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Specific leaf area and vapour pressure deficit control live fuel moisture content

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Abstract

1. The live fuel moisture content (LFMC) is an important precondition for wildfire activity, yet it remains challenging to predict LFMC due to the dynamic interplay between atmospheric and hydrological conditions that determine the plant's access to, and loss of water.

2. We monitored LFMC and a range of plant water-use traits (predawn and midday leaf water potentials [Ψ_{leaf}]), leaf traits (specific leaf area [SLA]), hydrological status (soil water content [SWC] in the shallow layer and full profile) and atmospheric variables (air temperature, vapour pressure deficit [VPD], CO_2 concentrations) in a mature eucalypt woodland at the *Eucalyptus* Free-Air CO_2 Enrichment (EucFACE) facility during a drought.

3. We combined plant traits, hydrological status and atmospheric variables into a biophysical model to predict LFMC dynamics, and compared these with predictions of LFMC based on a satellite model and established relationships between Ψ_{leaf} and LFMC from pressure–volume curves.

4. Predawn Ψ_{leaf} could be well predicted from changes in SWC, but variation in midday Ψ_{leaf} and LFMC were more responsive to atmospheric than hydrological variables. The biophysical model explained up to 89% of variability in LFMC and outperformed established approaches to predict LFMC. SLA was the single most important variable to predict LFMC, followed by VPD, which explained 33% of the remaining variability in LFMC.

5. Our study demonstrates that the co-variation of plant traits and atmospheric and hydrological conditions affect LFMC during drought, suggesting a new way forward for predicting LFMC by combining biophysical and satellite-based models of LFMC with seasonal forecasts of meteorological and hydrological variables.

1 | INTRODUCTION

Recent years have been characterized by an increase in the frequency of megafires in terms of burn area across forest ecosystems (Abram et al., 2021; Boer et al., 2020; Duane et al., 2021; Fidelis et al., 2018; Nolan et al., 2021; Varga et al., 2022). These events have been attributed to a combination of climate warming and associated changes in fire weather and ignition probability; antecedent droughts that resulted in unusually dry fuels and high-severity fires; and changes in land management and associated increases in fuel load (Abatzoglou et al., 2018; Canadell et al., 2021; Collins et al., 2021; Fidelis et al., 2018; Keeley & Syphard, 2021; Nolan et al., 2021; Stephens et al., 2014; Varga et al., 2022; Williams et al., 2019). Typically, multiple preconditions were exceeding moderate thresholds of fire risk rather than individual conditions reaching extreme magnitudes (Khorshidi et al., 2020), although the Australian 2019/2020 'Black Summer' bushfire season exemplified extreme magnitudes in multiple drivers (Nolan et al., 2021).

The recent megafires in Australian forests coincided with record low moisture levels in live fuels and average fuel loads (Nolan et al., 2021). The occurrence of widespread drought prior to major fire seasons has fueled efforts to transfer approaches from plant physiology to fire ecology to advance our understanding of how changes in plant water relations during drought affect the flammability of living canopy fuels and thus wildfire risk (Jolly & Johnson, 2018; Nolan et al., 2016, 2020; Pivovaroff et al., 2019; Resco de Dios, 2020; Rossa & Fernandes, 2018; Scarff et al., 2021). While established modelling approaches exist to predict the moisture content of dead fuels due to their close relationship with atmospheric meteorological conditions (Matthews, 2013; Ray et al., 2010; Resco de Dios et al., 2015) and soil moisture (Zhao et al., 2021, 2022), the moisture content of living fuels (LFMC; i.e. the tissue's water mass per unit dry mass) remains challenging to predict due to the dynamic interplay between hydrological and atmospheric conditions that determine the plant's access to, and loss of water (Cochard et al., 2021). In addition to leaf water mass, LFMC is also influenced by the tissue's dry mass, which is determined by net primary productivity, foliar starch, sugar and crude fat contents and leaf phenology (Brown et al., 2022; Jolly et al., 2014). Thus, the co-variation of leaf water and dry mass can introduce temporal fluctuations of LFMC at daily, seasonal, and inter-annual scales. As community compositions vary spatially and plants respond dynamically to changes in growing conditions, vegetation can introduce significant influence on LFMC and species-specific calibrations might be needed to predict variation in LFMC from environmental conditions (Jolly et al., 2014; Nolan et al., 2018, 2020; Pivovaroff et al., 2019; Qi et al., 2016; Scarff et al., 2021). For example, key hydraulic traits such as leaf-saturated moisture content and leaf water potentials (particularly at turgor loss point [TLP]) have been identified to introduce large variation in LFMC between woody species in south-eastern Australia (Nolan et al., 2020, 2022; Scarff et al., 2021) and Spain (Balaguer-Romano et al., 2022). In contrast, only a few studies have assessed the influence of leaf traits such as specific leaf area (SLA; the ratio of leaf area to leaf mass) on spatial and temporal predictions of LFMC and confirmed its influence on instantaneous LFMC across plant functional types (Brown et al., 2022) or on maximum LFMC at the species level (Nolan et al., 2022). This is surprising, given that SLA is an important indicator of the fitness of a species in their environment (Poorter et al., 2009) and SLA and LFMC both incorporate leaf dry weights in the denominator.

