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ORIGINAL RESEARCH

Decoupling between soil moisture and biomass drives seasonal variations in live fuel moisture across co-occurring plant functional types

Tegan P. Brown[1]* , Zachary H. Hoylman[2,3], Elliott Conrad[4], Zachary Holden[5], Kelsey Jencso[2,3] and W Matt Jolly[4]

Abstract

Background: Wildfires are important global disturbances influencing ecosystem structure and composition. The moisture content of living and senescent plant components are key determinants of wildfire activity, yet our understanding of how seasonal fluctuations in water availability and biomass control live foliar moisture content (LFMC) across co-occurring plant functional types is limited in diverse forested landscapes.

Results: We recorded root-zone volumetric water content (VWC) and sampled leaf mass area (LMA) and LFMC of three co-occurring plant functional types across six field sites. We used a linear mixed effects model to quantify the drivers of LFMC and understand whether LFMC dynamics were coupled or decoupled from site conditions. Both LMA and VWC were significant predictors of LFMC variability ($p < 0.001$), although the strength and direction of these relationships varied across functional types. LFMC dynamics of understorey plant functional types were strongly coupled to site conditions, where the site random effect explained 44.2% (shrub) and 74.8% (herb) of the variability in LFMC across the season respectively. In contrast, overstorey plants were decoupled from site conditions, which explained only 8.1% of the variability in LFMC.

Conclusions: LFMC of understorey plants responded to changes in soil water availability (VWC), while overstorey trees responded to biomass fluctuations (LMA). We present a conceptual model describing the influence of these factors on LFMC, which aligns with our findings and draws on the broader literature. This knowledge and conceptual approach can be used to improve our ability to characterize seasonal LFMC variation across different plant functional types, in turn improving our capacity to predict wildfire risk.

Keywords: Fuel moisture, Functional type, Leaf mass area (LMA), Live foliar moisture content (LFMC), Soil moisture

Resumen

Antecedentes: Los incendios son disturbios importantes que influencian la estructura y composición de los ecosistemas. El contenido de humedad de los componentes vivos y senescentes de las plantas es un determinante

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*Correspondence: tpbrown@student.unimelb.edu.au
[1] School of Ecosystem and Forest Sciences, Faculty of Science, The University of Melbourne, Baldwin Spencer Building, Parkville 3010, VIC, Australia
Full list of author information is available at the end of the article

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(Continued from previous page) clave en la actividad de los incendios. Sin embargo, nuestro conocimiento sobre cómo las fluctuaciones estacionales en la disponibilidad del agua y la biomasa controlan la humedad foliar en tejidos vivos (LFMC) en agrupaciones de tipos funcionales de plantas, es limitado en diversos paisajes forestales.

Resultados: Registramos el contenido volumétrico de agua en la zona radical (VWC), y muestreamos la masa del área foliar (LMA) y el LFMC de tres agrupaciones de tipos funcionales de plantas en seis sitios de muestreo en el campo. Usamos un modelo de efecto mixto linear para cuantificar los conductores del LFMC y entender el por qué la dinámica del LFMC estuvo acoplada o no a las condiciones del sitio. Tanto la masa foliar (LMA) como el contenido volumétrico de agua en la zona radical (VWC) fueron predictores significativos de la variabilidad en el LFMC (p<0,001), aunque la robustez y dirección de esas relaciones variaron a través de los tipos funcionales. La dinámica del LFMC de tipos funcionales del sotobosque se acopló fuertemente con las condiciones de sitio, en el cual el efecto aleatorio del sitio explicó el 44,2% (componente arbustivo) y el 74,8% (componente herbáceo) de la variabilidad en el LFMC a través de las estaciones, respectivamente. En contraste, las plantas del dosel superior estuvieron desacopladas de las condiciones de sitio, lo que explicó sólo el 8,1% de la variabilidad en el LFMC.

Conclusiones: El contenido de humedad del combustible vivo (LFMC) de las plantas del sotobosque, respondieron a los cambios en la disponibilidad de agua en el suelo (VWC), mientras que los árboles del dosel superior respondieron a las fluctuaciones de la biomasa (LMA). Presentamos un modelo conceptual que describe la influencia de esos factores en el LFMC, concordando nuestros resultados y productos con la amplia literatura en la materia. Este conocimiento y aproximación conceptual puede ser usado para mejorar nuestra habilidad para caracterizar la variación estacional del LFMC a través de diferentes tipos funcionales de plantas, y también mejorar nuestra capacidad para predecir el riesgo de incendios.

Background

Wildfire is an important global disturbance that influences the structure and composition of ecosystems (Bowman et al. 2009). A key determinant of wildfire activity is the moisture content of fine fuels such as foliage, small branches, and litter, which affects ignition probability, fire behavior, and resultant fire severity (Matthews 2014; Ellis 2015). Fuel moisture content is defined as the ratio of water mass to dry mass in a live or dead sample and can vary by an order of magnitude between live and dead fuels (Viney and Hatton 1991). In forested regions, fires typically burn through a mixture of living and dead vegetation and while the moisture content of both are important, the factors that govern spatial and temporal variability can be quite different (Jolly and Johnson 2018).

Dead fuel moisture content (DFMC) is a function of the weather conditions at the fuel interface and physical fuel properties that control the movement of water across the boundary layer (Anderson 1990). With the exception of decomposition processes, the dry mass of dead fuel is relatively constant (Grootemaat et al. 2015), so changes in DFMC primarily reflect changes in the water mass. In contrast, live foliar moisture content (LFMC) is determined by fluctuations in both dry mass and water mass, which vary independently over space and time. While factors governing variation in DFMC have been the subject of extensive research (Viney 1991; Matthews 2014), few studies exist that seek to understand mechanisms driving variation in live foliar moisture content.

LFMC variations relate to plant physiological properties that govern plant water and carbon cycles. Soil water uptake, transpiration rate, and plant water storage each influence the moisture status of foliage (Kozlowski et al. 1991), while fluctuations in dry mass are related to carbon cycling processes including photosynthesis, respiration, carbon allocation, and phenology (Barbour 2017; Larcher 2003). LFMC can be difficult to estimate because the water and dry mass components of foliage vary independently across different temporal and spatial scales. Temporal fluctuations in LFMC occur at daily, seasonal, and inter-annual scales (Bertin et al. 1999; Wever et al. 2002; Pellizzaro et al. 2007b), while spatial fluctuations are related to interspecific variability across species at the same site, intraspecific variation across environmental gradients, or interactive effects of both factors (Krix and Murray 2018; Nolan et al. 2018).

