again to determine saturated mass, then dried in a 70 °C oven for at least 72 h and reweighed to determine dry mass (Conrad et al. 2024). These measurements yield the fresh mass, dry mass, and turgid (saturated) mass values that were used to calculated the relative water content (Weatherley 1950) and the live fuel moisture content (Jolly et al. 2014).

Table 1 Description of sampling sites across Montana and Idaho, USA, used in the study. Temperature and precipitation summaries are 30-year annual means from the PRISM dataset (PRISM Climate Group 2025) and soil characteristics are from the USDA NCRS web soil survey (NRCS 2025)

Site name	Latitude (dec deg)	Longitude (dec deg)	Elevation m (ft)	Species	Mean Ann Prec mm (in)	Mean Ann Temp °C (°F)	Soil order	Drainage class
Spring Gulch	46.7359	−114.5362	1162 (3812)	PICO, PIEN	682.0 (26.9)	4.7 (40.5)	Inceptisol	Somewhat excessively drained
Blue Mountain	46.8298	−114.11812	1346 (4416)	PIPO, PSME	445.5 (17.5)	6.8 (44.3)	Inceptisol	Somewhat excessively drained
Jerry Johnson	46.4739	−114.88439	939 (3081)	ABGR, THPL	939.8 (37)	6.4 (43.5)	Inceptisol	Well drained
St Mary's Peak	46.5003	−114.20339	2091 (6859)	PIAL	989.1 (38.9)	4.0 (39.2)	Inceptisol	Excessively drained
White Pine Creek	47.7389	−115.67531	1024 (3360)	PIMO, THPL	1106.9 (43.6)	5.5 (41.9)	Inceptisol	Well drained
TV Mountain #2	47.0026	−114.00282	1564 (5131)	LAOC, ABLA	688.8 (27.1)	6.0 (42.8)	Inceptisol	Well drained

An additional 12 old and new needles were subsampled to determine surface area to volume ratio (SAV). Needle volume was determined using the Ohaus density kit as before. Surface area was determined by dipping needles in 70 °C paraffin (Paraplast, Leica Biosystems) and comparing the deposited wax mass to a regression made from wooden shapes of known surface area (Conrad et al. 2024). A factor to convert projected to all-sided surface area was determined by comparing the wax-dipping and ImageJ measurements for each needle and were summarized by species and foliage age class. These "projected to all sided ratio" factors can simplify future surface area determination for these species and they are commonly used in ecophysiology-based process models (White et al. 2000).

The mechanistic live fuel moisture model

Live fuel moisture content (LFMC) is defined as ratio of fuel particle's water mass and oven-dried mass as follows:

$$LFMC = \frac{kg_{H_20}}{kg_{DM}} \times 100 \tag{1}$$

We use the term particle to describe a single component of the plant, such as needles or leaves, fine branches, coarse branches, or stems that are measured for a given species and foliage age class at a given time. LFMC can be quantified for any plant particle.

LFMC can also be calculated using volumetric quantities by normalizing the numerator and denominator by the particle volume. If we consider the LFMC as a simple ratio of the volumetric water mass (VWM) and volumetric dry mass, which is equivalent to its density (ρ), the follow equation describes the LFMC:

$$LFMC = \frac{Volumetric\ Water\ Mass\ (VWM)}{Density\ (\rho)} \times 100 \tag{2}$$

VWM can be further decomposed using relative water content (RWC) if an additional scalar value is developed that describes the water mass that the particle can hold at saturation relative to its volume. First, RWC can be calculated from particle fresh, dry, and turgid mass measurements as follows (Weatherley 1950):

$$RWC = \frac{Fresh\ Mass - Dry\ Mass}{Turgid\ Mass - Dry\ Mass} = \frac{kgH_2O}{kgH_2OSat} \times 100 \tag{3}$$

where the numerator represents the sample water mass and the denominator is the sample water mass at saturation. RWC quantifies the hydration status of a plant and it is proportional to the amount of water a plant can hold. Thus, an RWC of 100% means the plant particle is fully saturated and a value of 0% would mean the plant is fully desiccated. In contrast, LFMC is unbounded and it commonly exceeds 100% when water mass exceeds dry mass.

Additionally, a new metric can be defined, which we will call kappa (κ), to describe the particle saturated water mass relative to its volume. κ can be calculated using measurements from the saturation step of RWC and normalized by the fresh particle volume as follows:

$$\kappa = \frac{Saturated\ Water\ Mass}{Volume} = \frac{Turgid\ Mass - Dry\ Mass}{Volume} = \frac{kgH_2OSat}{m^3} \tag{4}$$

where Turgid Mass is the mass of the fuel particle in kilograms after rehydration and Dry Mass is the the oven dry sample mass in kilograms and volume is the measured fresh sample volume (m^3). Kappa can then be used to scale the measured RWC to VMC as follows:

$$VWM = \frac{RWC}{100} \times \kappa = \frac{kgH_2O}{\cancel{kgH_2OSat}} \times \frac{\cancel{kgH_2OSat}}{m^3} = \frac{kgH_2O}{m^3} \tag{5}$$

where the volumetric water mass (VWM) is the product of RWC (scaled to fraction from percent by dividing by 100) and κ.

Continuing, the volumetric dry mass, or particle density (ρ), can be described as the product of the leaf mass area (LMA) and the surface-area-to-volume ratio (SAV):

$$\rho = LMA \times SAV = \frac{kgDM}{\cancel{m^2}} \times \frac{\cancel{m^2}}{m^3} = \frac{kgDM}{m^3} \tag{6}$$

Finally, this yields a simple, mechanistic form of LFMC that can be calculated from the four easily measured plant particle traits described above. The model can characterize variations in plant water stress, particle biomass, and morphology as follows:

$$LFMC = \frac{\frac{RWC}{100} \times \kappa}{LMA \times SAV} \times 100 \tag{7}$$

These primary plant descriptive metrics were chosen to build off of a wealth of existing physiological and combustion research. Previous work on other Intermountain West US conifers has shown that decoupling the seasonal water and dry mass dynamics helps explain more of the variation in LFMC both seasonally and across needle age classes (Jolly et al. 2014; Jolly and Johnson 2018). Informed by previous research (Jolly et al. 2014), we chose the relative water content (RWC) to represent the seasonal water variations (Weatherley 1950) and we chose leaf mass area (LMA) to capture the seasonal carbon, or dry mass, variations based on other recent research (Nolan et al. 2022; Brown et al. 2022; Griebel et al. 2023). LMA is a common ecophysiological metric of plant biomass per unit area (Poorter et al. 2009) and it is sometimes replaced with its reciprocal, specific leaf area (SLA), in LFMC-related literature but the two quantities are equivalent. We included the surface-area-to-volume ratio (SAV) because it is a well-known particle combustion trait that has been measured as a metric of wildland fuel flammability for decades (Brown 1970). κ is a novel fuel metric but it should be related to the internal morphology of a species and we would expect it to vary by species and foliage age class.

When combined, these four metrics of foliar physical and chemical properties yield the particle live fuel moisture in percent of dry mass as an emergent property. Full model parameters,units and descriptions are summarized in Table 2.

Exploratory data analysis

We first calculated the daily median values for LFMC, RWC, LMA, SAV, and κ for each sample period, species, and foilage age class (new or old) across the entire study period and we used those summarized daily values for all subsequent analysis and model variant explorations. Exploratory data analysis was performed in Python version 3.12.5. We plotted distributions of LFMC and the four model input variables using violin plots created using the Seaborn Python package (0.13.2) (Waskom 2021) and we explored seasonal variations in the intensively sampled Douglas fir plots using time series plots.

