Received: 27 February 2023 Accepted: 28 July 2023

DOI: 10.1111/1365-2435.14423

Functional Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Live fuel moisture and water potential exhibit differing relationships with leaf-level flammability thresholds

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Funding information
University of Califor Laboratories (UCNL) 5 Grant/Award Nu 85-4251 1 L

Handling Editor: Adam Martin

Abstract

1. In semi-arid regions where drought to cause mortality, wildfire in Southern California chaparral, relation and drought-related traits may cause live wildland flame and to examine these patterns, fire scientists and p plants have used metrics of water content, in pressure-based metrics of physiological status however, relationships across these metric unresolved.
2. To determine the impact of live fuel hydration on flammability (ignitability, combustibility, and sustainability) and plant hydraulic systems), we conducted laboratory dehydratio in which we simultaneously measured xylem and flammability. We tested two chaparral species, *Adenostoma fasciculatum* and *Ceanothus megacarpus*.
3. Live fuel moisture explained a substantial portion of variation in flammability (increased ignitability and combustibility with drought), but not sustainability. Drought-response traits (turgor loss point) likelihood and spread) identified at the l better predictor of flammability in linear
4. *A. fasciculatum* was more flammable than *C. megacarpus*, and in both species more flammable during the wet growing seas drought-related tissue characteristics other t or chemical content, are critical for dete
5. Our results suggest a mechanistic link between specific levels of drought-related traits, such as turgor loss point, might improve predictions of systems.

KEYWORDS
chaparral, drought, leaf flammability, live fuel moisture, pressure-volume curve, water potential

1 | INTRODUCTION

Climate change is expected to increase the frequency and severity of interactions between drought and fire (Littell et al., 2018). Drought amplifies wildfire dynamics by influencing community composition, fuel structure and water availability and flammability (Krawchuk & Moritz, 2011; Parks et al., 2016). Fire, in turn, can influence water availability while, can influence water availability by reducing plant cover and/or decreasing plant-community composition, including plant functional type and trait diversity (Nolan et al., 2022). Despite these feedbacks, the mechanisms that govern the connections between drought and fire, especially regarding how drought treatments might influence combustion characteristics (Nolan et al., 2021), are poorly understood. Plant physiology may help fill this gap: by using insights from plant physiology to explain patterns of vegetation flammability in the wildfire literature and by applying drought research (Anderegg et al., 2018; Jones & Johnson, 2018).

Progress in plant physiology requires communication between plant physiologists and fire ecologists, which has focused largely on questions within their respective fields between them. For example, fire behaviour models rate plant physiology beyond generalizations (Scott et al., 2014), functional groups, while relationships between various aspects of fire ecology, including fuel flammability and ecological effects of fire, are rarely (Jolly et al., 2015; Pausas & Johnson, 2018). Additionally, these two fields use different metrics to assess tissue hydration, which can impact vegetation characteristics (Table 1). Research on metrics of tissue water status has a tendency to focus on xylem water potential, a measure of the energy required to move water across the plant and an important physiological drought threshold, while fire scientists use metrics (e.g. live fuel moisture [LFM], the ratio of water to dry matter in fuels) that vary in their connection to plant physiology (Bartlett et al., 2016; Weatherspoon, 1996). The use of different metrics is specific to only a few species, which can challenge to integrating insights between LFM and xylem water potential (or other metrics) and the degree to which they are related to ecological processes. For example, LFM has been clearly linked to physiological drought (Nolan et al., 2018), while live fuel moisture is not to flammability, while live fuel moisture estimates of fire risk even though they are not physiological drought status or the range of variation in physiological drought (Nolan et al., 2021). Recent studies have begun to develop models connecting LFM with plant water status to explain patterns of flammability in some species (e.g. Nolan et al., 2018, 2022; Pellizzaro et al., 2017), yet the potential is entirely driven by the integrative studies have yet to investigate both metrics and flammability (Dennison et al., 2008; Jolly et al., 2014; Nolan et al., 2018). Additionally, fire behaviour models are parameterized with LFM (Scott et al., 2014), which can be challenging to measure (Pellizzaro et al., 2007). Physiological drought metrics may be more easily measured and modelled (Nolan et al., 2020), thereby supporting a more 'ecosystem' for both fire behaviour and fire effects models.

Adenostoma fasciculatum (chamise) is a model species. The relationship between LFM (~70%–600%) and LWP (~−1 to −6 MPa) is well established (Jolly et al., 2014; Nolan et al., 2018). Chamise is also a model species for plant physiology (Jacobsen et al., 2007; Pratt et al., 2007), with a well-established relationship between LWP and percent loss of conductivity (PLC) (Jacobsen et al., 2007; Pratt et al., 2007). Chamise is a drought-deciduous species that sheds leaves during the dry season (Jacobsen et al., 2007; Pratt et al., 2007), which can alter the relationship between LFM and LWP (Nolan et al., 2018). Chamise is also a model species for fire ecology, with a well-established relationship between LFM and fire behaviour (Jolly et al., 2014; Nolan et al., 2018). Chamise is also a model species for fire ecology, with a well-established relationship between LFM and fire behaviour (Jolly et al., 2014; Nolan et al., 2018).

TABLE 1 Measured raw flammability metrics and associated aspects of flammability.