The importance of both water and dry mass changes in estimating LFMC has been understood for decades (Kozlowski 1964), yet to date this knowledge has not be consistently applied in studies exploring variation in LFMC. Jolly et al. (2014) suggest that decoupling dry and water mass components when estimating LFMC, and exploring their variability independently using principles of ecophysiology will enable a more accurate understanding of seasonal fluctuations in foliage moisture status and flammability (Pivovaroff et al. 2019). Nolan et al. (2020) extended this by relating LFMC to plant physiological traits governing changes in dry mass, ultimately suggesting that LFMC models could be improved by incorporating plant morphological traits, such as leaf mass area (LMA). However, estimating LFMC variability at landscape-scales using ecophysiological principles

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is difficult because we currently lack a conceptual framework describing the dominant controls on water and dry mass fluctuations in LFMC at different scales and across plant functional types. Consequently, estimating LFMC remains challenging across topographically complex landscapes with diverse species assemblages.

Current methods for estimating LFMC typically focus on changes in moisture content using drought indices (Viegas et al. 2001; Schunk et al. 2017; Ruffault et al. 2018) or remote sensing (Yebra et al. 2013; Caccamo et al. 2012; Qi et al. 2012). Drought indices reflect long-term soil moisture deficits and have shown useful correlations with LFMC for some plant functional types. However, this approach is limited because drought indices do not capture changes in dry mass, or differing responses to moisture availability across co-occurring plants. For example, LFMC has been strongly correlated with drought indices for shallow-rooted plant functional types (Dimitrakapoulos and Bemmerzouk 2003; Pellizzaro et al. 2007a), while woody plants with limited seasonal fluctuation in LFMC related poorly to similar indices (Nolan et al. 2018; Viegas et al. 2001; Caccamo et al. 2012).

Remote sensing approaches enable broad-scale estimates of LFMC to be captured at useful temporal scales (Yebra et al. 2013) and calibrated spectral approaches can differentiate between dry and water mass components (Qi et al. 2014). However, sensors typically capture only the upper-most layer of vegetation and omit contributions to overall leaf area from near-surface vegetation. While this may be suitable for estimates of canopy or grassland LFMC, it limits the utility of remote sensing approaches in multi-layered forests with diverse species assemblages.
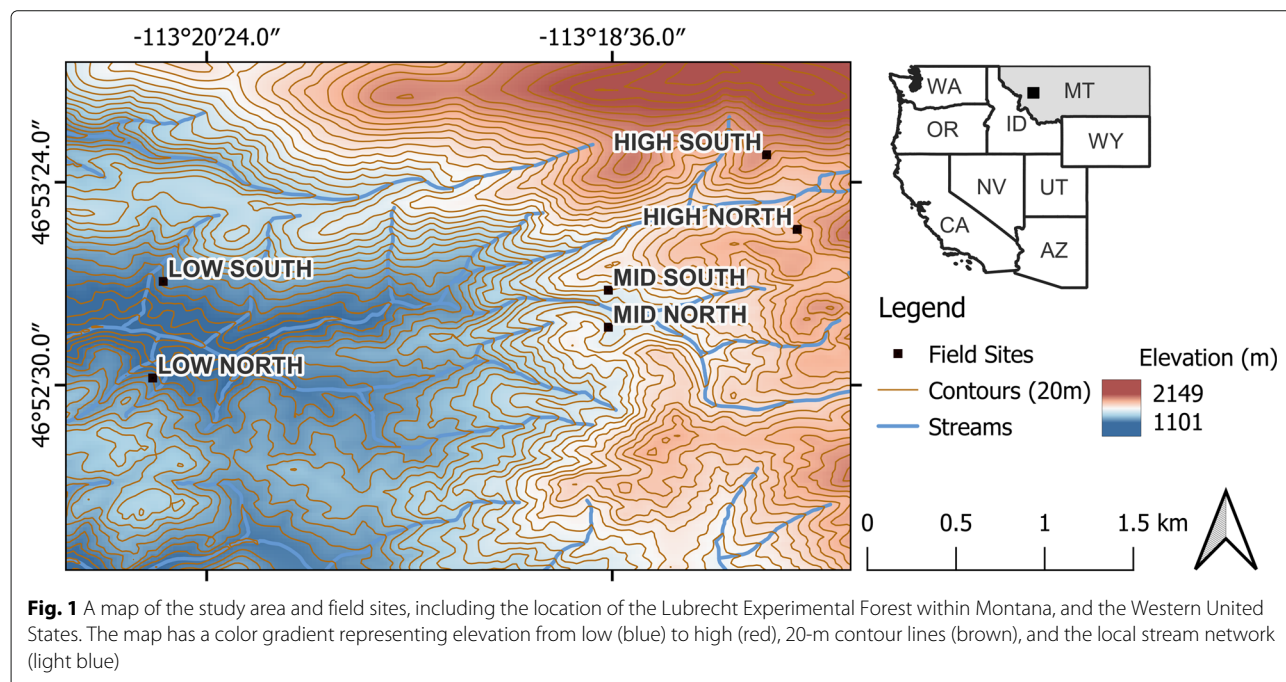
Accurate estimations of LFMC are critical for understanding landscape-scale fire risk and potential fire behavior (Rothermel 1972; Dennison et al. 2008). Here, we present a study aimed at quantifying seasonal LFMC variability in three co-occurring plant functional types and relate this to water and dry mass controls. We explore ecophysiological principles in a field-based experimental context to explore the key physical drivers that should be incorporated to constrain the application of remote sensing or drought index approaches to LFMC estimation at spatial and temporal scales relevant for fire managers.

Overall, we assess the degree to which LFMC variability is coupled, or decoupled from site conditions in a complex forested landscape. Finally, we present a simple, conceptual model that frames the combined influences of water and dry mass variations on LFMC dynamics across three plant functional types.

Methods

Study area

This study was conducted in the North Fork of the Elk Creek catchment, in the Lubrecht Experimental Forest, Western Montana, USA (Fig. 1). Precipitation in the area is snow-melt dominated and typically increases with elevation. Two snow survey telemetry (SNOTEL) sites (#604 and #657) are located in the catchment, recording mean annual precipitation of 514 mm and 664 mm, and mean annual temperature of 4.2 °C and 3.0 °C, respectively (between 1981 and 2010) (NRCS 2021). Annual precipitation in 2019, the year field data were collected for this study, 757mm and 709mm, for SNOTEL stations #604 and #657 respectively, which are higher than average

Fig. 1 A map of the study area and field sites, including the location of the Lubrecht Experimental Forest within Montana, and the Western United States. The map has a color gradient representing elevation from low (blue) to high (red), 20-m contour lines (brown), and the local stream network (light blue)

(NRCS 2021). The underlying lithology of the catchment is quartz monzonite, with well-drained silty-loam soils (USDA 2001). Hoylman et al. (2018) report consistent soil depths across 54 wells driven to bedrock within the catchment, ranging between ∼ 0.5 and 1.0m and 1.0 and 2.0m on side-slope and hollow landscape positions respectively.