Testing mechanistic live fuel moisture model simplifications

We evaluated ten mechanistic LFMC mode variants in order to choose a parsimonious model that captures seasonal LFMC dynamics but that does not require every parameter to be estimated precisely. Based on previous work, we assumed that seasonal dry mass dynamics would be most important for conifers (Brown et al. 2022) and that relative water content would help explain additional variability (Jolly et al. 2014). For fixed parameters, we calculated the median value across all data, stratifying by species and foliage age class. The time-variant and fixed parameters of each model variant are listed in Table 3. For each of the ten mechanistic model variants, we substituted either time-varying or fixed values into Eq. 7 as detailed in Table 3. The first four models tested have a single time varying input and the other three mechanistic model inputs are fixed. The last six models allow two variables to change with time while fixing the two other mechanistic model variables using species and foliage age class medians. This analysis was

Table 2 Mechanistic live fuel moisture variable definition

Variable	Abbreviation	Description	Units
Live fuel moisture content	LFMC	Percent of dry mass	$\frac{kgH_2O}{kgDM} \times 100$
Relative water content	RWC	Percent of saturated moisture	$\frac{kgH_2O}{kgH_2OSat} \times 100$
Leaf mass area	LMA	Leaf mass per unit surface area	$\frac{kgDM}{m^2}$
Surface area to volume ratio	SAV (SVR)	All-sided surface area to volume ratio	$\frac{m^2}{m^3}$
Kappa	κ	Volumetric saturated water mass	$\frac{kgH_2OSat}{m^3}$

Table 3 Model simplification variants evaluated using both the seasonal Douglas fir and the 11 Intermountain West US conifer data

	Model ID	Time-variant parameters	Fixed parameters
Single time varying parameter models	**Model 1**	LMA	RWC, SAV, k
	Model 2	RWC	LMA, SAV, k
	Model 3	SAV	LMA, RWC, k
	Model 4	k	LMA, RWC, SAV
Two time varying parameters models	**Model 5**	LMA,RWC	SAV, k
	Model 6	SAV, RWC	LMA, k
	Model 7	RWC, k	LMA, SAV
	Model 8	LMA, SAV	RWC, k
	Model 9	LMA, k	RWC, SAV
	Model 10	SAV, k	LMA, RWC

performed for both the intensively sampled Douglas fir seasonal time series and for the 11 Intermountain Western US conifers dataset.

Each model variant from Table 3 was compared to field-measured LFMC using ordinary least squares regressions. Both the r^2 of linear regression fit with an intercept of 0 (1:1 line) and mean absolute error (MAE) for both the seasonal Douglas fir model and the pooled 11 inter-species Intermountain conifer model were calculated in Python using the LinearRegression routine from the scikit learn package (SKLearn version 1.5.2) (Pedregosa et al. 2011).

Results

Projected to all-sided surface area conversions

Results of conversion factors from projected to all-sided surface area are given in Table 4. Conversion factors ranged from a low of 2.0 to a high of 2.7 depending on species and foliage age class with except for Western larch. Larch surface area was difficult to characterize using the wax dipping method and yielded a conversion factor less than 2.0 (0.8) which is not physically possible. Therefore, we use a simple conversion of 2.0 for all larch surface areas. With the exception of larch, the range of conversion factors were similar to those reported for evergreen needleleaf forests with White et al. (2000) who reported a mean value of 2.6 with values 2.37 to 3.14 for similar species. These projected to all-sided surface area conversions are used to calculate all-sided leaf mass area and surface-area-to-volume ratios for all 11 tree species.

Fixed model parameters across 11 conifer species

Median mechanistic LFMC model parameters for Douglas fir and the remaining 10 species tested are presented in Table 5. These values are used in the Douglas fir high temporal frequency seasonal LFMC model evaluations and also in the model evaluations across the 11 Intermountain Western US conifer species that were sampled.

Douglas fir exploratory data analysis

We collected 741 individual foliage samples from Douglas fir between 2021 and 2022 which yielded 62 daily median values for LFMC, RWC, LMA, SAV, and k for both new and old foliage by sample date. One artifact was noted in some of the RWC for old foliage of Douglas fir across all measurements where preliminary exploration showed that some of the samples effectively "over-rehydrated" yielding unrealistic RWC values (lower than 75%) (Arndt et al. 2015). This bimodality was also seen in new foliage but the two peaks were less distinct. We therefore filtered the dataset for RWC values within published valid ranges

Table 4 Projected to all-sided surface area conversion factors for new and old foliage of 11 tree species

Species	Common name	Abbreviation	Median conversion factor		*n*
			New	Old	(New, Old)
Abies grandis	Grand fir	ABIGRA	2.1	2.5	(32, 32)
Abies lasiocarpa	Subalpine fir	ABILAS	2.2	2.2	(48, 48)
Larix occidentalis	Western larch	LAROCC	0.8 (2.0)	NA	(43,NA)
Picea englemannii	Englemann spruce	PICENG	2.4	2.7	(48, 47)
Pinus albicaulis	Whitebark pine	PINALB	2.5	2.5	(47, 48)
Pinus contorta	Lodgepole pine	PINCON	2.2	2.4	(45, 47)
Pinus monticola	Western white pine	PINMON	2.0	2.0	(48, 45)
Pinus ponderosa	Ponderosa pine	PINPON	2.2	2.3	(23, 24)
Pseudotsuga menziesii	Douglas-fir	PSEMEN	2.3	2.3	(12, 12)
Thuja plicata	Western redcedar	THUPLI	NA	2.3	(NA,36)
Tsuga heterophylla	Western hemlock	TSUHET	2.0	2.2	(46, 48)

Factors were determined by comparing photogrammetric projected surface area to all-sided surface area measured using wax deposition for individual needles. Note: Western larch values are unrealistically low but the needles are typically very flat so we assume a value of 2.0 for that species

Table 5 Median model parameters by species and foliage age class for 11 Intermountain Western US conifers

Species code	Foliage age	LFMC (% dry wt)	RWC (% sat)	LMA (kg m^{-2})	SAV (m^{-1})	k (kg H_2O m^{-3})
ABIGRA	**New**	218.5	92.5	0.062	4234.2	653.71
	Old	125.4	91.1	0.096	4191.0	699.0
ABILAS	**New**	145.5	88.9	0.081	4269.4	595.3
	Old	114.6	87.3	0.106	4013.8	536.4
LAROCC	**New**	219.9	85.0	0.049	4899.6	687.5
PICENG	**New**	158.6	89.2	0.091	3405.3	681.0
	Old	108.7	89.3	0.131	3725.2	585.0
PINALB	**New**	137.9	86.2	0.090	4193.7	678.0
	Old	119.1	86.3	0.110	4021.7	677.2
PINCON	**New**	188.4	83.6	0.082	4507.1	783.1
	Old	110.3	79.5	0.098	4564.8	676.8
PINMON	**New**	179.2	85.1	0.078	4339.8	684.7
	Old	135.7	81.1	0.076	4323.3	721.4
PINPON	**New**	161.2	82.0	0.088	4195.2	744.0
	Old	120.0	78.6	0.114	3947.3	686.7
PSEMEN	**New**	170.1	87.2	0.082	4298.6	662.0
	Old	132.3	89.2	0.089	4499.7	671.4
THUPLI	**Old**[a]	118.2	81.5	0.089	4101.2	575.4
TSUHET	**New**	179.0	89.6	0.066	4678.7	618.6
	Old	136.6	90.6	0.079	4730.2	580.7

These values were used as fixed model parameters for all mechanistic model variants tested (see Table 3 for model variant descriptions)

[a]Note: THUPLI was not separated into new and old and all foliage was lumped into the old category

($RWC \geq 75\%$). The distribution of live fuel moisture content for new and old foliage shows that old foliage LFMC is generally distributed around 100% but new foliage peak around 160% and was also right skewed (Fig. 1). Live fuel moisture content followed a seasonal pattern similar to that of other conifers where the new growth continually declined during the needle maturation period and the old foliage showed a pronounced season dip prior to new needle emergence (Fig. 1). This drop and recovery in LFMC of old foliage is consistent with the "spring dip" measured in other conifers (Jolly et al. 2016).