Flammability axis	Flammability metric	Definition
Ignitability	Time to ign	Time (sec.) from sample place
	Glow to ign	Time (sec.) from first glow t
	Temp. at ig	Temperature (°C) at first fla
Combustibility	Maxtemp	Maximum temperature (°C) betw
	Max time	5 s plus time to extinction
	Flame height	Height (cm) of tallest flame
Consumability	Time to fir	Time (sec.) from sample place
	Glow duration	Time (sec.) from first glow t
	Post-flame glo	Time (sec.) from last flame t
		final ember
Sustainability	Flame duration	Time (sec.) from first flame

increasingly negative osmotic potentials (Bartlett et al., 2012; Pivovaroff et al., 2014; Turner, 1988; Tyree & Hammel, 1972). Although the relationships between water levels above the TLP a change in water potential may initially vary across species as a change in water content compared to values below the TLP, as well as different functional forms (Bartlett et al., 2012). Because TLPs remain-d nonlinear below the TLP, relationships between pressure and water content (Bartlett et al., 2012; Martin-StPaul et al., 2017; Meinzer et al., 2014; Sack et al., 2003) could even changes in leaf chemistry near the TLP, suggest that a species' TLP may be adjusted in response to drought (Bartlett et al., 2014; Sack et al., 2003). Sample collection, study in flammability the TLP is thus a key trait for understanding how species respond to drought (Bartlett et al., 2014; Pivovaroff et al., 2021). Plant tissue samples were collected

Seasonal phenology can also affect the flammability of chaparral species (Anderegg et al., 2018; Jolly et al., 2014; Pivovaroff et al., 2019). Many species undergo a period of new growth and solute accumulation in response to winter rains (Bartlett et al., 2014; Jacobsen et al., 2008; Pivovaroff et al., 2019). We expected that LFM and leaf dry matter content (LDMC, the ratio of dry weight to saturated weight relative to saturated weight) would increase during the growing season (Jolly et al., 2014; Pivovaroff et al., 2019). Because plants in chaparral ecosystems typically experience drought conditions during the summer and fall (Jacobsen et al., 2008; Pivovaroff et al., 2019), we expected that LFM would decrease during the summer and fall (Jolly et al., 2014; Qi, 2016). In some plant-ts (*Ostrea fasciculatum* and *Ceanothus megacarpus* (Keeley, 1992; Pivovaroff et al., 2019), seasonal changes in flammability can affect quantities of flammable volatile organic compounds (VOCs) either stored or actively emitted (Jolly et al., 2014; Pivovaroff et al., 2019). Typically, plant tissues (Bar-Massada et al., 2014; Chetehouna et al., 2009; Owens et al., 1998; Pivovaroff et al., 2019). Other seasonal changes, such as shifts in tissue allocation during growth, may also affect the structure and composition of plant tissues (Bar-Massada et al., 2014; Pivovaroff et al., 2019; Plaza et al., 2018; Scott et al., 2014; Tarlugma et al., 2019). Seasonal changes in temperature (Pivovaroff et al., 2019) and photoperiod (Pivovaroff et al., 2019) might also influence flammability. While some studies have examined the importance of including physiological traits when modeling the relationship between live fuel moisture and flammability (Nolan et al., 2018, 2022; Pivovaroff et al., 2019), few studies have explicitly investigated if flammability changes (e.g., shifts in physiology and morphology occur.

To identify how physiological drought response might inform flammability via associations between drought-related traits, we assessed chaparral shrub flammability, tissue water status and xylem water potential across wet and dry seasons. We asked: (1) Do leaf flammability metrics vary with potential predictive flammability, and (3) do linear mixed-effects models with flammability metrics vary with functional forms with flammability metrics vary with Are there thresholds flammability metrics vary with samples were harvested

taxa (23 samples; 48 samples). Samples were temporarily stored (<2 h) in two thick plastic bags from which excess air was removed and were stored in a dark cooler until processing (DPV: 306–0 min after collection. Pressure–volume curves (Wade et al., 1970), which were used to estimate 0.1 MPa/s and xylem exudation was added to the solution to minimize microbial growth.

2.3 LFM measurements

To characterize water content in the leaves and terminal stems, LFM measurements were collected at the same time as water potential measurements. Sampling was guided by the National Fire Danger Rating System (Deeming et al., 1978), which associated local and regional measurements with topographic features; this project was accomplished by sampling at Sedgwick Reserve and Santa Barbara Botanic Garden's LFM 2016, plus image analysis (ImageJ; Rueden et al., 2017; Schneider et al., 2012; Weis et al., 2008). Approximately 25 g of leaves and terminal stems were collected from each plant, avoiding dead plant matter or reproductive tissue. Samples were placed in pre-weighed airtight plastic Nalgene containers. Samples were weighed (fresh weight) and then dried at 100 °C for 24 h, and then re-weighed (dry weight). LFM was calculated as the ratio of water weight (fresh weight − dry weight) and dry weight, expressed as a percentage (i.e., LFM = (fresh weight − dry weight)/dry weight × 100). LFM values <100% indicate greater dry matter than water, and values >100% indicate greater water- than dry matter. Flammability tests the protocol for measuring LFM in the same as the field except for a single sample was taken at each timepoint.

2.4 Benchtop flammability and water potential measurements

Simultaneous measurements of LFM, water potential and flammability were conducted on leaves and stems of each species (Table 1) during benchtop drydowns. Branches (~20 cm) were collected and shipped overnight in coolers with ice packs. Upon arrival, branches were cut underwater into smaller segments (~15 cm) and allowed to rehydrate underwater for 2 h or until water potential was <−1.2 MPa (Kaufmann & Ryan, 1986; Pivovaroff et al., 2014). Over the course of a benchtop drydown, leaves and stems were removed from the branch at approximately intervals of 1 MPa. Tests were conducted until samples had reached between −9 and −10 MPa, leaving samples at a range of water potentials (i.e., hydration) for flammability measurements.

Flammability tests were performed using a radiant heater (Quartzall, 500 W). The heater was positioned 4 cm above the heated surface (~50 kW/m²). The entire experiment was conducted within a laboratory fume hood to control for humidity and airflow. Ambient conditions were recorded at the beginning and end of each day using a digital thermometer and hygrometer (Extech RH520A). Flammability tests were performed on leaves and stems (Table 1) during benchtop drydowns. Branches (~20 cm) were collected and shipped overnight in coolers with ice packs. Upon arrival, branches were cut underwater into smaller segments (~15 cm) and allowed to rehydrate underwater for 2 h or until water potential was <−1.2 MPa (Kaufmann & Ryan, 1986; Pivovaroff et al., 2014). Over the course of a benchtop drydown, leaves and stems were removed from the branch at approximately intervals of 1 MPa. Tests were conducted until samples had reached between −9 and −10 MPa, leaving samples at a range of water potentials (i.e., hydration) for flammability measurements.