The area is dominated by three conifer species in the overstorey: Douglas fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), and western larch (*Larix occidentalis*) (Rowell et al. 2009). The understorey vegetation is dominated by white spirea (*Spiraea betulifolia* var. *lucida*) and common huckleberry (*Vaccinium globulare*), while the ground cover is comprised primarily of heartleaf arnica (*Arnica cordifolia*) (Nimlos et al. 1968; Habeck 1991). The forested region was clear-fell harvested from 1904 to 1934, resulting in present-day stands of similar age, ranging from 70 to 100 years. While no major fires have occurred recently in the study area, the historical return interval for non-stand replacing, low intensity fire was every 7 years (Grissino-Mayer et al. 2006). The landscape has historically been purposefully managed with fire by the Confederated Salish and Kootenai Tribes (CSKT 2021).

Field sites and sampling
Six field sites were located across an aspect (north/polar and south/equatorial) and elevation (low, mid, high) gradient (Table 1; Fig. 1). Further information about the field sites is available in Hoylman et al. (2019). Each site was instrumented with one capacitance-based volumetric water content (VWC m^3 m^{-3}) probe (Decagon 5TE) at 0.5-m depth, connected to a custom-built circuit board data logger (Hoylman et al. 2019). Values were recorded at 30-min intervals.

Three species representing different plant functional types were common to the field sites throughout the catchment: *P. menziesii* (tree), *S. betulifolia* (shrub), and *A. cordifolia* (herb). *P. menziesii*-dominated forest is an

important and widely distributed overstorey tree throughout the Intermountain West (Mathys et al. 2014). Habeck (1974) listed *S. betulifolia* as an understorey shrub of "major importance" to this forest community, while *A. cordifolia* is frequently co-recorded with these species throughout their distribution (Schuler 1968). The rooting depth of *P. menziesii* is largely determined by soil structure, with maximum root depth typically ranging between 0.6 and 1.0m (Mauer and Palatova 2012). However, a substantial volume of the root mass is contained in roots extending laterally from the stem. Mauer and Palatova (2012) measured lateral roots of *P. menziesii* individuals between 10- and 80-year-olds and reported mean depths ranging from 0.082 m ($\pm$ 0.021 m) to 0.146 m ($\pm$ 0.029 m). We were unable to obtain root-zone data for *S. betulifolia* specifically. However, Nimlos et al. (1968) reported rooting depths up to 1.2 m in *Rosa woodsii* plants located in the Lubrecht Experimental Forest, which are small native shrubs in the same Family (Rosaceae) as *S. betulifolia*. The majority of *A. cordifolia* roots are within 0.3 m of the surface; however, in a study using radio-iodine absorption at different depths, *A. cordifolia* roots were present at a depth of 0.61m (Nimlos et al. 1968).

Foliar samples were collected from three co-occurring species that were identified at each site in pre-sampling surveys. *P. menziesii* (tree), *S. betulifolia* (shrub), and *A. cordifolia* (herb) were sampled ten times over a 12-week period from June to August 2019. At each field site, twenty herb and shrub samples, and ten tree (needle) samples were collected from randomly selected individual plants within 20m of the middle of the site, demarcated by the logging station. The number of samples required per collection was determined by assessing foliage LFMC variability in the pre-sampling surveys, balanced with the number of samples that could be analyzed in the laboratory each week. To control for variability within the canopy due to shading (Gebauer et al. 2012), tree foliage samples were always collected from the outer crown up to 3m from the ground. All samples were immediately sealed in an airtight bag and transported to the laboratory in a cooler. Needles were left on the branch for transportation.

Laboratory analysis
Laboratory analyses were conducted on the afternoon of collection. Tree needle samples were separated from the branch, taking care to select only 1-year-old foliage, to control for variability related to the age of the needle (Jolly et al. 2014). One-year-old needles were utilized because they are easily identified on the branch by selecting needles on the first node back from the bud. Fresh foliage samples were weighed (FW) using scales accurate to the nearest 10 mg (herb and shrub) and 1 mg (tree needles). The samples were dried in a convection oven for 48 h at

Table 1 Site descriptions of the six field sites utilized in this study

Site name	Description	Elevation (m asl)	Coordinates
LENA	Low elevation north aspect	1401	46.875523, -113.343993
LESA	Low elevation south aspect	1402	46.882649, -113.343217
MENA	Mid elevation north aspect	1598	46.879283, -113.310282
MESA	Mid elevation south aspect	1602	46.882002, -113.310284
HENA	High elevation north aspect	1747	46.886507, -113.296316
HESA	High elevation south aspect	1787	46.892029, -113.298578

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70 °C and re-weighed to determine the dry weight (DW). LFMC was determined using the following equation:

$$LFMC\ (\%) = \frac{FW - DW}{DW} \times 100 \qquad (1)$$

Before drying, the samples were photographed against a plain white background. To determine the one-sided (projected) surface area (SA) of each leaf or needle, the images were analyzed using Image J software following Ferreira and Rasband (2012). LMA was calculated from one-sided SA and DW using the following equation:

$$LMA\ \left(g\ m^{-2}\right) = \frac{DW}{SA} \qquad (2)$$

Equation 3 presents a simplified formula to estimate LFMC from Eq. 1, highlighting the importance of both the water mass numerator (FW-DW) and dry mass denominator (DW) for LFMC variability. Further, we outline assumptions tested in this study: (a) that soil moisture (VWC) is a proxy for changes in the water mass of live fuels and (b) that LMA is a proxy for changes in the dry mass of live fuels.

$$LFMC \approx \frac{\text{Water Mass}}{\text{Dry Mass}} \approx \frac{f(VWC)}{f(LMA)} \qquad (3)$$

Data analysis

VWC was calculated from the sensor output (dielectric permittivity) following Topp et al. (1980) using the manufacturer's suggested equation. VWC was summarized for each site and sample period by taking the daily mean value. Prior to averaging, VWC data were visually inspected for missing data and errors associated with sensor failures. A small number of missing data points at the HENA field site (between August 14 and 27) were estimated using linear interpolation.