Distributions of relative water content (RWC), leaf mass area (LMA), surface-area-to-volume ratio (SAV), and maximum volumetric water holding capacity (κ) are shown in the left column of Fig. 2. LMA showed a distinct shift between new and old foliage where old foliage LMA

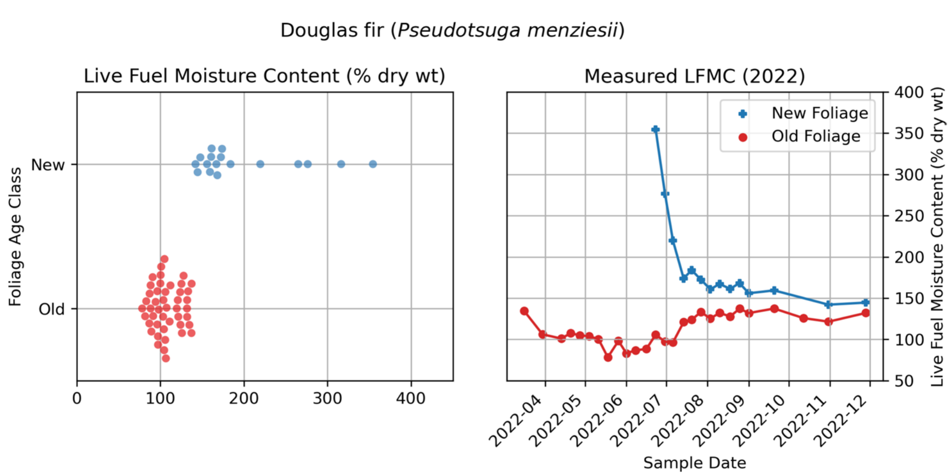

Fig. 1 Swarm plots (left) of new and old Douglas fir foliage sampled at Blue Mountain in 2021 and 2022 and a time series plot of new and old foliage LFMC for 2022 (right) ($N = 62$)

was consistently higher than new foliage LMA. SAV for new and old foliage were distributed roughly equally but new foliage SAV was right skewed. Max water holding capacity followed the inverse of LMA where new foliage had a higher water holding capacity than old foliage.

Seasonal variations of RWC, LMA, SAV, and k are shown in the right column of Fig. 2. There was a small seasonal cycle of RWC for old foliage and more pronounced seasonal variability of RWC in new foliage. LMA followed an inverse trend of LFMC where old foliage LMA peaked during the period of the lowest measured LFMC in old foliage and as LMA in new foliage increased over the season, new foliage LFMC decreased. SAV variations for old foliage were mostly constant over the season but new foliage SAV declined quickly after needle emergence. Finally, κ stayed relatively constant for old foliage and declined until it was approximately equal to old foliage κ by the end of the growing season.

Performance of the Douglas fir mechanistic live fuel moisture model

A summary of the ordinary least squares, no intercept regressions between measured and modeled LFMC for each Douglas fir model variant is shown in Table 6. All of the top 3 models contained time-varying leaf mass area (LMA). The best fit model (model 8) used time-varying LMA and SAV and fixed values for RWC and k ($r^2 = 0.95$). The second best model (model 5) fit uses time-varying LMA and RWC and fixed values for k and SAV ($r^2 = 0.91$). Model 5 is also the most generalized version of the models tested because it includes a time-varying proxy for both water content and dry matter variations, while still controlling for potential species-variations using foliage age class medians values for κ and SAV. Notably, the third-best model (model 1) used only time-varying LMA to predict LFMC with fixed values for RWC, κ, and SAV ($r^2 = 0.90$), highlighting the strong dependence of LFMC on changes in dry matter.

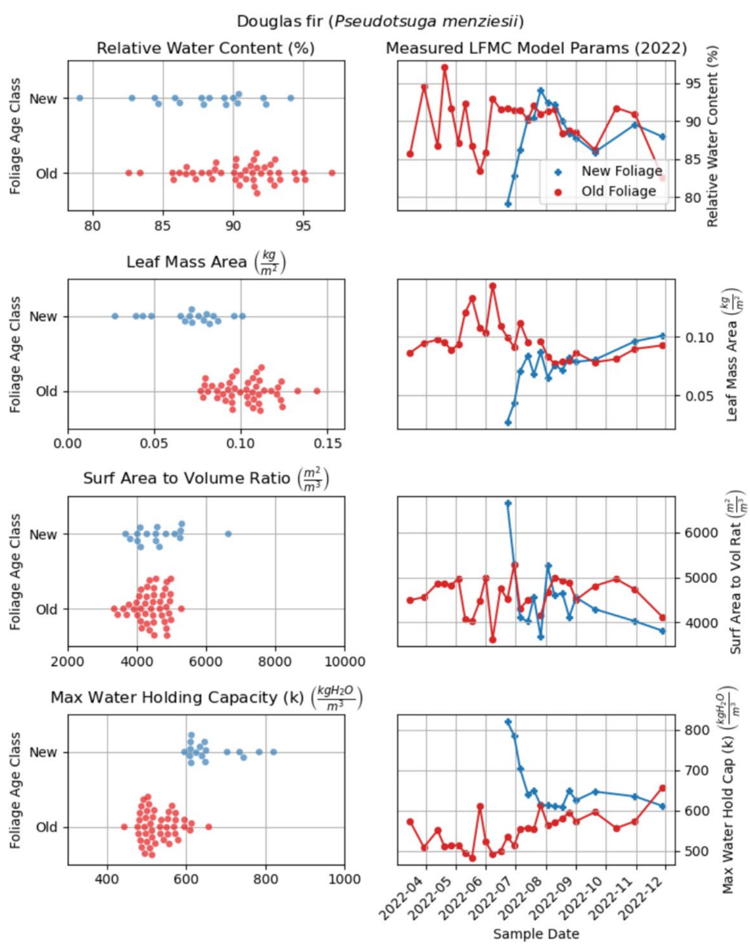

Fig. 2 Swarm plots (left column) and example time series plots (right column) of relative water content, leaf mass area, surface-area-to-volume ratio, and maximum water holding capacity for new and old Douglas fir foliage sampled at Blue Mountain in 2022 ($N = 41$)

Table 6 Ordinary least squares, no intercept regression comparisons of modeling and predicted LFMC for each model variant (Table 3) calculated using seasonal Douglas fir (*Pseudotsuga menziesii*) data

Model ID	Time-variant parameters	Fixed parameters	r^2	MAE
Model 1	LMA	RWC, SAV, k	0.90	12.9
Model 2	RWC	LMA, SAV, k	-0.37	27.0
Model 3	SAV	LMA, RWC, k	-0.45	30.8
Model 4	k	LMA, RWC, SAV	0.52	16.5
Model 5	LMA,RWC	SAV, k	0.91	12.9
Model 6	SAV, RWC	LMA, k	-0.56	33.0
Model 7	RWC, k	LMA, SAV	0.32	19.0
Model 8	LMA, SAV	RWC, k	0.95	8.3
Model 9	LMA, k	RWC, SAV	0.84	17.5
Model 10	SAV, k	LMA, RWC	0.04	24.0

Shaded rows show the top 3 best model fits based on the highest r^2 of the 1:1 line and the lowest MAE

A time series of measured and predicted Douglas fir LFMC for model 5 is shown in Fig. 3. Model 5 showed the best fit for the most generalized model version and it was strongly correlated with measured LFMC. Model 5 sufficiently reproduced the seasonal trends in both new and old foliage and the mean absolute error was low (12.9% across all observations).

Eleven Intermountain US tree species exploratory data analysis

We measured 712 individual foliage samples across the 11 species and four sample periods which yielded 78 daily median values for LFMC, RWC, LMA, SAV, and k for both new and old foliage by sample date after filtering for relative water content values above 75% as mentioned in the Douglas fir data prep description above. LFMC measured across species closely resembled the distributions for Douglas fir but central tendency for old foliage with slight higher at about 120%. New foliage moisture content values peaked slightly higher at about 150% and they were were heavily right skewed with maximum values near 500% (Fig. 4). LFMC values above 500% only occurred when we sampled very new foilage within 1 or 2 weeks of needle flushing, thus measurements this high are not common throughout the growing season.