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were determined using the protoco[illegible] (Sack et al., 2018).

2.6 | Statistical analyses

2.6.1 | Relationships between flammability metrics and derived flammability proxies

To investigate the relationships [illegible] flammability traits (Table 1), a principal component [illegible] used (Jolliffe, 2002). The PCA was conducted [illegible] set that included both species [illegible] nents (i.e. PC1 and PC2) were used [illegible] 'flammability proxies'. The PCA was conducted using the *stats* package in R (R Core Team, 2022). All analyses were performed in R version 1.4.1717, with [illegible] repository https://doi.org/10.5281/zenodo.8269574 (Celebrezze, 2023).

2.6.2 | Relationships between plant hydration and flammability

To assess the effects of plant hydration on flammability, linear mixed-effects models were used to predict flammability principal component scores representing [illegible] assessments ('flammability proxies') [illegible] flammability metrics of interest using the *lme4* package in R (Bates et al., 2012). As the impacts [illegible] woodiness on flammability were of primary interest, [illegible] variables (water potential, LFM, RWC and [illegible]) [illegible] ple dry weight were used as predictors, [illegible] covariate.

During model selection, the variance inflation factor (VIF) was used to ascertain the presence of [illegible] (Zuur et al., 2009). [illegible] weight, dry weight, LDMC and LFM (VIF > 4) [illegible] while water potential, wet weight [illegible] collinear (VIF < 2) and were therefore considered [illegible]. Exploratory model selection revealed that [illegible] date significantly improved model fit [illegible]; other covariates (2-month average prior precipitation [illegible] and Monthly Rainfall, 2021), the starting temperature of [illegible] flammability chamber) rarely improved the model [illegible] ing either flammability proxies or [illegible] of the hydration metrics. In [illegible] was treated as a random effect [illegible] servations = 486). All numeric [illegible] tred and scaled to facilitate [illegible].

The most parsimonious model [illegible] (2014) [illegible] lected using Akaike's information criterion (Akaike, 1987) [illegible] simpler model structures chosen when [illegible] of one another. P-values were obtained [illegible] (2022) [illegible] per cent confidence [illegible]

[illegible] models using the R package *lmerTest* (Kuznetsova et al., 2017). The marginal R^2 and the conditional R^2 were also extracted from [illegible] (Nakagawa & Schielzeth, 2012). The *remef* package was used to visualize the partial effects of water status [illegible] removing the site and date fixed and random effects [illegible] (Hohenstein & Kliegl, 2021). To analyse differences in the relationship [illegible] and plant hydration between species [illegible] (PCA) [illegible] to seasonal [illegible] set by species prior to the model [illegible] isolate the effect of season on the [illegible]

While investigating differences [illegible] September 2020 [illegible] also allowed for us to [illegible] Likewise, while investigating seasonal [illegible]

2.6.3 | Threshold detection: mixed-effects models

[illegible] flammability metrics [illegible] to predict flammability [illegible] collected during [illegible] assessing water potential (and a co[illegible] water potential [illegible] −1 MPa) [illegible] RWC and LF[illegible] (Muggeo, 2020) [illegible] segmented [illegible] *segmented* package in R [illegible]

the breakpoints were plotted alongside with their 95% CI garnered from bootstrapping (see Table 2a). Then, possible overlap between flammability traits was assessed. To test whether the thresholds were driven by outliers, distributions, separate analyses were conducted without bootstrapped data to coerce an equal sample size for *A. fasciculatum* and *C. megacarpus*. This was done by randomly resampling points from the species with the greater number of observations (*C. megacarpus* (12% bins for *A. fasciculatum* (6% bins for LFM), randomly resampling points from the species with the greater number of observations (*C. megacarpus*, 8; *A. fasciculatum*, 19), and had a standard deviation not included segmented regressions on the resampled data. This process was iterated 1000 times for each species and the average breakpoint was presented (Tables S4 and S5).

3 | RESULTS

3.1 Relationship between flammability metrics

In the PCA, the first axis (PC1) one explained 37.2% of the variation in flammability metrics and was positively correlated with metrics used to describe sustainability (flame duration) and combustibility (flame height and maximum temperature), and negatively

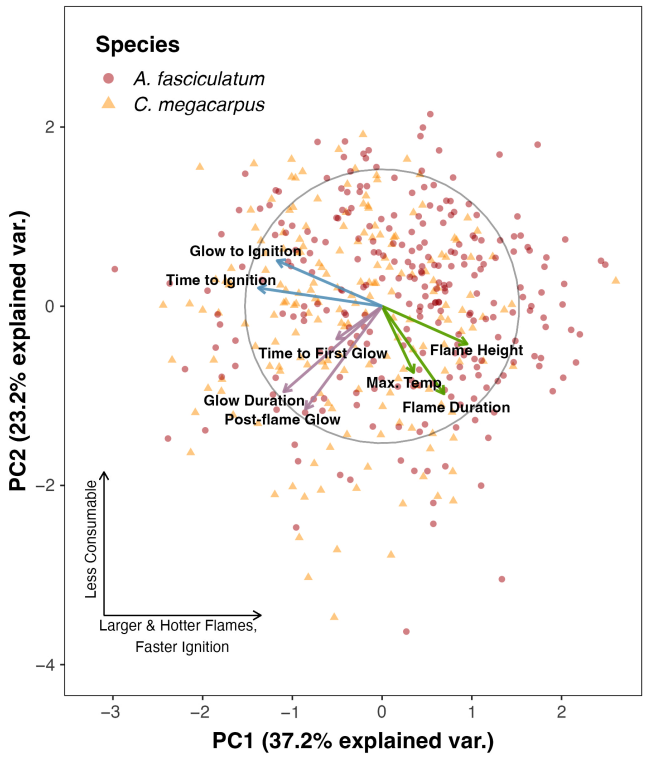

FIGURE 2 Principal component analysis of flammability parameters (*n* = 20) for individual plants. Individual points represent a single sample, with shape and colour indicating species. Arrows indicate flammability metrics and arrow colour indicates flammability parameters are indicated in blue, combustibility in green and consumability in purple.