LFMC and LMA data were visually assessed for the presence of outliers. Data were grouped by functional type, sampling week, and site. At this level, LFMC and LMA values in the top and bottom tenth percentile were assumed to be associated with sampling and laboratory errors and removed from subsequent analysis. In total, 2161 individual foliage samples are presented in the results.

We used one way analysis of variance (ANOVA) to assess interspecific differences of LFMC and LMA means across plant functional types, and intraspecific differences across aspect and elevation. To explore the water and dry mass controls on seasonal variation in LFMC, we used a linear mixed effects model. LMA and VWC were tested as fixed effects in the model, while the individual site effect (site ID) was included as a random effect. The repeated samples were nested as auto-correlated data within the random effects (site ID) grouping. The random effects in this model therefore describes factors influencing LFMC

that vary with site at a localized scale. Mixed effects models are appropriate for this experimental design given the repeated temporal sampling nested within sites, and to account for site-specific controls on variability through the random effects term. In addition to understanding relationships between LFMC, LMA, and VWC, we apportioned observed variance in LFMC to site conditions (random effect term). To do this, we divided the variance attributed to the site by the total variance (site ID + residual) and multiplied the value by 100. These values represent the degree to which seasonal fluctuations in LFMC are coupled (high variance explained) or decoupled (low variance explained) from the site. All data analyses were performed using the R statistical software, version 3.6.3 (R Core Team 2016).

Results

Grouped across all sites, there were significant interspecific variation in LFMC between plant functional types ($F_{2,2158}$=5719.65, $p < 0.05$) (Fig. 2). Seasonal mean LFMC for the ground-cover herb was 393% (SD $\pm$ 88.8%), more than double the LFMC of shrubs (137%, SD $\pm$ 25.1%) and tree foliage (124%, SD $\pm$ 25.3%) (Fig. 2). Intraspecific variation in LFMC was estimated across sites using the elevation and aspect gradient; there were significant across-site aspect and elevation effects within each functional type, although the magnitude of these differences were smaller than interspecific differences between functional types at the same site (Table 2; Fig. 3). LMA, a proxy for dry mass differences in this study, was also significantly different across functional types ($F_{2,2158}$=17930.17, $p < 0.05$) (Fig. 2). Seasonal mean LMA was 180 gm^{-2} (SD $\pm$ 27.4) for tree foliage, 40.0 gm^{-2} (SD $\pm$ 8.04) for shrub, and 36.7 gm^{-2} (SD $\pm$ 6.45) for herb foliage (Fig. 2). LMA typically increased with elevation, with diverging results across aspects (Table 2; Fig. 3). As with LFMC, interspecific variation in LMA was greater than intraspecific across the aspect and elevation gradient (Table 2).

There were significant differences in seasonal mean VWC between all sites (Table 3), with the exception of mid- and high-elevation sites on polar slopes. VWC typically increased with elevation and was higher on north-facing (polar) slopes (Fig. 4).

Controls of LFMC variability

LMA and VWC were significant predictors of LFMC ($p < 0.001$) (Table 4) in the linear mixed effects model for all plant functional types. In each case, LMA had a negative relationship with LFMC; in other words, an increase in LMA resulted in a decrease in LFMC. While the strength of this relationship was greatest for ground-cover herbs and weakest for tree foliage (Table 4), this likely relates to the magnitude of differences observed in the raw values of LMA. The *t*-values reported highlight the standard-
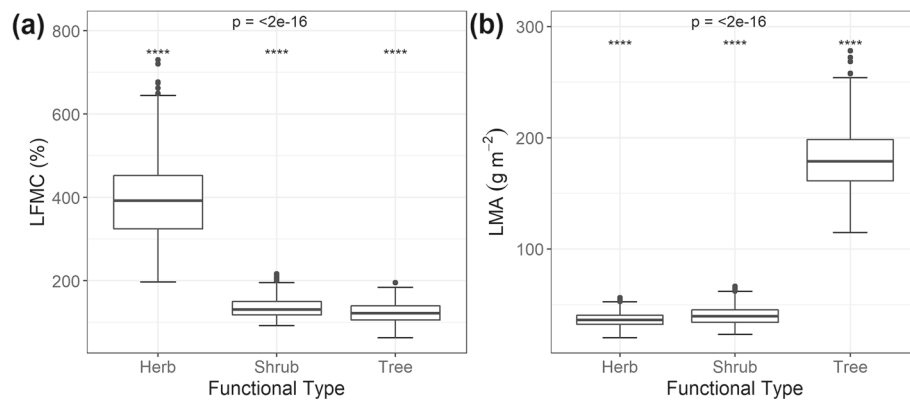
Fig. 2 Box and whisker plots depicting the median, interquartile range and minimum and maximum observed values for **a** measured live foliar moisture content (LFMC) and **b** leaf mass area (LMA) for herb, shrub, and tree functional types. Data are grouped across all sites and sampling periods. The *p*-value denotes results of one-way analysis of variance across all functional types, while asterisks denote statistically significant difference of means between paired functional type groups. $^{****} = p < 0.0001$, $n = 2161$

ized effect, demonstrating that the relative importance of LMA (a proxy for dry mass) to LFMC variability is highest for tree foliage. There were distinct differences across functional types related to the effect of VWC on LFMC. While statistically significant relationships were observed for each functional type, the coefficient of the model for tree foliage was negative, describing a relationship where a reduction in soil moisture related to an increase in foliar moisture content. While the strength of the relationships were substantially different, LFMC for herb and shrub foliage had a positive relationship with VWC (Table 4), such that lower soil moisture related to lower LFMC for these functional types.

Within the linear mixed effects model, the proportion of variance explained by the site random effects term describes the degree to which LFMC variability is coupled, or decoupled from site conditions (Table 5). The site-based random effects term explained 8.1%, 44.2%, and 74.8% of the LFMC variability for tree, shrub, and herb plant functional types respectively.