Histograms of RWC, LMA, SAV, and κ across all 11 tree species are shown in Fig. 5. Model input variables across all species were distributed similarly to Douglas fir. RWC values were slightly higher for new foliage. LMA was consistently higher for old foliage shifting from a peak of about 0.075 $kg\ m^{-2}$ for new foliage to a peak of about 0.10 $kg\ m^{-2}$ for old foliage after full foliar maturation. SAV was similar across foliage age classes. Similar to Douglas fir, new foliage SAV was right skewed and showed a tail in the distribution above 6000 m^{-1}. Max volumetric water holding capacities (κ) were highest for new foliage and lowest for old foliage. Overall, sample distributions across the 11 Intermountain species were similar to those observed for Douglas fir.

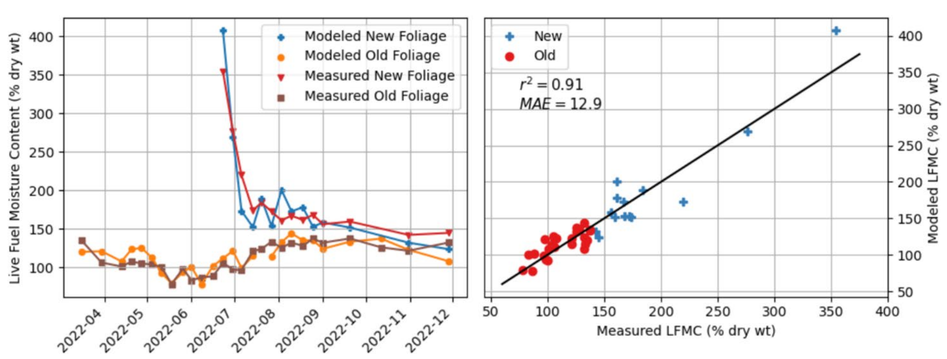

Fig. 3 Model comparison for model variant 5 which models seasonal Douglas fir live fuel moisture content using time-varying RWC and LMA and fixed SAV and κ by foliage age class as mechanistic LFMC model inputs. The model adequately characterizes the disparate seasonal dynamics between new and old foliage as well as the period of the "spring dip" seen in the old foliage prior to new needle flushing (left panel) and it accounts for about 91% of the variation in live fuel moisture across the entire season regardless of foliage age class with a mean absolute error of 13% across the full range of LFMC values (right panel)

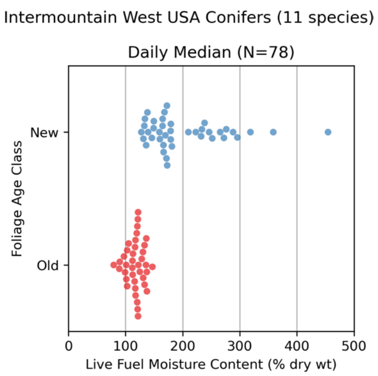

Fig. 4 Swarm plots of new and old live fuel moisture content for all 11 conifers sample across the Intermountain Western US in 2022 (N = 78)

Performance of the mechanistic live fuel moisture model across 11 Intermountain US tree species

A summary of the ordinary least squares, no intercept regression tests for each model variant calculated across all 11 conifer species is shown in Table 7. Consistent with the seasonal tests for Douglas fir, the best three models all included LMA (models 1, 5, and 8). Additionally, the most general model with the best fit for Douglas fir (model 5) was also the most general and best fit model across 11 Intermountain Western US conifers. This generalized model captured the between species variations of new and old LFMC using only time-varying LMA and RWC and species-specific, fixed parameters for SAV and k (Table 5). A plot of the measured and modeled LFMC values calculated across all 11 Intermountain US conifer species is shown in Fig. 6.

Discussion

This study presents a mechanistic model for conifer live fuel moisture content (LFMC) that moves beyond traditional correlative approaches with meteorological data. It unveils LFMC as an emergent property directly derived from established physiochemical parameters. This framework integrates current knowledge on the drivers of LFMC variation and lays the foundation for

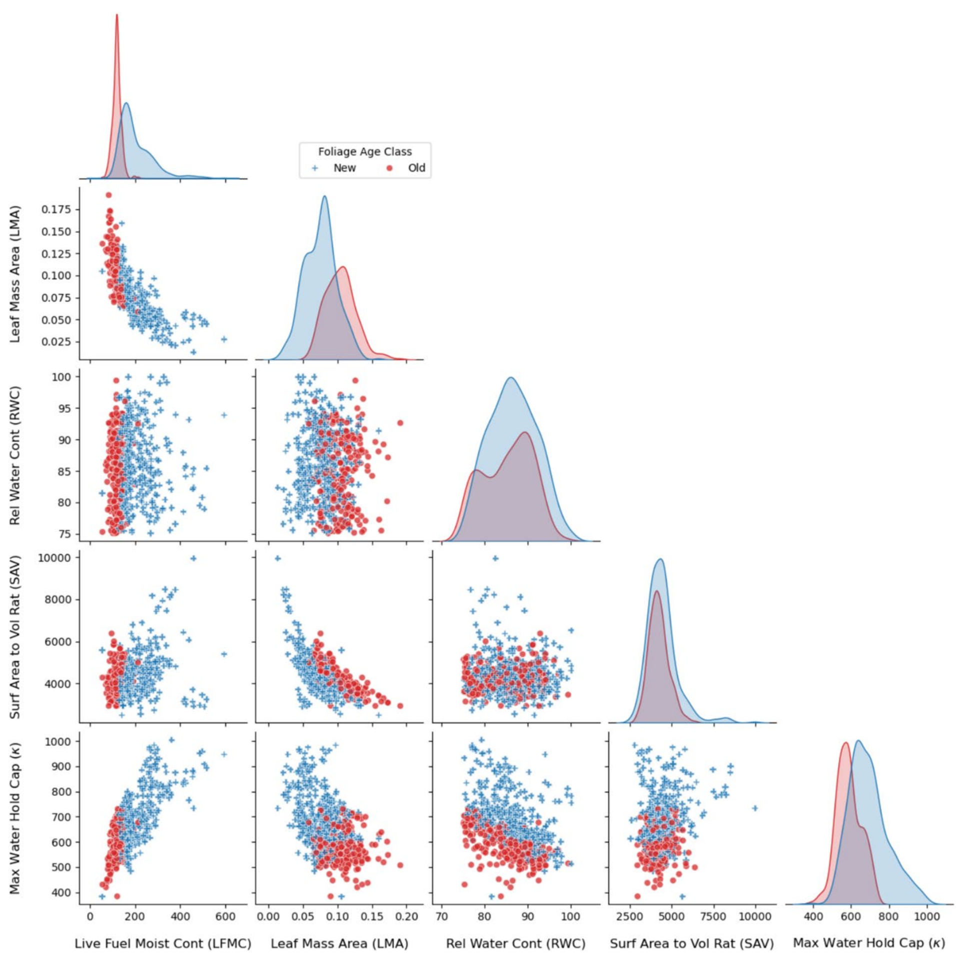

Fig. 5 Pairplot of all measurements of LFMC, LMA, RWC, SAV, and κ across 11 conifers sample across the Intermountain Western US in 2022 (N = 712). Variables descriptions and units are given in Table 2

Table 7 Statistical comparisons of modeling and predicted LFMC for each model variant (Table 3) calculated using seasonal data from 11 Intermountain US conifer species