3.2 Relationship between hydration and flammability

Our linear mixed-model selection identified combustibility proxy (PC1) and rics (time to ignition, flame-duration) ily contributed to PCA axes. Water most important metric in models as (ΔAIC < 2) for all flammability metrics ignition, combustibility proxy, longer t glow durations and shorter flame dur (Table 3). These results were simi-lar f cies separately (models of glow dura taining RWC was equally parsimonious as a covariate.

3.3 Threshold detection

While water potential was consisten of flammability metrics (particular LFM showed stronger evidence for th flammability in segmented models (Figure 3). Models of all flammability metrics exhibited signi with LFM (1.0 for *A. fasciculatum* and 8 of 11 for *C. megacarpus*, Table S4), and about half *A. fasciculatum* and 6 of 11 for *C. megacarpus* (Table S5). Meanwhile, few flammability metrics had signif threshold relationships with water

	Component 1	Component 2	Component 3
Flame duration	**0.76**	−0.17	−0.05
Flame height	**0.62**	0.14	−0.31
Maximum temp.	**0.51**	−0.16	0.11
Time to ignition	−0.72	−0.41	0.45
Glow to ignition	−0.82	−0.39	−0.23
Glow duration	−0.11	−0.99	0.04
Postflame glow	0.11	−0.93	0.15
Time to first glow	0.01	−0.09	0.98
Proportion of variance	**37.17%**	**23.23%**	**14.72%**
Cumulative proportion	**37.17%**	60.39%	**75.11%**

TABLE 2 Principal component (PCA) loadings following for PCA. Bold text indicates instances where metric is loaded upon the by an absolute value grea indicating that the flamm has a relatively large ir principal component.

TABLE 3 Top models relating plant hydration metrics (water potential, relative water content, leaf dry matter content (LDMC) covariates to selected dependent variables: combustibility principal component 1 (PC1), time to ignition, glow duration across both species for all dates. Each model includes included in some but not all models. Hydration and dry weight estima change of the dependent variable from models fit with only a random intercept. ΔAIC represents the variation in AIC from the model with lowest AI models ΔAIC < 2 (in bold) are presented in addition to LFM, RWC and water po

Dependent variable	Model fixed effects	Hydration	Dry matter	ΔAIC	Marg. R^2/Cond. R^2
PC1	Water potential + LDMC	−0.459***	**4.721**	**0**	0.259/0.305
	Water potential	−0.456***		**0.626**	**0.243/0.305**
	RWC	−0.404***		9.937	0.227/0.282
	LFM	−0.334***		21.605	0.204/0.276
Time to ignition (s)	Water potential + LDMC	4.940***	2.988**	**0**	0.382/0.412
	Water potential	4.927***		6.973	0.362/0.416
	RWC	4.220***		36.120	0.320/0.359
	LFM	3.259***		70.144	0.263/0.327
Flame duration (s)	**Water potential**	−0.677**		**0**	**0.076/0.131**
	Water potential + Dry Weight	−0.494	**0.331**	1.369	0.078/0.131
	Water potential + LDMC	−0.674***	**0.272**	**1.404**	0.078/0.137
	Dry weight		0.762**	1.758	**0.072/0.121**
	LFM	−0.658**		2.395	0.071/0.121
	RWC	−0.574**		3.507	0.068/0.122
Glow duration (s)	Water potential + LDMC	−2.020	**4.721**	**0**	**0.253/0.312**
	RWC + LDMC	−1.866	4.942	0.844	**0.252/0.311**
	Water potential	−2.063		4.694	0.248/0.293
	LFM	−1.950		5.317	0.242/0.303
	RWC	−1.846		5.384	0.248/0.293

for *A. fasciculatum* and *C. megacarpus* respectively; Table S6 and Table S5). Trends also remained similar detected breakpoints for water potential (Figure S2). When we removed extremely high or low water potential values that had a moderate influence on the model fit (Cook's distance > 1; Figure S3), six data points, whereas the breakpoints for *A. fasciculatum* and *C. megacarpus* more often in the middle of the data range (Table S7). These breakpoints were still significant (*p* < 0.05) after removing potential outliers.

Most significant breakpoints in the LFM–TTI relationship were robust to bootstrap resampling to minimum sample size at LFM values of 37% (Table S4). For *A. fasciculatum*, the *C. megacarpus*, but *A. fasciculatum*. For *A. fasciculatum*, the