Discussion

LFMC variability across co-occurring functional types

The moisture content of live foliage is a key determinant of wildfire ignition, propagation, and severity (Rossa et al. 2016). Therefore, it is important to understand LFMC dynamics and the factors controlling these dynamics across plant functional types at different spatial and temporal scales. In our study, we found significant differences in LFMC among co-occurring plant functional types. Similar to Scarff et al. (2021), these differences were greater between different species at the same site compared to differences across an environmental gradient. Differences in LFMC were strongly related to seasonal fluctuations in water availability (VWC) and dry mass (LMA), yet the strength of the relationships of each plant functional type to these controls varied (Table 4). Overall, this results in distinct differences in the moisture dynamics of tree, shrub, and herb plant functional types, and we suggest that this can be conceptualized as these plant functional types being coupled, or decoupled from site

Table 2 Site seasonal mean and standard deviation (in parentheses) of live foliar moisture content and leaf mass area for tree, shrub, and herb functional types. These summary data were computed from 2161 individual foliage samples, comprising tree ($n = 529$), shrub ($n = 867$), and herb ($n = 765$)

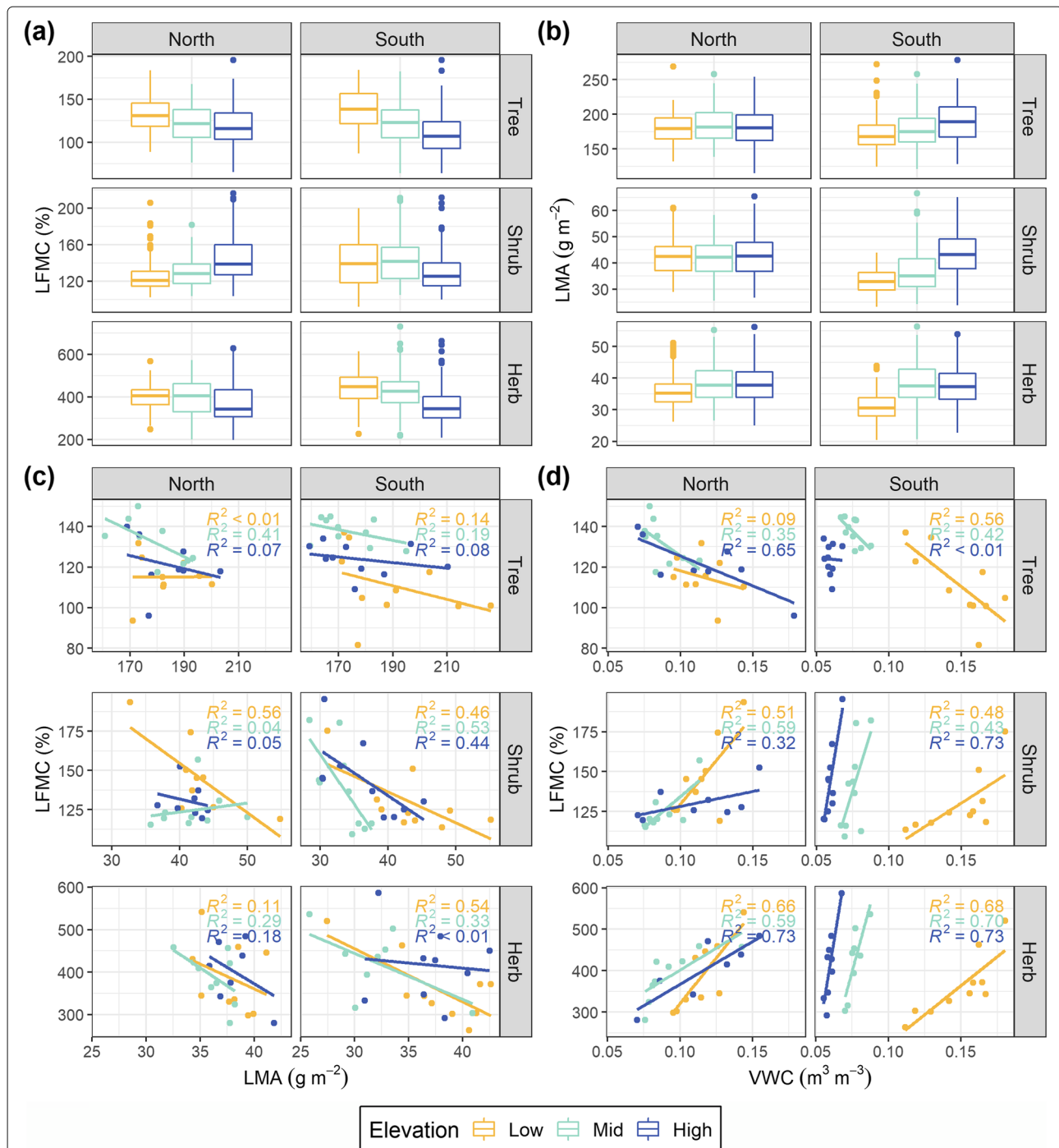| Site ID	LFMC (%)			LMA (gm^{-2})		
	Tree	Shrub	Herb	Tree	Shrub	Herb
LENA	131.8 (20.5)	125.3 (16.9)	399.3 (59.5)	179.2 (24.5)	42.2 (7.1)	35.7 (5.3)
LESA	138.5 (24.6)	141.0 (27.4)	438.6 (77.1)	173.4 (27.1)	33.0 (4.9)	31.1 (4.6)
MENA	122.9 (22.3)	129.3 (15.3)	395.4 (83.7)	183.7 (25.4)	41.6 (6.7)	38.3 (5.9)
MESA	124.4 (25.8)	143.9 (25.8)	423.6 (83.9)	177.8 (26.5)	36.7 (8.0)	37.9 (6.2)
HENA	118.5 (24.4)	145.9 (27.0)	369.4 (87.0)	180.0 (27.5)	42.7 (7.5)	38.0 (6.7)
HESA	110.1 (25.2)	130.5 (24.1)	360.4 (86.6)	190.2 (30.9)	43.1 (9.3)	37.4 (6.7)

Fig. 3 Summary plots describing observed live foliar moisture content (LFMC) and leaf mass area (LMA). The box and whisker plots for LMFC (**a**) and LMA (**b**) for each plant functional type are grouped by aspect and elevation; the colors correspond to low (yellow), mid (teal), and high (blue) elevation. Data for **a** and **b** are combined for all sites and sampling periods, $n = 2161$. The relationship between LFMC and LMA and LFMC and volumetric water content (VWC) are presented in **c** and **d**, respectively, with a linear model and R^2 for each aspect and elevation group. Plots **c** and **d** used averaged data as included in the linear mixed effects model ($n =$)

Table 3 Site seasonal mean and standard deviation (in parentheses) of volumetric water content, measured at 0.5m depth. Summary data presented were computed from VWC data recorded at 30-min intervals between June 12 and August 27, 2019 ($n = 23755$). The number of data points per site are approximately equal ($n = 3649 - 3674$), except for HENA related to missing data between August 14 and 27 ($n = 3054$). The interpolated values for this site were not included in the summary

Site ID	VWC (m³ m⁻³)
LENA	0.090 (0.017)
LESA	0.074 (0.005)
MENA	0.117 (0.034)
MESA	0.059 (0.003)
HENA	0.114 (0.014)
HESA	0.148 (0.021)

conditions. These findings have important implications for how we estimate LFMC across complex forested landscapes, and the methods to determine landscape wildfire risk.