Model ID	Time-variant parameters	Fixed parameters	r^2	MAE
Model 1	LMA	RWC, SAV, k	0.890	13.5
Model 2	RWC	LMA, SAV, k	-0.646	35.9
Model 3	SAV	LMA, RWC, k	-0.583	39.9
Model 4	k	LMA, RWC, SAV	0.387	23.3
Model 5	LMA,RWC	SAV, k	0.887	12.5
Model 6	SAV, RWC	LMA, k	-0.645	41.5
Model 7	RWC, k	LMA, SAV	0.257	25.1
Model 8	LMA, SAV	RWC, k	0.901	12.5
Model 9	LMA, k	RWC, SAV	0.874	16.8
Model 10	SAV, k	LMA, RWC	0.094	29.5

Shaded rows show the top 3 best model fits based on the highest r^2 of the 1:1 line and the lowest MAE

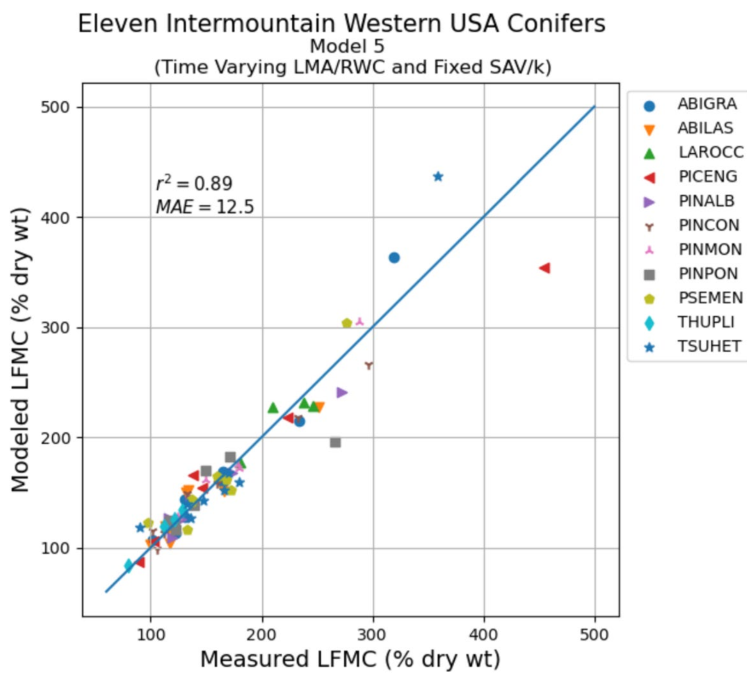

Fig. 6 Performance of mechanistic live fuel moisture model variant 5 for 11 tree species across the Intermountain Western US. This model uses only time-varying LMA and RWC with fixed SAV and κ by species and foliage age class from Table 5. This model variant adequately captures LFMC variations across all species while remaining sufficiently general to promote potential testing and application across a range of plant functional types

future research by bridging ecophysiology and combustion science in the context of live fuel dynamics.

By incorporating established metrics like relative water content, leaf mass area, surface-area-to-volume ratios, and maximum water holding capacity, the model provides a robust and transparent framework. This framework not only integrates current knowledge on environmental drivers of LFMC variation; it also lays the foundation for future research by bridging ecophysiology and combustion science in the context of live fuel dynamics. Ultimately, this novel model paves the way for a more comprehensive, pyroecophysiology-based exploration of the complex, interdisciplinary factors governing live fuel dynamics and flammability globally.

Leaf mass area

Leaf mass area, or its reciprocal specific leaf area (SLA), has been measured in plant physiology studies for decades. Consistently throughout this study, LMA was the best single predictor of LFMC variations across conifers. LMA alone account for about 90% of the LFMC variations both within and between species (Tables 6 and 7), highlighting its dominance in the seasonality of LFMC. LMA variations have been shown to capture the complex dynamics of leaf economics and are strongly linked to leaf construction cost, leaf longevity, photosynthetic capacity, and suite of other plant traits (Reich et al. 1997). Other LFMC dynamics studies have also found that LMA is a strong predictor of LFMC variations (Nolan et al. 2018, 2022; Griebel et al. 2023). Leveraging LMA/SLA allows us to better understand LFMC variations in the context of global distributions of plant leaf morphological traits and thus deepens our understanding of how LFMC might vary across plant functional types or biomes (Reich et al. 1997) and it may also help us understand linkages to key ecological traits such as leaf lifespan, foliar nitrogen content, and net photosynthetic rates (Lambers and Poorter 1992; Reich et al. 1997).

Additionally, LMA is a metric of fuel availability per unit crown volume and leaf area. As LMA increases, the amount of fuel per unit leaf area increases because canopy biomass (fuel) can be estimated from LMA if the Leaf Area Index (LAI) of the plant is known (Fang et al. 2019). More work is needed to better characterize LMA differences across species or fuel types but our mechanistic model is a first step towards linking important physiological plant characteristics to factors that may influence the burning rate and/or fire behavior of a particular species at a given point in space and time.

Relative water content

Relative water content is a very common and easy-to-measure metric of physiological water stress in plants (Martinez-Vilalta et al. 2019) and it has been measured for over 70 years (Weatherley 1950). It can characteritize, for example, total cell relative water content below 75% severely inhibits photosynthesis and protein production (Lawlor and Cornic 2002). RWC at the turgor loss point (TLP) is more consistent than the leaf water potential at TLP (Bartlett et al. 2012), suggesting that studies exploring relationships between leaf water potential at turgor loss and live fuel moisture dynamics may also benefit from using RWC (Pivovaroff et al. 2019; Boving et al. 2023; Nolan et al. 2018). Finally, RWC is strongly related to leaf water potential which is know to influence a variety of physiological processes such as stomatal conduction. Ultimately, RWC captures periods of plant stress, thus making it an important component of a model meant to capture the response of live fuels to drought.

One challenge we found with RWC was an occasional potential for the foliage samples to over-saturate, requiring us to filter the data over a "valid" range of values greater than 75%. This over-saturatation could be caused by the submersion method we used for rehydration. Arndt et al. (2015) found that the choice of rehydration methods could affect the final measured RWC value and they suggested that standing the foliage base in water or floating them could result reduce the chance of over-saturation and the resulting uncharacteristically low RWC values we observed in some samples. Clausen and Kozlowski (1965) suggest some an effective, standing rehydration method for conifer that may reduce or eliminate oversaturation and subsequent unrealisitcally low RWC values. Future work should explore these standing rehydration techniques to help reduce potential error sources and provide robust seasonal measures of water stress.

Surface area to volume ratio

Leaf surface area to volume ratio (SAV or sometimes SVR in literature) is also an important leaf trait that varies based on the plants growing environment. Research has found that SAV can be characterized by the availability of light, water, nutrients, and carbon and thus SAV, similar to LMA, is an emergent property of a plants environment (Roderick et al. 2000). Further, SAV/SVR is also the reciprocal of "characteristic length" commonly used in combustion research to calculate the Biot, Nusselt, and Reynolds numbers (Bergman et al. 2011). Biot numbers, for example, are often used to assess the validity of different types of solutions to model transient heat transfer. SAV has been an important component of wildland fuel measurements for over 50 years (Brown 1970) and it used to characterize fuels for wildland fire behavior models such the Rothermel fire spread model (Rothermel 1972) as well as CFD-based wildfire simulators such as FIRETEC (Linn et al. 2002), the Wildland Urban Interface Fire Dynamics Simulator (WFDS) (Mell et al. 2007), and newer models such as Quic-FIRE (Linn et al. 2020) and QES-Fire (Moody et al. 2022). Thus, SAV is a property that is closely linked to form and function of plants across environmental gradients as well as the thermal heat behavior, making it an ideal variable to capture in a mechanistic description of live fuel dynamics.