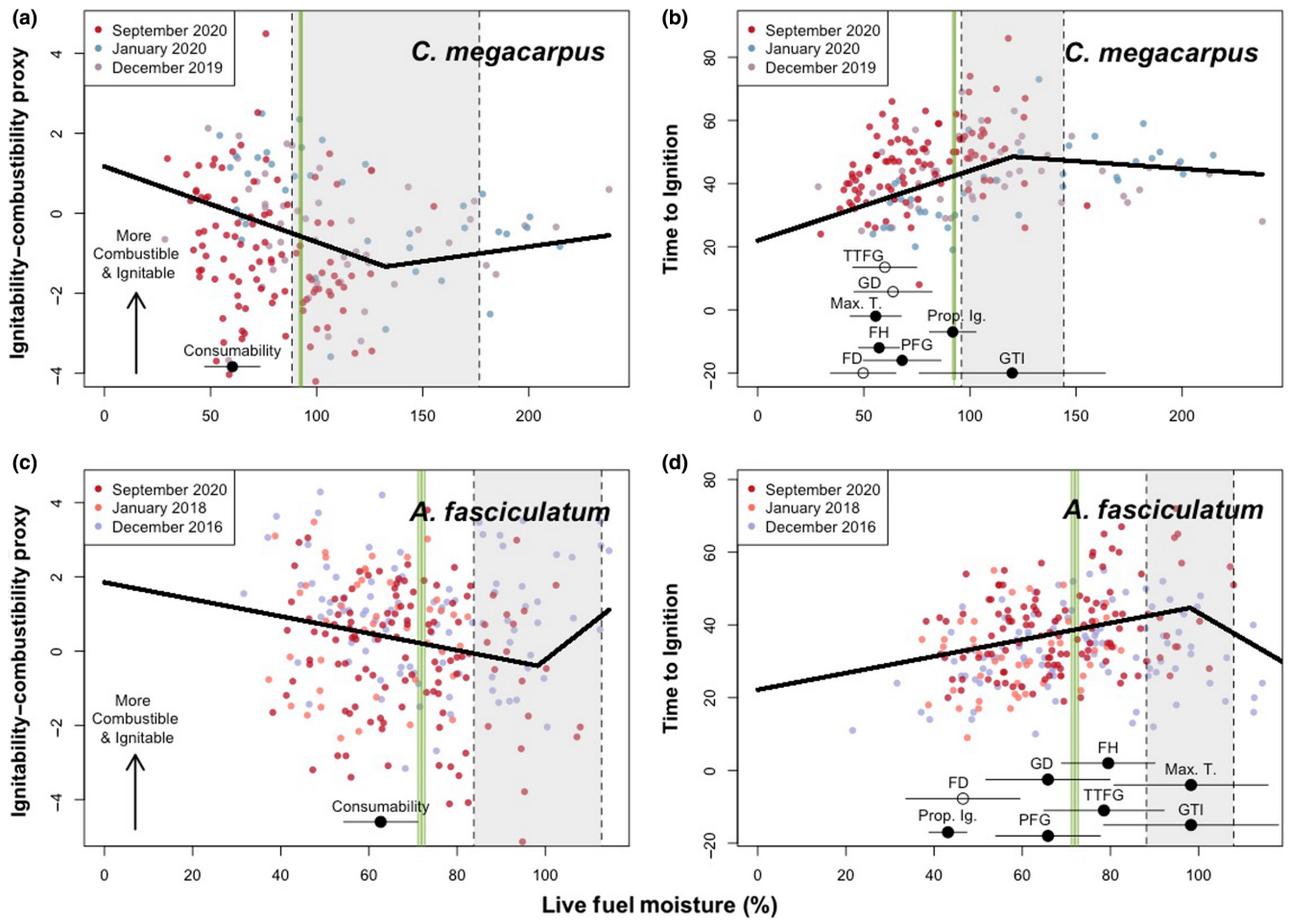

FIGURE 2 Segmented regression models for *Ceanothus megacarpus* (a, b) and *Adenostoma fasciculatum* (c, d), where dark red lines represent segmented regression mixed effects models of ignitability proxy (a, c) and ignition time (b, d) as a function of live fuel moisture. Shaded green areas represent 95% confidence intervals for identified thresholds. Green vertical lines and associated shaded green areas represent thresholds and confidence intervals for the consumability proxy (PC2) and ignitability proxy (PC1). Fuel moisture thresholds for fuel drying rate (FD), glow duration (GD), flame height (FH), proportion of flaming (Prop. Ig.), time to glow (TTFG), maximum temperature (Max. T.) and glow to ignition (GTI) are also shown. Open circles represent the predictor and closed circles represent cases where LFM was a significant

and 84.83 +/− 2.13% RWC. Additional measurements of live fuel moisture relationship with LFM below parameters (Table S3) are in a positive relationship (Figure 2a,b; Figure S2).

For *A. fasciculatum*, the mean value for each of the flammability metrics with significant LFM was a significant +/− 19.4 (ranging from 78.8% to 84.8% for all metrics), these breakpoint median value was 70% the mean value for the TFLP (Figure 2). For *Ceanothus megacarpus*, all thresholds where LFM was a significant predictor of flammability metrics, thresholds occurred at 74.3% +/− 7.6% for *C. megacarpus*. Mean thresholds +/− 32.1, while the median value was 80.0%. Specific time: ranged from 89.4 to 78.8% bility metrics, thresholds occurred at 74.3% +/− 7.6% for *C. megacarpus*. Mean thresholds all were significantly different (ANOVA: F_{TLP} = 25.04, p < .001; Figure 3). glow to ignition and proportion of samples ignited) had a mean threshold at 79.8% for *A. fasciculatum*, while consumability and combustibility occurred at 63.9% and 56.4% for *C. megacarpus* and 70.1% and 88.9% for *A. fasciculatum* respectively. The strength of the relationships (slope) did not differ between species, with the exception of flammability metric; however, flammability metrics were consistently higher when measured

(an increased wet season consumability for *C. megacarpus*, the relationship between LFM for *A. fasciculatum* and 0.460 for *C. megacarpus*, with decreased leaf water potential by χ^2 (1) = 2.13, p = 0.144) and wet season consumability for *C. megacarpus* and dry season consumability for *A. fasciculatum* (χ^2 (1) = 1.75, p = 0.186) (Figure 3). For both species, the relationship between LFM and water potential did not significantly differ between the wet season and dry season (χ^2 (1) = 0.768, p = 0.381) or through time for this relationship (χ^2 (1) = 0.0, p = 0.998). Species significantly affected the relationship between LFM and water potential (χ^2 (1) = 9.60, p = 0.002), with *A. fasciculatum* having a steeper slope than *C. megacarpus* (Figure 3). Species significantly improved the predictive ability of models of water potential versus LFM (χ^2 (1) = 23.5, p < 0.001), but it did not significantly improve the predictive ability of the water potential versus ignitability models (χ^2 (1) = 2.60, p = 0.107) or consumability models (χ^2 (1) = 0.0, p = 0.961). Species significantly improved the predictive ability of models relating water potential to ignitability (χ^2 (1) = 14.1, p = 0.011, Figure 3a,b; *A. fasciculatum*: χ^2 (1) = 6.007, p = 0.0143). Season did not significantly improve the predictive ability of models relating water potential to ignitability (χ^2 (1) = 3.40, p = 0.065) or consumability (χ^2 (1) = 0.0, p = 0.961). Species did significantly improve the predictive ability of models relating water potential to flammability (χ^2 (1) = 4.10, p = 0.043, Figure 3e,f; *A. fasciculatum*: χ^2 (1) = 1.4, p = 0.236). However, a proxy for flammability (PTA2) (Table S9) for more flame