Water mass controls on LFMC variability

Access to soil moisture was significantly related to foliar moisture content in each plant functional type, although the strength and direction of the relationships varied. LFMC of the herbaceous ground cover *A. cordifolia* was tightly coupled to changes in VWC at 0.5m, while fluctuations in shrub (*S. betulifolia*) LFMC were moderately related (Table 4). In contrast, the negative relationship between tree foliage moisture content and VWC suggests soil moisture at this depth has a limited effect on LFMC dynamics of *P. menziesii* needles.

The significant differences in LFMC and relationships with water availability across co-occurring plant func-

tional types observed in this study align with research in forested ecosystems in other locations. Dimitrakapoulos and Bemmerzouk (2003) reported strong relationships between plant moisture status and drought indices for herbaceous shallow-rooted species (analogous to *A. cordifolia* measured here), and comparatively poor relationships of the same indices with the moisture dynamics of deep-rooted *Pinus brutia* trees. Pellizzaro et al. (2007a) compared LFMC with the Keetch-Byram Drought Index (KBDI) (Keetch and Byram 1968) and Drought Code (DC) (van Wagner 1987), finding strong correlations between these indices and LFMC for herbaceous species in the Mediterranean-type ecosystem, while observing weak correlations for deep-rooted sclerophyllous species at the same location. Nolan et al. (2018) and Pivovaroff et al. (2019) provide a mechanistic basis for these findings, demonstrating that moisture variability in co-occurring plants is largely related to differences in the ecophysiological traits that mediate access to and uptake from water in the soil, and water storage capacity and regulation within the plant. This aligns with our observations of herb and shrub seasonal LFMC decline, and the limited variation observed in *P. menziesii* needle moisture status. However, unlike Nolan et al. (2018) we did not find a positive relationship between overstorey tree moisture variability and deep (in their study > 0.25m; in our study 0.5m) soil moisture. This may be related to the age of the foliage sampled, or the depth of the sensors, or a combination of both factors. A limitation of our study is that we only sampled tree foliage from one age category (1-year-old). While mixing new and old foliage can confound LFMC results (Agee et al. 2002), it may explain the divergence in soil moisture and LFMC relationships across the literature. The observed lack of variability in tree foliage LFMC, and the divergent relationship with VWC may also be related to the depth of the soil moisture sensors. Although
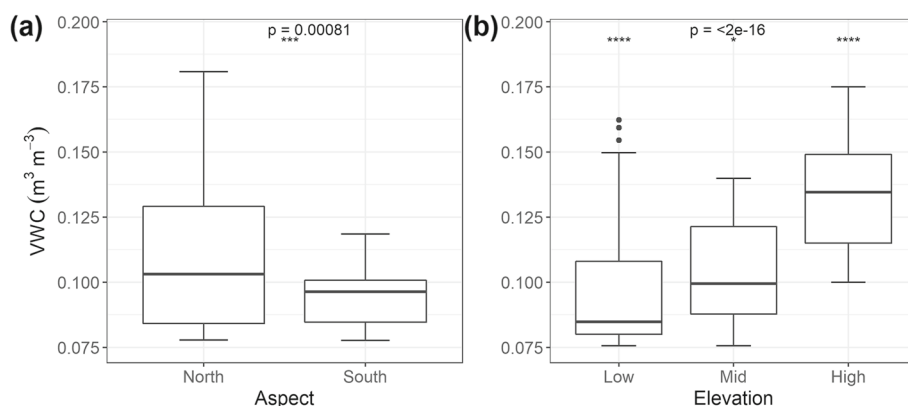

Fig. 4 Box and whisker plots depicting the median, interquartile range, and minimum and maximum observed values for seasonal mean volumetric water content (VWC) grouped by aspect (**a**) and elevation (**b**).The global *p*-value denotes results of one-way analysis of variance across all groups, while asterisks denote statistically significant difference of means between sets of pairs. * = $p < 0.05$, *** = $p < 0.001$, **** = $p < 0.0001$, $n = 2161$

Table 4 Fixed effects estimated from the linear mixed effects model for tree, shrub, and herb functional types. All data points were pooled for this model ($n = 2161$)

Functional type	Variable	Estimate	SE	df	t-value	p <t-value
Tree	Intercept	214.10	7.59	97.38	28.19	***
	LMA	−0.35	0.03	501.96	−10.20	***
	VWC	−269.46	45.00	68.52	−5.98	***
Shrub	Intercept	135.33	8.98	12.87	15.08	***
	LMA	−1.12	0.09	831.84	−12.76	***
	VWC	480.96	37.96	764.49	12.67	***
Herb	Intercept	271.93	46.14	7.60	5.89	***
	LMA	−3.54	0.37	730.48	−9.53	***

*** = p< 0.001

the soil profile between surface and 0.5m contains ∼ 60–70% of the total root mass of conifer trees (Jackson et al. 1996), and our soil moisture values align with other studies in the region (Martin et al. 2018; Hoylman et al. 2019), our sensors were located above the maximum rooting depth of *P. menziesii* (0.6–1.0m) (Mauer and Palatova 2012) and they may be accessing deeper water stores than we were able to measure. However, overall LFMC variability in 1-year-old tree foliage was more strongly related to changes in biomass, estimated from LMA, which may also explain the divergent VWC/LFMC relationship for tree foliage. Plant regulation of water loss is facilitated through a range of traits that, overall, correspond to greater investment in the leaf and subsequently higher LMA (Poorter et al. 2009). This affirms our findings of comparatively lower moisture values and variability in tree needles, with correspondingly higher LMA.

Dry mass controls on LFMC variability
LMA is a morphological plant characteristic commonly used to summarize a suite of traits related to plant functioning and resource storage and is directly related to changes to foliage dry weight (Eq. 2) (De La Riva et al.