Implications for improved field sampling of live fuel moisture content

Historically, field measurements of live fuel moisture content have been used to infer potential seasonal shift in expected fire behavior (Dennison et al. 2008). A tremendous effort has been put forth to measure LFMC across many global species (Yebra et al. 2019, 2024). Our work suggests that measuring LFMC alone may be insuffient to characterize the resulting seasonal changes in live fuel water content and biomass and, subsequently, live fuel flammability. We observed that the overwhelming majority of LFMC variations could be explained by changes in foliar biomass and not changes in foliar water content. Additionally, the same LFMC value could be derived from different combinations of RWC and LMA. Therefore, it is important to consider the implications of the work presented here in the context of LFMC field sampling programs. Our protocols were designed to be relatively straightforward to perform in the laboratory. For conifers, if median SAV and κ values and a conversion from projected to all-sided leaf area exist for a given species, then samplers would only weigh live fuel samples fresh, snap a digital planar image of the sample, and rehydrate the sample to obtain a turgid mass for RWC determination. When combined with oven drying of the sample, it would yield sufficient information to calculate both LMA and RWC. If SAV, κ, or the area scalar values are not available for a given species in the literature, they can be measured using a single set of foliar samples during the middle of the growing season by following the methods presented above. Future work should explore ways to streamline this field sampling to provide metrics that more completely describe live fuel dynamics while not adding much additional work to field sampling efforts that are common across the world.

Scaling live fuel moisture content using remote sensing

There is considerable interest in leverage remote sensing to map and scale live fuel moisture content across landscapes (Danson and Bowyer 2004; Yebra et al. 2019). These data are used to constrain landscape-scale fire behavior simulations to better assess real-time risk (García et al. 2020). A mechanistic model similar to the one presented here was described by Yebra et al. (2013) using metrics common to remote sensing such as equivalent water thickness (EWT) and dry matter content (DMC). Hunt et al. (1987) explored the use of infrared reflectance to measure the relative water content and proposed the development of a Leaf Water Content Index. Additionally, some work has been done to relate spectral reflectance to specific leaf area (Lymburner et al. 2000). Recent work has focused on the decoupling of water mass and dry mass dynamics to improve predictions of live fuel moisture content with remote sensing (Rao et al. 2020). A hybrid approach that explores additional scaling parameters such as SAV and κ may significantly improve those remotely sensed estimates of LFMC and aligning physiological measurements such as LMA and RWC with remote sensing-based proxies like EWT and DMC stands to significantly improve our ability to map important live fuel variations across the planet. This would ultimately aid in more complete understanding of the factors to drive live fuel flammability across global ecosystems and it would allow better spatial and temporal monitoring of fuel dynamics that could link to real-time estimates of wildfire risk.

Ecophysiologically-based process modeling

An overarching objective of this study is to provide a framework for the decomposition of live fuel moisture content into variables that are physiologically-relevant and that can be modeled across species, space, and time. Terrestrial ecosystem models that merge ecosystem dynamics with landscape wildfire disturbances, such as FATES (Koven et al. 2020), BIOME-BGC (White et al. 2000), or FIRE-BGC (Keane 1996), among many others, would benefit from the implementation of this mechanistic live fuel moisture model. These models commonly use LMA or SLA to describe leaf form and they also model seasonal variations in leaf water potential (ψ_l) which can be used to estimate RWC using a pressure-volume curve. This would allow LFMC to be modeled historically and forecast using future climate scenarios. To do that, we must consider each of the model variables in the context of their driving processes. A conceptual figure of these variations is shown in Fig. 7. The RWC is primarily controlled by changes in the leaf water content and these changes are a balance of water uptake from the soil and water lost through transpiration. LMA variations are ultimately controlled by the uptake of carbon and conversion to non-structural carbohydrates through photosynthesis and the allocation/translocation of these resources throughout the plant. Ultimately, a model that captures the dynamics of non-structural carbohydrate (NSC) pools, the development of new foliage and the allocation of key elements, such as nitrogen could be coupled with a leaf water balance model to suitably model LFMC over space and time and across species. This type of LFMC modeling improvement could facilitate more accurate predictions of vegetation response to climate and disturbance.

Fire behavior modeling

Each mechanistic model input is an important components to fire behavior models. A recent synthesis has suggested that a mechanistic approach to live fuel dynamics characterization can improve our ability to model fire behavior and fire effects (Dickman et al. 2023). Most fire behavior models used fuel moisture content as an direct input, along with fuel geometry descriptors such as surface area to volume ratio, particle density and fuel amount, or loading (Linn et al. 2002; Mell et al. 2007; Rothermel 1972). The mechanistic model can provide key fire behavior model inputs while also keep the input

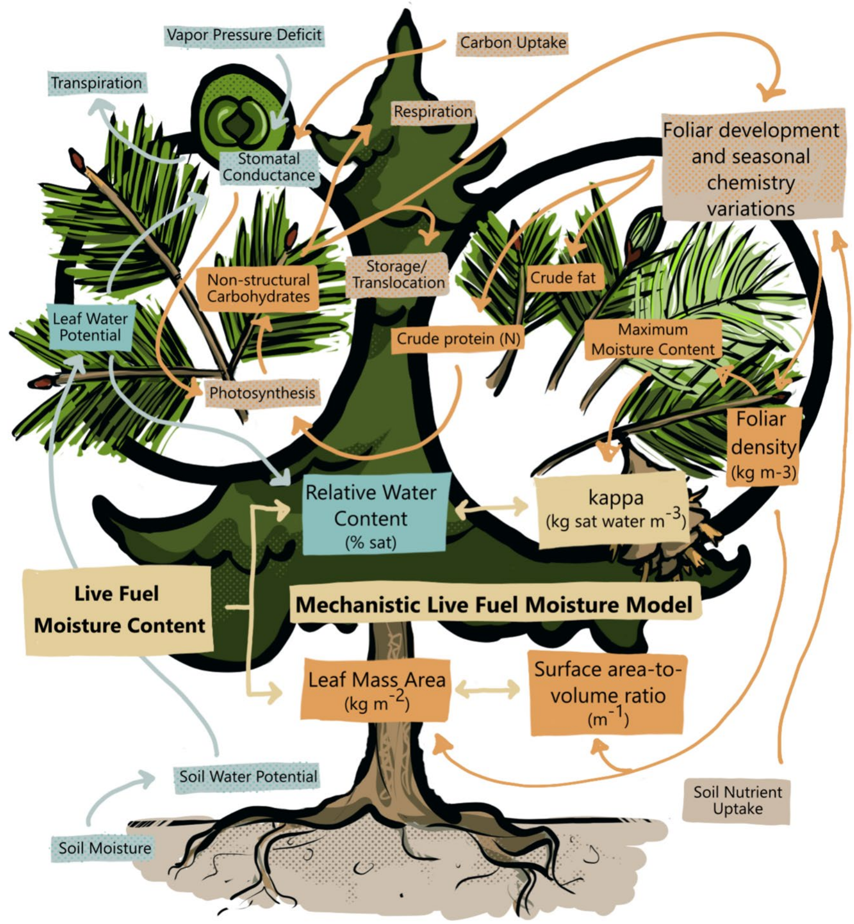

Fig. 7 Conceptual framework of ecophysiological processes that drive seasonal and inter-species variations in mechanistic live fuel moisture model inputs. LFMC is a balance between the flow of carbon and water in a plant and the allocation of carbon to various plant components. Colored arrows represent various flows from compartments or interactions between key variables in the mechanistic model. Blue arrows are generally flows of water and orange arrows are flows of biomass or nutrients. Credit: Elliott Conrad, USFS

parameters in balance. Ultimately, the SAV, LMA, and computed LFMC from the mechanistic model can be used as direct inputs to fire behavior models. Also, other characteristics can be derived, such as particle density, with is simple the product of LMA and SAV and seasonal density variations have been used to explore the impact of canopy fuel variations on potential fire behavior (Jolly et al. 2016). LMA can be used directly with plant characteristics such as Leaf Area Index (LAI) to compute the canopy fuel load. As mentioned above, canopy foliar biomass can be computed as the product of LAI and LMA when LAI is corrected for foliar orientation or fractional cover (Bahrami et al. 2022). Ultimately, this mechanistic live fuel moisture model can ensure that fire behavior model inputs are balanced and that they represent the combined physio-chemical characteristics of live plants at any given time during their lifecycle.