In Australian forests and woodlands, LFMC has been linked to variation in leaf flammability by modifying ignition times (Scarff et al., 2021) and cumulative area burnt by wildfire (Dennison & Moritz, 2009; Nolan et al., 2016; Yebra et al., 2013). Rises in vapour pressure deficit (VPD) cause declines in the moisture content of live fuels and increases in the flammability of dead fuels, both of which have been positively correlated with increases in burn area in forested ecosystems in Australia, North America and Europe (Boer et al., 2017; Clarke et al., 2022; Nolan et al., 2016; Rao et al., 2022; Resco de Dios et al., 2022; Williams et al., 2019). A number of recent studies focused on disentangling the importance of VPD for global wildfire risk, e.g. by influencing burn area (Rao et al., 2022), sustaining active fire when flammable conditions are sustained through the night (Balch et al., 2022; Chiodi et al., 2021) or by increasing the frequency of days above critical forest flammability thresholds due to rising temperatures with a changing climate (Clarke et al., 2022). Models that predict instantaneous variation in LFMC based on hydrological variables (such as soil moisture; Vinodkumar et al., 2021) or meteorological drought indices (Pellizzaro et al., 2007; Ruffault et al., 2018; Viegas et al., 2001) fail to account for dynamic plant physiological adjustments and species-specific plant water-use strategies or leaf traits, and to our knowledge the combined influence of plant traits, atmospheric and hydrological variables on the instantaneous variability in LFMC have not been assessed anywhere in forest ecosystems in Australia, or elsewhere.

Remotely sensed data provide an opportunity for estimating LFMC over large areas at fine spatial and temporal resolutions (Cunill Camprubí et al., 2022; Nolan et al., 2016; Yebra et al., 2018), but species-specific calibrations are still required to link remotely sensed estimates of vegetation water content to LFMC (Yebra et al., 2013). Models of LFMC based on spectral observations hold promise to overcome this gap, with good results in ecosystems where species-specific calibration and validation data are available (Yebra & Chuvieco, 2009; Yebra et al., 2013, 2018). Moreover, soil moisture-based relationships of LFMC (Vinodkumar et al., 2021) might enable near-term to seasonal forecasts of continental LFMC, as forecasts of hydrological variables at high spatial resolution are being integrated into Australia's national ensemble forecasting system (Vogel et al., 2021). Yet, the in situ variability of plant traits that control the

moisture content of living fuels remains to be tested in many ecosystems, particularly during extreme environmental conditions such as severe drought.

We monitored LFMC and a range of plant water-use traits (predawn and midday leaf water potentials [Ψ_{leaf}]), leaf traits (SLA and leaf mass per leaf area [LMA]), hydrological status (soil water content [SWC] in the shallow layer and full profile) and atmospheric variables (air temperature, VPD and CO_2 concentrations) in a mature eucalypt woodland at the *Eucalyptus* Free-Air CO_2 Enrichment (EucFACE) facility. The observation period included a severe drought that directly preceded the 'Black Summer' bushfires in southeastern Australia (2019/2020). EucFACE is Australia's only CO_2-enrichment experiment in a mature dry-sclerophyll woodland, providing us not only with the unique opportunity to assess the influence of elevated atmospheric CO_2 concentrations (eCO_2) on plant traits during a severe drought, but also to determine how increases in future CO_2 concentrations will affect fuel moisture, a key component of wildfire risk, based on *in situ* observations from mature trees. Elevated CO_2 is predicted to increase organic solute concentrations in leaves (Li et al., 2018; Zheng et al., 2019) and leaf thickness due to greater carbon accumulation per unit leaf area (Ainsworth & Long, 2005; Epron et al., 1996; Wujeska-Klause et al., 2019a). Thus, eCO_2 should in theory affect leaf dry matter content and plant water-use traits, both of which would affect the rate of decline in leaf water potentials during drought. Moreover, eCO_2 can increase plant moisture status during drought (Saxe et al., 1998), suggesting that LFMC might be maintained at a higher level under eCO_2 in the face of drought as well.