Table 5 The random effects estimated from the linear mixed effects model for tree, shrub and herb functional types. All data points were pooled for this model ($n = 2161$)

Functional Type		Variance	SD
Tree	Site	37.11	6.09
	Residual	419.80	20.49
Shrub	Site	287	16.94
	Residual	358	18.92
Herb	Site	10234	101.16
	Residual	3447	58.71

2016). Seasonal fluctuations in LMA were significant in explaining LFMC for all functional types (Table 4). However, the relative importance of LMA (compared to VWC) was higher for tree foliage compared to shrubs and herbs. There is a sound physical basis for this because plant investment in foliage is related to its longevity (Falster et al. 2012), which differed between the plants measured in this study. *P. menziesii* is an evergreen tree, and needle longevity is between 5 and 8 years (Balster and Marshall 2000). In contrast, *S. betulifolia* and *A. cordifolia* replace foliage annually, and similar to many other shrubs and herbs in this region, this results in lower plant investment in each leaf and correspondingly lower LMA values (Prior et al. 2003; Poorter et al. 2009). High LMA relates to higher foliage density within the leaf organ, which consequently leaves less room for water (Poorter et al. 2009). Nolan et al. (2020) demonstrated that high LMA values are related to lower maximum LFMC values and our results align with these findings.

Changes in dry matter were a more important predictor of LFMC fluctuations of overstorey tree needles compared to understorey foliage (Table 5). Consequently, processes affecting dry mass variability are likely to be more important in mediating LFMC fluctuations in tree needles than shrub and herb foliage — where soil moisture predominates LFMC variability. This also accounts for the statistically significant, yet seemingly contradictory relationships between decreasing VWC and increasing tree foliage LFMC (Table 5). Despite the strong relationship, we suggest it is a correlated, not causal one. Consequently, we infer that the relationship is the result of two disconnected processes: seasonal decreases in VWC, and seasonal increases in LFMC controlled by dry mass changes, not water availability.

Variation in dry matter is strongly related to phenological events that influence foliage chemistry (Jolly et al. 2016; Little 2011), which describes changes in the relative proportions of crude fat, carbohydrate, protein, and starches. Phenology is a common tool used to manage fire by traditional owners (Armenteras et al. 2021), and its relationship with fire behavior has been widely documented (Chrosciewicz 1986; Bajocco et al. 2015; Jolly et al. 2016). In conifer forests, the timing of new needle emergence and development has been related to an increase in dry mass in old needles before budbreak, and subsequent decline as stored energy and nutrients are released into new needles. This process is illustrated in the LMA dynamics of tree needles in Fig. 5, where LMA peaks in early July and then declines. New needles typically have lower carbon content and higher relative water content until the cell walls elongate and harden (Riding and Aitken 1982). However, a limitation of our study is that we only sampled established, 1-year-old foliage. While hardened needles constitute a larger proportion of the crown than
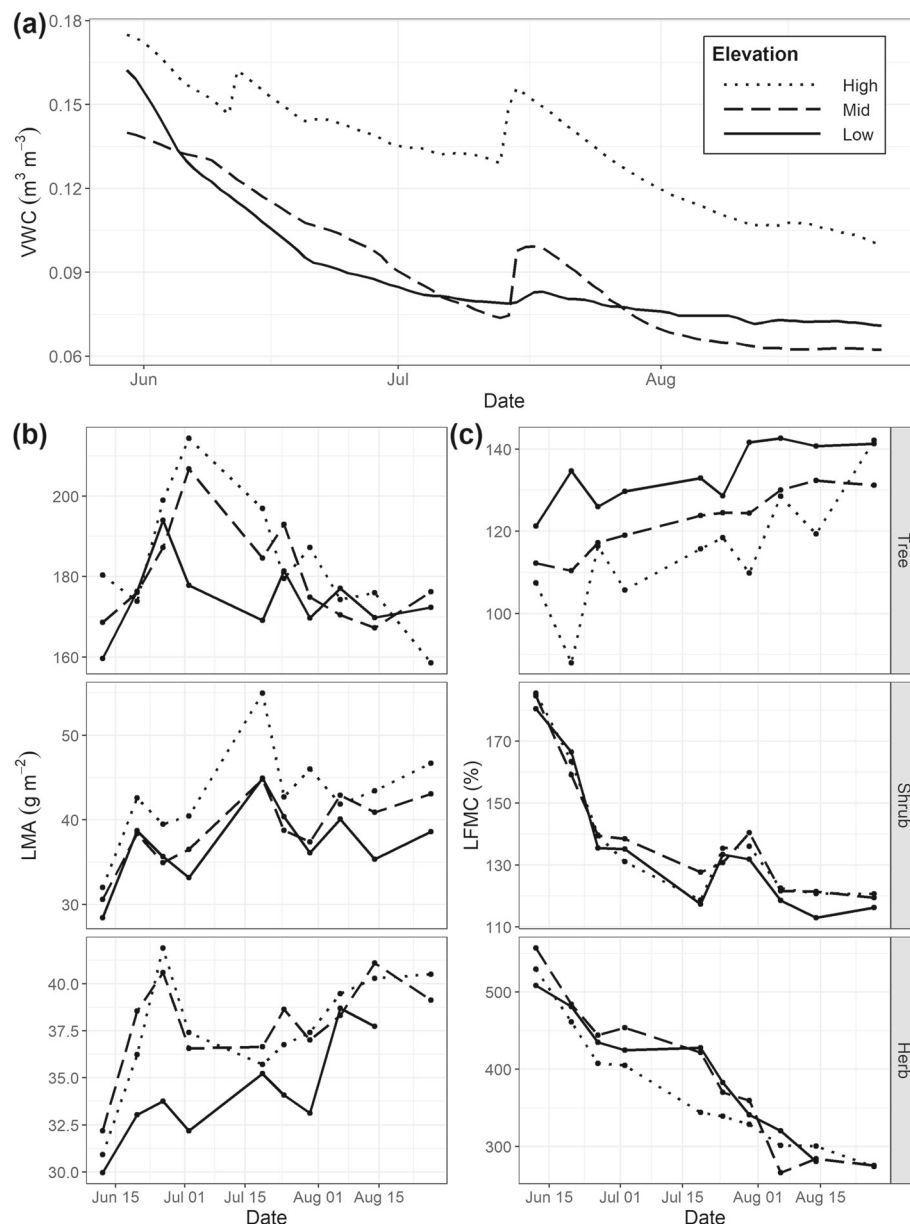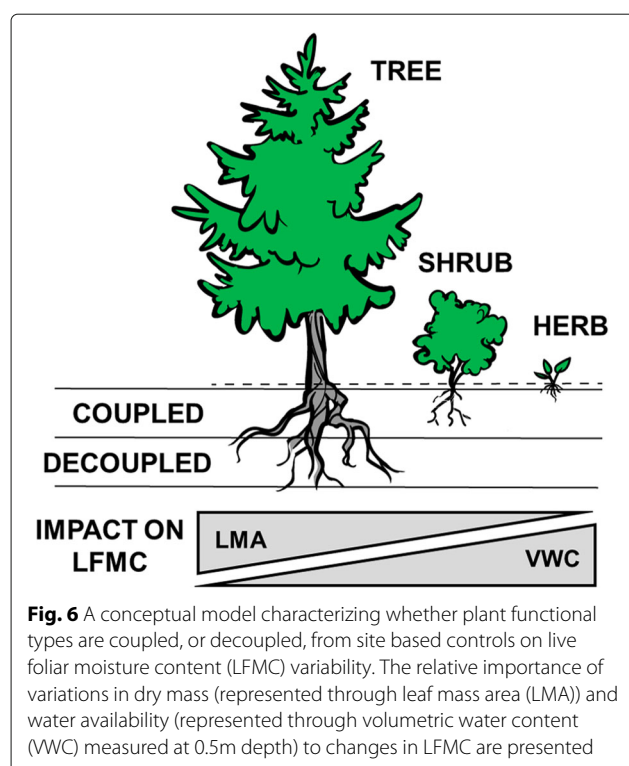
Fig. 5 Seasonal fluctuations in mean volumetric water content (**a**) per elevation group. Leaf mass area (**b**) and live foliar moisture content (**c**) are presented as means across each elevation group separated by plant functional type