Conclusion

Here we have presented a novel, pyroecophysiology-based model of live fuel moisture content. The model blends plant ecophysiology and combustion traits to adequately characterize seasonal and inter-species variations in moisture content across a wide cross section of Intermountian Western US conifers. Ultimately, this new model harmonizes decades of disparate live fuel moisture research and lays a foundation for more fruitful live fuel dynamics explorations worldwide.

Authors' contributions

W.M.J. designed the study, developed the mechanistic model, supervised data collection, performed data analysis, created figures, wrote manuscript, and worked with co-authors for edits. E.T.C. lead the data collection and data summarizing, created the conceptual diagram figure, assisted with data analysis, and edited the manuscript. T.P.B. assisted with data collection and edited the manuscript. S.C.H. assisted with data interpretation and contextualization and edited the manuscript.

Funding
This work was funded in part by DOD SERDP Grant Number RC-19-1092 titled "Live Fuels: Identification of Key Processes Controlling Ignition and Fuel Consumption."

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

Declarations

Ethics approval and consent to participate
Not applicable.

Competing interests
None.

Author details
[1]Missoula Fire Sciences Laboratory, US Forest Service, Rocky Mountain Research Station, 5775 Hwy 10 W, Missoula 59808, MT, USA. [2]Department of Energy, Environment and Climate Action, Government of Victoria, PO Box 500, East Melbourne, VIC 3002, Australia.

Received: 15 October 2024 Accepted: 28 February 2025
Published online: 07 April 2025

References

Ackley, W. B. 1954. Seasonal and diurnal changes in the water contents and water deficits of bartlett pear leaves. *Plant Physiology* 29 (5): 445.

Arndt, S. K., A. Irawan, and G. J. Sanders. 2015. Apoplastic water fraction and rehydration techniques introduce significant errors in measurements of relative water content and osmotic potential in plant leaves. *Physiologia Plantarum* 155 (4): 355–368.

Bahrami, B., A. Hildebrandt, S. Thober, C. Rebmann, R. Fischer, L. Samaniego, O., et al. 2022. Developing a parsimonious canopy model (pcm v1.0) to predict forest gross primary productivity and leaf area index of deciduous broad-leaved forest. *Geoscientific Model Development* 15 (18): 6957–6984. https://doi.org/10.5194/gmd-15-6957-2022.

Balaguer-Romano, R., R. Díaz-Sierra, M. De Cáceres, R. H. Àngel Cunill-Cam-prubí, M. M. Nolan, J. Voltas Boer, et. al. 2022. A semi-mechanistic model for predicting daily variations in species-level live fuel moisture content. *Agricultural and Forest Meteorology* 323:109022. https://doi.org/10.1016/j.agrformet.2022.109022.

Bartlett, M. K., C. Scoffoni, and L. Sack. 2012. The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis. *Ecology Letters* 15 (5): 393–405. https://doi.org/10.1111/j.1461-0248.2012.01751.x. https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1461-0248.2012.01751.x.

Bergman, T.L., A.S. Lavine, F.P. Incropera, and D.P. DeWitt. 2011. *Introduction to heat transfer*, 6th ed. Hoboken: John Wiley and Sons Inc.

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., J. K. Balch, P. Artaxo, W. J. Bond, J. M. Carlson, M. A. Cochrane, et. al. 2009. Fire in the earth system. *Science* 324 (5926): 481–484. https://doi.org/10.1126/science.1163886. https://www.science.org/doi/pdf/10.1126/science.1163886.

Bradshaw, L. S., J. E. Deeming, R. E. Burgan, D. Jack, et al. 1984. The 1978 national fire-danger rating system: technical documentation. *General Technical Report INT-169. Ogden, UT: US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station*. 44 p. 169.

Brown, J. K. 1970. Ratios of surface area to volume for common fine fuels. *Forest Science* 16 (1): 101–105.

Brown, T. P., Z. H. Hoylman, E. Conrad, Z. Holden, K. Jencso, and W. M. Jolly. 2022. Decoupling between soil moisture and biomass drives seasonal variations in live fuel moisture across co-occurring plant functional types. *Fire Ecology* 18(1). https://doi.org/10.1186/s42408-022-00136-5.

Byram, G. M. 1943. Solar radiation and forest fuel moisture[1]. *Journal of Agricultural Research* 67:149.

Chuvieco, E., C. Yue, A. Heil, F. Mouillot, I. Alonso-Canas, M. Padilla, et. al. 2016. A new global burned area product for climate assessment of fire impacts. *Global Ecology and Biogeography* 25 (5): 619–629. https://doi.org/10.1111/geb.12440. https://onlinelibrary.wiley.com/doi/pdf/10.1111/geb.12440.

Clausen, J., and T. Kozlowski. 1965. Use of the relative turgidity technique for measurement of water stresses in gymnosperm leaves. *Canadian Journal of Botany* 43 (2): 305–316.

Conrad, E T., W M. Jolly, T P. Brown, and S C. Hillman. 2024. Branching out: species-specific canopy architecture limits live crown fuel consumption in Intermountain West USA conifers. *Fire Ecology* 20 (1): 28.

Countryman, C.M. 1972. *The fire environment concept*. La Verne: Pacific Southwest Forest and Range Experiment Station.

Danson, F., and P. Bowyer. 2004. Estimating live fuel moisture content from remotely sensed reflectance. *Remote Sensing of Environment* 92 (3): 309–321. https://doi.org/10.1016/j.rse.2004.03.017.

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 (1): 18–27.

Dickman, L. T., A. K. Jonko, R. R. Linn, I. Altintas, A. L. Atchley, A. Bär, et. al. 2023. Integrating plant physiology into simulation of fire behavior and effects. *New Phytologist* 238 (3): 952–970. https://doi.org/10.1111/nph.18770. https://nph.onlinelibrary.wiley.com/doi/pdf/10.1111/nph.18770.

Fang, H., F. Baret, S. Plummer, and G. Schaepman-Strub. 2019. An overview of global leaf area index (lai): methods, products, validation, and applications. *Reviews of Geophysics* 57 (3): 739–799. https://doi.org/10.1029/2018RG000608. https://agupubs.onlinelibrary.wiley.com/doi/pdf/10.1029/2018RG000608

Finney, M A., C W. McHugh, I C. Grenfell, K L. Riley, and K C. Short. 2011. A simulation of probabilistic wildfire risk components for the continental United States. *Stochastic Environmental Research and Risk Assessment* 25: 973–1000.

Fons, W. L. 1950. Heating and ignition of small wood cylinders. *Industrial & Engineering Chemistry* 42 (10): 2130–2133.

García, M., D. Riaño, M. Yebra, J. Salas, A. Cardil, S. Monedero, et. al. 2020. A live fuel moisture content product from landsat tm satellite time series for implementation in fire behavior models. *Remote Sensing* 12(11).

Gisborne, H. T. 1936. The principles of measuring forest fire danger. *Journal of Forestry* 34 (8): 786–793.

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 (3): 719–731. https://doi.org/10.1111/1365-2435.14271. https://besjournals.onlinelibrary.wiley.com/doi/pdf/10.1111/1365-2435.14271.

Hunt, E. R., B. N. Rock, and P. S. Nobel. 1987. Measurement of leaf relative water content by infrared reflectance. *Remote Sensing of Environment* 22 (3): 429–435. https://doi.org/10.1016/0034-4257(87)90094-0.

Jolly, W M., P H. Freeborn, W G. Page, and B W. Butler. 2019. Severe fire danger index: a forecastable metric to inform firefighter and community wildfire risk management. *Fire* 2 (3): 47.

Jolly, W. M., A. M. Hadlow, and K. Huguet. 2014. De-coupling seasonal changes in water content and dry matter to predict live conifer foliar moisture content. *International Journal of Wildland Fire* 23:480–489.