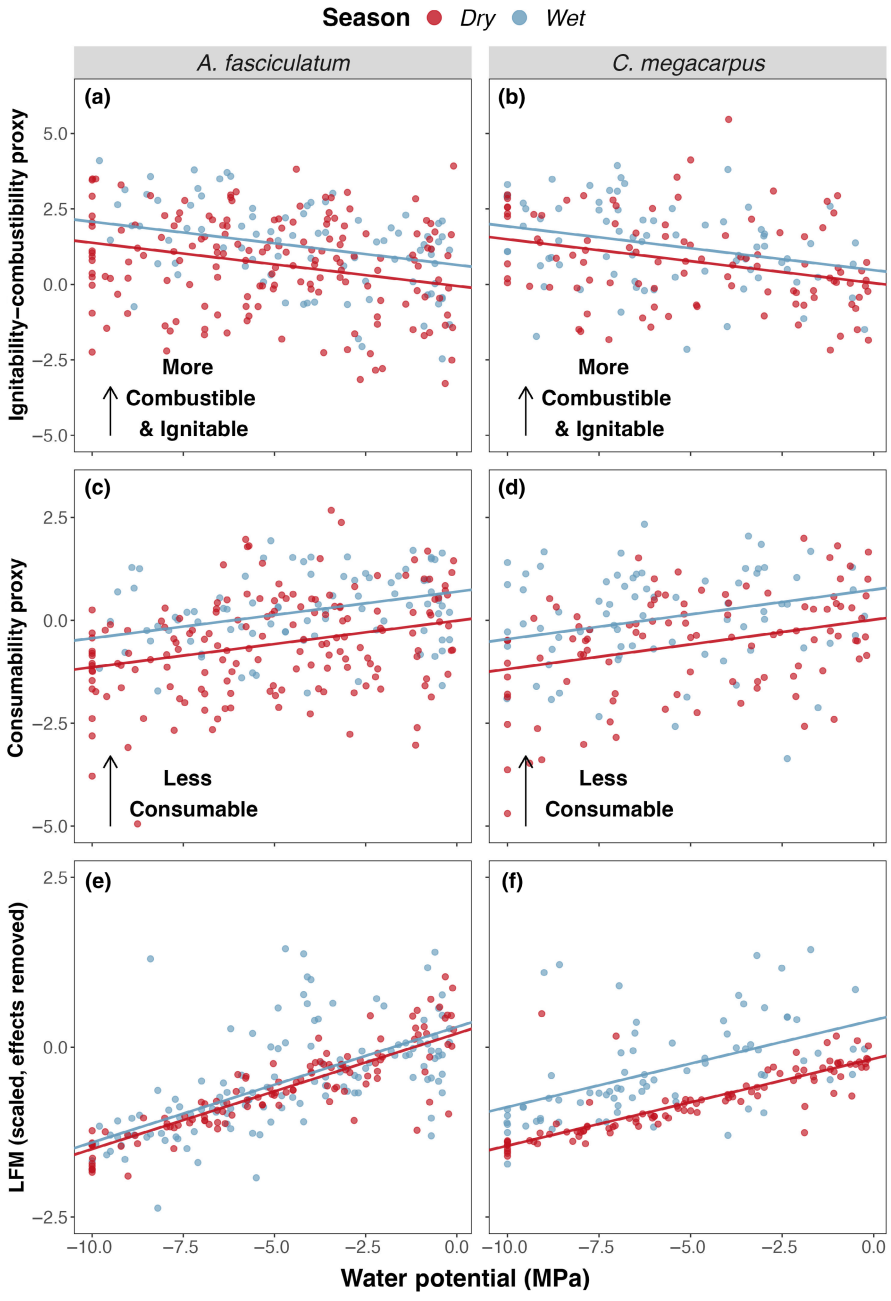

FIGURE 3 The effect of season on the relationship between water potential and two flammability proxies: ignitability–combustibility proxy (a, b) and consumability (c, d), as well as the relationship between water potential and live LFM (e, f) *Adenostoma fasciculatum* (a, c, e) and *Ceanothus megacarpus* (b, d, f). Trend lines are from linear mixed models, showing the partial effect of season with random effect removed using the package.