new needles, future research should include needles of multiple ages to understand dominant drivers of LFMC across all components of tree foliage. Overall, our research suggests that estimating seasonal fluctuations in dry matter may be a more useful metric for understanding LFMC variability in mature overstorey tree foliage than water mass dynamics.

Conceptual model

The combination of divergent dry- and water mass controls on LFMC offers an explanation as to why overstorey

trees often exhibit less seasonal variation in LFMC compared to co-occurring plants in the understorey (Fig. 5) (Viegas et al. 2001; Pellizzaro et al. 2007a). Ultimately, these relationships may be well-served by a conceptual approach depicting different LFMC dynamics related to plant functional type (Fig. 6). Figure 6 illustrates the relative importance of dry (LMA) and water (VWC) mass controls on LFMC across the plant functional types observed in this study, that draws on the body of literature related to LFMC dynamics across different plant functional types. The figure describes relationships where

Fig. 6 A conceptual model characterizing whether plant functional types are coupled, or decoupled, from site based controls on live foliar moisture content (LFMC) variability. The relative importance of variations in dry mass (represented through leaf mass area (LMA)) and water availability (represented through volumetric water content (VWC) measured at 0.5m depth) to changes in LFMC are presented

fluctuations in live foliar moisture content are coupled (herb and shrub functional types) or decoupled (trees) from site conditions effects on LFMC variability.

The relationships between LFMC variability, plant functional type, and site conditions have implications for how we might best estimate LFMC in diverse forested environments. Functional types that are coupled to site conditions (e.g., herb and shrubs) may be estimated using correlative drought indices or broad scale soil moisture models. In contrast, LFMC variability in established tree or overstorey foliage, which were decoupled from site-based controls here, could be estimated from remote sensing approaches (e.g., Qi et al. 2014) or knowledge of species distribution, mean seasonal LFMC, and phenology, as suggested by Pellizzaro et al. (2007a). Ultimately, understanding LFMC of the entire forest profile in diverse species assemblages may be well served by a combination of methods, guided by the conceptual model presented in Fig. 6.

Implications for monitoring and interpretation

Changes to the foliar moisture content of living vegetation is a function of two related, yet distinct components expressed in Eq. 1: the amount of water that is in the foliage and the amount of dry matter. To date, studies of live foliar moisture content have largely focused on changes to water content only, while omitting fluctuations in dry matter from experimental design.

Estimating fluctuations in LFMC from changes to the water mass alone has important limitations, because LFMC is calculated *relative* to the dry weight of a sample (Eq. 1). Therefore, two foliage samples with the same LFMC value could have vastly different absolute amounts of dry and water mass. This is important because of the physical differences that dry and water mass have on fire activity. Energy must be expended to evaporate water before a fuel sample can burn; therefore, the water mass acts as an energy sink. In contrast, the dry matter in a fuel sample provides chemical elements that support flaming combustion, acting as an energy source. Studies assessing the flammability of live vegetation should routinely record both water and dry mass components of LFMC.

LFMC is an important driver of flammability in forested landscapes (Nolan et al. 2016; Dennison and Moritz 2009) and has been related to fire metrics such as rate of spread (Rossa et al. 2016), fire extent (Chuvieco et al. 2009), and severity (Hudspith et al. 2017). In an operational context, the research presented in this manuscript provides a conceptual methodology to estimate LFMC across diverse species assemblages in forested regions for use in landscape fire risk assessments and assist in predicting wildfire spread and in the execution of planned burning. Future research could add to this approach by assessing the controls on LFMC fluctuations across different ages of foliage (e.g., new needles), adding different plant functional types and testing the predictive capacity of this conceptual approach.

Conclusion

We present a new conceptual model that brings together new data and existing literature to understand the drivers of live foliar moisture content across three plant functional types in western Montana, USA, and relate this to the site-based controls on moisture variability. The conceptual approach describes whether seasonal LFMC dynamics are coupled, or decoupled from localized (i.e., site-based) conditions. Seasonal fluctuations in LFMC of understorey shrubs and herbs are strongly related to site conditions (coupled), whereas moisture variation in established overstorey trees in this study were decoupled from localized drivers, and more strongly influenced by changes in dry mass. This new knowledge can be used to improve our ability to characterize seasonal live fuel moisture content variations across plant functional types which, in turn, would improve our ability to predict wildfire spread, intensity and subsequent risk across landscapes.

Abbreviations

DFMC: Dead fuel moisture content; DW: Dry weight; FW: Fresh weight; LFMC: Live foliar moisture content; LMA: Leaf mass area; SA: Surface area; VWC: Volumetric water content

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Availability of data and materials
The data used in the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

Author details
[1] School of Ecosystem and Forest Sciences, Faculty of Science, The University of Melbourne, Baldwin Spencer Building, Parkville 3010, VIC, Australia. [2] Montana Climate Office, W.A. Franke College of Forestry and Conservation, University of Montana, 32 Campus Drive, Missoula 59812, MT, USA. [3] W.A. Franke College of Forestry and Conservation, University of Montana, 32 Campus Drive, Missoula 59812, MT, USA. [4] US Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, 5775 Highway 10 West, Missoula 59803, MT, USA. [5] USDA Forest Service, Northern Region, Missoula 59807, MT, USA.

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