Jolly, W. M., J. Hintz, R. L. Linn, R. C. Kropp, E. T. Conrad, R. A. Parsons, et. al. 2016. Seasonal variations in red pine (Pinus resinosa) and jack pine (Pinus banksiana) foliar physio-chemistry and their potential influence on stand-scale wildland fire behavior. *Forest Ecology and Management* 373:167–178.

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

Keane, R. E. 1996. *FIRE-BGC, a mechanistic ecological process model for simulating fire succession on coniferous forest landscapes of the northern Rocky Mountains*, Volume 484. Ogden: US Department of Agriculture, Forest Service, Intermountain Research Station.

Koven, C D., R G. Knox, R A. Fisher, J Q. Chambers, B O. Christoffersen, S J. Davies, et. al. 2020. Benchmarking and parameter sensitivity of physiological and vegetation dynamics using the functionally assembled terrestrial ecosystem

simulator (fates) at Barro Colorado Island, Panama. *Biogeosciences* 17 (11): 3017–3044. https://doi.org/10.5194/bg-17-3017-2020.
Kozlowski, T. T., and J. J. Clausen. 1965. Changes in moisture contents and dry weights of buds and leaves of forest trees. *Botanical Gazette* 126 (1): 20–26. https://doi.org/10.1086/336289.
Lambers, H., and H. Poorter. 1992. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences, Volume 23 of *Advances in Ecological Research*, 187–261. Academic Press. https://doi.org/10.1016/S0065-2504(08)60148-8.
Lawlor, D. W., and G. Cornic. 2002. Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. *Plant, Cell & Environment* 25 (2): 275–294.
Linn, R. R., S. L. Goodrick, S. Brambilla, M. J. Brown, R. S. Middleton, J. J. O'Brien, et. al. 2020. Quic-fire: a fast-running simulation tool for prescribed fire planning. *Environmental Modelling & Software* 125:104616.
Linn, R., J. Reisner, J. J. Colman, and J. Winterkamp. 2002. Studying wildfire behavior using firetec. *International Journal of Wildland Fire* 11 (4): 233–246.
Lymburner, L., P. J. Beggs, C. R. Jacobson, et al. 2000. Estimation of canopy-average surface-specific leaf area using landsat tm data. *Photogrammetric Engineering and Remote Sensing* 66 (2): 183–192.
Martinez-Vilalta, J., W. R. Anderegg, G. Sapes, and A. Sala. 2019. Greater focus on water pools may improve our ability to understand and anticipate drought-induced mortality in plants. *New Phytologist* 223 (1): 22–32.
Mell, W., M. A. Jenkins, J. Gould, and P. Cheney. 2007. A physics-based approach to modelling grassland fires. *International Journal of Wildland Fire* 16 (1): 1–22.
Moody, M. J., J. A. Gibbs, S. Krueger, D. Mallia, E. R. Pardyjak, A. K. Kochanski, et. al. 2022. Qes-fire: a dynamically coupled fast-response wildfire model. *International Journal of Wildland Fire* 31 (3): 306–325.
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. https://doi.org/10.1016/j.agrformet.2022.108941.
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. https://doi.org/10.1016/j.agrformet.2018.09.011.
NRCS. 2025. NRCS web soil survey. https://websoilsurvey.nrcs.usda.gov/app/. Accessed 15 Jan 2025.
Pedregosa, F., G. Varoquaux, A. Gramfort, V. Michel, B. Thirion, O. Grisel, et. al. 2011. Scikit-learn: machine learning in Python. *Journal of Machine Learning Research* 12:2825–2830.
Pellizzaro, G., C. Cesaraccio, P. Duce, A. Ventura, and P. Zara. 2007. Relationships between seasonal patterns of live fuel moisture and meteorological drought indices for Mediterranean shrubland species. *International Journal of Wildland Fire* 16 (2): 232–241.
Perry, G. L. 1998. Current approaches to modelling the spread of wildland fire: a review. *Progress in Physical Geography: Earth and Environment* 22 (2): 222–245. https://doi.org/10.1177/030913339802200204.
Pivovaroff, A. L., N. Emery, M. R. Sharifi, M. Witter, J. E. Keeley, and P. W. Rundel. 2019. The effect of ecophysiological traits on live fuel moisture content. *Fire* 2 (2): 28.
Poorter, H., Ü. Niinemets, L. Poorter, I. J. Wright, and R. Villar. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist* 182 (3): 565–588.
PRISM Climate Group. 2025. Prism gridded climate data. https://prism.oregonstate.edu. Accessed 15 Jan 2025.
Rao, K., A. P. Williams, J. F. Flefil, and A. G. Konings. 2020. Sar-enhanced mapping of live fuel moisture content. *Remote Sensing of Environment* 245:111797. https://doi.org/10.1016/j.rse.2020.111797.
Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences* 94 (25): 13730–13734.
Resco de Dios, V. 2020. *Plant-fire interactions: applying ecophysiology to wildfire management*. Cham: Springer International Publishing.
Roderick, M., S. L. Berry, and I. Noble. 2000. A framework for understanding the relationship between environment and vegetation based on the surface area to volume ratio of leaves. *Functional Ecology* 14 (4): 423–437.
Rothermel, R.C. 1972. *A mathematical model for predicting fire spread in wildland fuels*, vol. 115. US: Intermountain Forest & Range Experiment Station, Forest Service.
Ruffault, J., J. M. Limousin, F. Pimont, J. L. Dupuy, M. De Càceres, H. Cochard, et. al. 2023. Plant hydraulic modelling of leaf and canopy fuel moisture content reveals increasing vulnerability of a Mediterranean forest to wildfires under extreme drought. *New Phytologist* 237 (4): 1256–1269. https://doi.org/10.1111/nph.18614. https://nph.onlinelibrary.wiley.com/doi/pdf/10.1111/nph.18614.
Ruffault, J., N. Martin-StPaul, F. Pimont, and J. L. Dupuy. 2018. How well do meteorological drought indices predict live fuel moisture content (lfmc)? An assessment for wildfire research and operations in mediterranean ecosystems. *Agricultural and Forest Meteorology* 262:391–401.
Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. Nih image to imagej: 25 years of image analysis. *Nature methods* 9 (7): 671–675.
Stocks, B J., B. Lawson, M. Alexander, C V. Wagner, R. McAlpine, T. Lynham, and D. Dube. 1989. The Canadian forest fire danger rating system: an overview. *The Forestry Chronicle* 65 (6): 450–457.
Viney, N. R. 1991. A review of fine fuel moisture modelling. *International Journal of Wildland Fire* 1 (4): 215–234.
Waskom, M. L. 2021. seaborn: statistical data visualization. *Journal of Open Source Software* 6 (60): 3021. https://doi.org/10.21105/joss.03021.
Weatherley, P. 1950. Studies in the water relations of the cotton plant. I. The field measurement of water deficits in leaves. *New Phytologist* 49 (1): 81–97.
White, M A., P E. Thornton, S W. Running, and R R. Nemani. 2000. Parameterization and sensitivity analysis of the biome-bgc terrestrial ecosystem model: net primary production controls. *Earth Interactions* 4 (3): 1–85.
Yebra, M., P. E. Dennison, E. Chuvieco, D. Riaño, P. Zylstra, E. R. Hunt, et. al. 2013. A global review of remote sensing of live fuel moisture content for fire danger assessment: moving towards operational products. *Remote Sensing of Environment* 136:455–468. https://doi.org/10.1016/j.rse.2013.05.029.
Yebra, M., G. Scortechini, K. Adeline, N. Aktepe, T. Almoustafa, A. Bar-Massada, et al. 2024. Globe-LFMC 2.0, an enhanced and updated dataset for live fuel moisture content research. *Scientific Data* 11 (1): 332.
Yebra, M., G. Scortechini, A. Badi, M. E. Beget, M. M. Boer, R. Bradstock, et al. 2019. Globe-LFMC, a global plant water status database for vegetation ecophysiology and wildfire applications. *Scientific Data* 6 (1): 155.

Publisher's Note