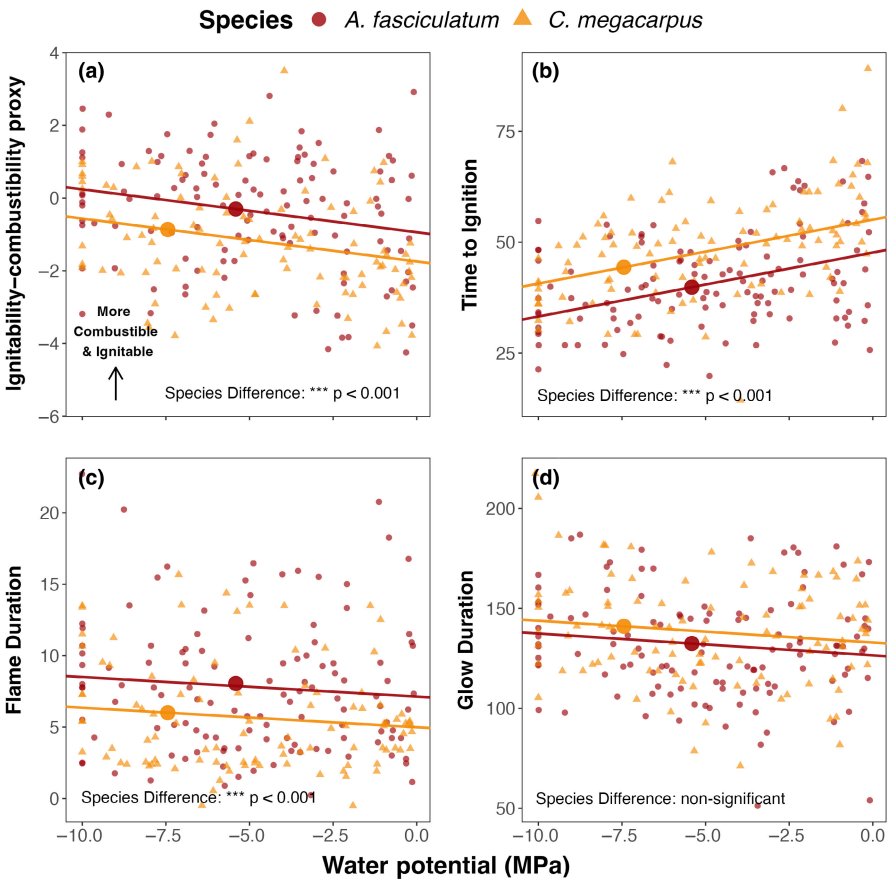

FIGURE 4 Interspecific differences in the relationship between the ignitability–combustibility proxy (a), time to ignition (b), flame duration (c) and glow duration (d) in 2020. Red circles and lines represent *Adenostoma fasciculatum*, while orange triangles and lines represent *Ceanothus megacarpus*. The partial effect of site was included in the model but the effect associated with it was removed during the plotting process to aid visualization. Large points along the lines represent the mean midday water potential for each species in September 2020 (see Figure 3 for more detail).

detail). The best models indicated that there was a significant interaction between water potential and flammability and across species, with *A. fasciculatum* being generally more flammable and showing greater changes in dry matter than *C. megacarpus* (higher PC1 value, faster time to ignition, shorter flame duration, and greater glow duration; Figure 4; Table S4). Water potential was the most important secondary effect in likelihood ratio tests, with inclusion of species-specific morphologies and seasonality improving the predictive power of time to ignition ($\chi^2(1) = 92.2$, $p < 0.001$), flame duration ($\chi^2(1) = 10.4$, $p = 0.00125$), and combustibility proxy ($\chi^2(1) = 11.0$, $p = 0.0009$), but not glow duration ($\chi^2(1) = 2.6$, $p = 0.107$). We found similar results using LFM as the primary predictor of flammability, with improved model predictions for all four metrics (Figure S4). Relationships between flammability proxy and fuel moisture content (Figure S5) were also similar to those between flammability and water potential (Figure 4).

4 | DISCUSSION

We conducted laboratory dehydration trials to examine the relationship between fuel moisture and flammability in two shrub species over multiple years. We found that hydration is an obvious but underappreciated driver of flammability, and that two commonly measured metrics of hydration (live fuel moisture and water potential) had significant but different relationships with flammability. Species differences in these relationships were predicted by their hydraulic behaviour in most flammability metrics near the turgor loss point, with *A. fasciculatum* generally more flammable than *C. megacarpus*. Species differences in flammability were also evident at the landscape scale, where *A. fasciculatum* dominated more frequently burned areas.

'Flammability' writ large is a complex suite of characteristics. Previous attempts to quantify flammability across groups (i.e. species or time points) using individually measured flammability components (e.g. Anderson et al., 2015; Dibble et al., 1994; Fletcher et al., 2014; Gill & Zylstra, 2005; Grootemaat et al., 2015; Schwilk, 2015; Simpson et al., 2014; Tanskanen et al., 2005; Trabaud, 1979; Van Altena et al., 2012; Wyse et al., 2016) have found that no single metric can capture the full range of flammability characteristics (Anderson et al., 2015; Dibble et al., 1994; Gill & Zylstra, 2005; Schwilk, 2015; Simpson et al., 2014; Tanskanen et al., 2005; Trabaud, 1979; Van Altena et al., 2012; Wyse et al., 2016). Instead, flammability is a multivariate concept that is best described by a suite of metrics (Anderson et al., 2015; Dibble et al., 1994; Gill & Zylstra, 2005; Schwilk, 2015; Simpson et al., 2014; Tanskanen et al., 2005; Trabaud, 1979; Van Altena et al., 2012; Wyse et al., 2016). Similarly, we found that no single metric of hydration can capture the full range of flammability characteristics. Instead, flammability is a multivariate concept that is best described by a suite of metrics (Anderson et al., 2015; Dibble et al., 1994; Gill & Zylstra, 2005; Schwilk, 2015; Simpson et al., 2014; Tanskanen et al., 2005; Trabaud, 1979; Van Altena et al., 2012; Wyse et al., 2016). Similarly, we found that no single metric of hydration can capture the full range of flammability characteristics. Instead, flammability is a multivariate concept that is best described by a suite of metrics (Anderson et al., 2015; Dibble et al., 1994; Gill & Zylstra, 2005; Schwilk, 2015; Simpson et al., 2014; Tanskanen et al., 2005; Trabaud, 1979; Van Altena et al., 2012; Wyse et al., 2016).

and flame-related metrics (ignitabil… ability, PC1) … As fire likelihood (i.e. ignitability) and intensity (i.e. combusti… and sustainability) are the prim… fire risk, PC1 parsimoniously cap… of flammability for translating … bility to begin to inform w… 2019) … Additionally, we provide eviden… capture multiple components of f… to measure metrics, and that, by … using only time to ignition and … combustibility, and glow duratio… be simplified and made more acces… metrics to be measured. This fol… Varner et al. (2015) focus on individual … marized scores.

4.2 | Both plant hydration and dry matter content affect flammability

We found that higher plant hydra… bility both in terms of flammabi… Hydration, dry matter content an… tors of flammability metrics, … tential) acting as an overall … flammability than either tissue … sample dry weight; Table 3). Leaf dry matter … the water potential model when … not the primary predictor of … metrics. The insight that water … predictor of flammability than LFM … hibits potential for physiology … scape fuels monitoring. While … existing large LFM databases, … water potential measurements would … tial drought-related shifts in flammabi… chemistry, structure and physiolo… both water potential and LFM should … tored concurrently. Advances in our ability to quickly measure water potential may increase the feasibility of switching to water potential-based fire risk sampling, with the … equipment (i.e. pressure chamber) … tation (Nolan et al., 2022). Additionally, having a predictable relationship between LFM and water … fire-risk landscapes might … drought and wildfire risk. … 2018 … 2022; Pivovaroff et al., 2019) … has been … paired LFM and water potential … base of drought-related indicators … leveraged for large-scale analysis of … landscape wildfire risk modelling.

4.3 | Tissue-level flammability … landscape-level wildfire patterns

At the landscape level, LFM has been … fire size, likelihood and rate … 2009; … Dennison & Moritz, 2009) … 2019) … Additionally … LFM … 2022) … (Pimont et al., 2022) … mability metrics were from ignitabi… *only* axis investigated where all-flamma… nificant predictor in segmented regr… landscape-level patterns, we found evide… old related to spread rates (susta… (50%–80% for *C. megacarpus* and 47%–79% for *A. fasciculatum*; Table S4) …

4.4 | Flammability thresholds a… water content at the TLP

The thresholds across species … Most of these … (Figure 2) … (Table S5) … contribution of physiology to the thre…

When hydration levels are in range, seasonal changes in water content are driven by both increased solute concentrations and stomatal adjustments; once the TLP is exceeded, water content is directly related to solute-accumulation (Figure 4a) and mediated by stomatal control (Figure 4b). We observed flammability via hydration and ignitability at a constant water content during trials conducted (Arndt, 2012; Turner, 2018). Seasonal dynamics in leaf water potential and leaf chemistry also adjust the TLP (Figure 2). Higher LFMs in early wet season samples with high water contents early in the season (Figure 3) were driven by differences in interacting seasonal and physiological mechanisms between water potential and water content. Once the TLP was exceeded, shifts as seasonal changes in water potential no longer altered water content in place above and below the TLP, with flammability (ignitability, sustainability, combustibility) effect of hydration on flammability (Dimitrakopoulos, 2001; Pausas, 2015; Pivovaroff, 2018; Quan, 2021) and timeframes. As we found constant flammability metrics when LFMs differed in water potential with high water content, it is likely that differences in flammability near the TLP are driven by associations with the TLP and not solely by water content adjustments alone.

4.3 | Seasonal differences

We found significant differences in flammability dynamics and flammability, with samples observed during the wet season more combustible and ignitable at a given water potential than those during the dry season (Figure 3). This is likely due to a combination of changes (increased osmotic concentration, increased apoplastic space in cells), chemical shifts related to the release of volatile organic compounds (e.g., monoterpenes) (Pivovaroff, 2021; Seco, 2011; Schlesinger, 1985), and seasonal changes in physical adjustments in dry matter content (e.g., changes in cellulose) (Gao, 2021; Pausas & Millán, 2019). Adjustments in dry matter content allow plants to maintain low water potentials during the dry season and can impact the relationship between water potential and water content, and dry weight, and thus flammability (Pivovaroff, 2014; Scholander, 1965). Changes in leaf chemistry and physiology and predicted flammability (Pivovaroff, 2021; Schlesinger, 1985), consumability (Pivovaroff, 2021), and combustibility (Pivovaroff, 2021) could be related to higher lignin content in new tissues could drive the observed seasonal variability in the wet season (Figure 3). More ignitable and combustible tissues during the wet season (Figure 3) are likely due to changes in emissions and/or storage of volatile organic compounds (VOCs). Mediterranean plants typically have maximum concentrations of VOCs in the coldest, wettest months, with peak concentrations during periods (Llusià & Peñuelas, 2000). The flash points of terpenoids can be as low as flammability when increased VOC emissions are observed (Ormeño, 2009; Pausas, 2016). Trends were less apparent in leaf to stem ratios (and therefore systems) or to the total chemical composition of individuals (Pivovaroff, 2021), *megacarpus*.

particularly the Chumash on whose traditional territory UC Santa Barbara sits.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data presented in this study, along with the code necessary for statistical analyses, data visualization, tables and with the metadata are openly available on GitHub via Zenodo repository: https://doi.org/10.5281/zenodo.8269574. Additional metadata and README an external publicly available dataset is noted for precipitation data from Santa Barbara County - www.countyofsb.org/2155/Rainfall-Information and County of Santa Barbara, Daily and Monthly Rainfall www.countyofsb.org/4407/Daily-Rainfall.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Principal component analysis of stress-related natural products.

Figure S2. Segmented regression plots.

Figure S3. Effect of season on LFM and flammability.

Figure S4. Effect of species on LFM and flammability.

Figure S5. Measured water potential and LFM.

Table S1. Top model details for PC1.

Table S2. Top models per species.

Table S3. Pressure–volume curve parameters.

Table S4. Summary of segmented regressions.

Table S5. Summary of segmented regressions with ...

Table S6. Summary of segmented regression results for water potential.

Table S7. Summary of segmented regression results for −1/water potential.

Table S8. Summary of models using site and season.

Table S9. Summary of models using site and species.

Table S10. Top models for effect sizes in meadow and mixed-shrub with leaf-level flammability thresholds.

How to cite this article: Boving, I., Celebrezze, A., Ramirez, A., Anderegg, L. D. L., & Dawson, T. E. (2024). Summer moisture and water potential exhibit thresholds in Table 3. *Functional Ecology*, *37*, 2770–2785. https://doi.org/10.1111/1365