The aims of this study were to (i) identify environmental conditions that influence the temporal dynamics of plant water-use traits, leaf traits and LFMC, (ii) determine if eCO_2 influences the temporal variability of plant traits and LFMC, (iii) derive a biophysical model that predicts variation in LFMC based on changes in plant traits, hydrological and atmospheric conditions and (iv) compare the biophysical model with existing approaches to predict LFMC based on a satellite model (Rozas-Larrondo et al., 2021) and pressure–volume curves (linear and two-phased *p*–*v* curve model; Nolan et al., 2022).

We hypothesize that (i) variation in predawn Ψ_{leaf} and LFMC can be predicted from SWC, whereas midday Ψ_{leaf} and LFMC will be more strongly influenced by atmospheric variables, (ii) stomatal closure in response to eCO_2 leads to less negative Ψ_{leaf} and, thus, higher LFMC and (iii) concurrent variation in SLA and Ψ_{leaf} will become the dominant influence on instantaneous LFMC when soil moisture becomes limiting during drought.

2 | MATERIALS AND METHODS

2.1 | Site description and experimental design

Data were collected at the *Eucalyptus* Free-Air CO_2 Enrichment (EucFACE) facility located in remnant Cumberland Plain Woodland near Richmond, NSW, Australia (33°37′S and 150°44′E, 23m

elevation). Permission was not needed for fieldwork and the site is fully described elsewhere (Duursma et al., 2016; Ellsworth et al., 2017; Gimeno et al., 2016). Briefly, the vegetation consists of an open canopy dominated by *Eucalyptus tereticornis* Sm. and an understory dominated by grasses with a sparse layer of sclerophyllous plants, short trees and shrubs. The leaf area index varies seasonally between 1.2 and 2.2 m^2 m^{-2}, with new shoots emerging in late spring to early summer (Duursma et al., 2016; Wujeska-Klause et al., 2019a). The soil is a well-draining, nutrient-poor Clarendon loamy sand (Crous et al., 2015).

The site is characterized by a humid temperate to subtropical climate, with a mean daily maximum temperature of 24.0°C, and a mean annual rainfall of 796mm over the 1960–2021 period. Soil drought between 2017 and 2020 coincided with numerous heatwaves in the summers of 2017/2018 and 2019/2020 (Griebel et al., 2022). The EucFACE experiment consists of six circular plots of 25m diameter (hereafter termed 'rings'). Each ring is surrounded by a 28m tall fibre-glass frame with perforated pipes that release CO_2 (Ellsworth et al., 2017). Since February 2013, three rings have been continuously exposed to an ambient CO_2 concentration of ≈400μmol mol^{-1} (hereafter termed 'aCO_2') and three rings to ≈550μmol mol^{-1} (aCO_2 + 150μmol mol^{-1}; hereafter termed 'eCO_2'). Each ring is equipped with a crane that facilitates access to the upper tree canopy.

2.2 | Leaf-level measurements

Leaf water potentials and leaf traits were collected from May 2012 in regular sampling campaigns targeting the months of February, May and October each year. In each campaign, we sampled fully expanded, mature leaves from the upper canopy of three co-dominant trees per ring. Three replicate shoots per tree were collected and stored in zip seal bags in a cooler during transport before midday leaf water potentials (Ψ_{leaf}) were measured to the nearest 0.1 MPa with a pressure chamber (1505D; PMS Instrument Company) immediately after sampling was completed. Since the cranes can only be operated during daytime, predawn Ψ_{leaf} were collected from the mid to upper portion of the canopy using 23m tall walk-up scaffolding units within each ring (two-three trees were within reach from each scaffold). All leaves that were sampled for water potentials were scanned to calculate leaf area (LA), before they were dried in an oven at 105°C for at least 48 h (Matthews, 2010) to obtain dry weights (D_w). We then calculated the SLA (m^2 kg^{-1}) as:

$$SLA = \frac{LA}{D_w}. \tag{1}$$

We further calculated LMA (gm^{-2}), which is the inverse of SLA. We commenced more frequent sampling of leaf-level measurements and concomitant LFMC in August 2018 to capture the dry period during the drought as well as the wet period following substantial rains in early 2020. Thus, all leaves that were sampled since August 2018 were also weighed to obtain fresh weights (F_w), and we then used the F_w and D_w to calculate live fuel moisture content (LFMC in %):

$$\text{LFMC} = \frac{(F_w - D_w)}{D_w} \times 100. \tag{2}$$

We used all available data from 2012 to 2021 to investigate the seasonality of Ψ_{leaf} and their relationship with SWC and data from 2018 to 2021 to investigate the seasonality of LFMC and SLA as well as relationships between LFMC and SWC, and between LFMC and leaf traits. For all analyses, trees were nested within plots when averaging by CO_2 treatment, and the standard error (SE) refers to the standard error of the mean when averaging campaigns by treatment (3 rings per treatment, thus $n = 3$). Note that prolonged lockdowns and facility closures during the coronavirus pandemic restricted sampling in the 2020–2021 period (Figures S.1–S.3).

2.3 | Soil moisture and atmospheric measurements

Volumetric water content (VWC in %) between 0.25 and 4.5 m depth was measured in 25 cm depth increments using neutron probes at approximately monthly intervals since May 2012. Measurements were taken at two locations within each ring and subsequently averaged by ring and treatment. Monthly measurements were further re-sampled to daily using linear interpolation accounting for irregular spacing between observations. Measurements of VWC were converted to SWC (mm) and summed for the shallow layer (0–1 m depth; $SWC_{shallow}$) and the full soil profile (0–4.5 m depth; SWC_{total}). We further derived daily minimum and daily maximum air temperature (T_{air} in °C) and VPD from half-hourly measurements at the nearby Cumberland Plain flux tower (AU-Cum; ≈1.5 km from study site; Griebel et al., 2020).

2.4 | Statistical analyses of CO_2 effects and individual relationships between leaf-level measurements, soil moisture and atmospheric variables

EucFACE has three replicate treatment plots for ambient and elevated CO_2 treatments, with three sampled trees per ring. Trees were nested within rings as random factors for mixed-model repeated-measures analysis of variance ('LME4' package; Bates et al., 2015), which was used to assess differences in CO_2 treatments and season (spring, summer, autumn and winter) for predawn and midday Ψ_{leaf}, SLA and LFMC. We accounted for SWC, VPD and sampling height as covariates in our models. If interactions in the mixed-model repeated measures ANOVA were significant, then differences between means were followed up with a Tukey HSD post hoc test (*glht* from the 'MULTCOMP' package; Hothorn et al., 2008). We used Levene's test (*leveneTest* from the 'CAR' package; Fox & Weisberg, 2019) to assess the homogeneity of variances. If applicable, data were log-transformed to correct for non-normal data distributions and residual plots confirmed constant variance in all three cases. We further assessed the relationships between Ψ_{leaf} and SWC, LFMC and shallow SWC, and

LFMC and SLA using self-starter functions for nonlinear regressions from the 'AOMISC' package (Onofri, 2020) and the 'DRC' package (Ritz et al., 2015). The relationship between predawn Ψ_{leaf} and SWC in the full profile was best described using asymptotic regressions, whereas all other relationships between Ψ_{leaf} and SWC were best described using logarithmic regressions. We further used a second-order polynomial function to assess relationships between LFMC and shallow SWC, and exponential growth functions to assess relationships between LFMC and SLA. All statistical analyses were performed in R version 4.0.3 (R Core Team, 2020) and due to the low replication associated with FACE sites (see Gimeno et al., 2016), p-values <0.1 were considered statistically significant.

2.5 | Predictions of live fuel moisture content from a statistical biophysical model

We used random forest regression models (Breiman, 2001) to predict LFMC based on hydrological status ($SWC_{shallow}$, SWC_{total}), atmospheric variables (T_{air}, VPD, CO_2 concentrations), plant water-use traits (predawn and midday Ψ_{leaf}) and leaf traits (SLA, LMA). We used the 'RANGER' package version 0.13.1 (Wright & Ziegler, 2017) and used minimum VPD/T_{air} for predawn observations, and maximum VPD/T_{air} for midday observations. We tested the model performance with VPD instead of T_{air}, $SWC_{shallow}$ instead of SWC_{total}, and SLA instead of LMA. We discarded T_{air} due to its high correlation with VPD (Spearman's $r > 0.75$; Figure S.4), and because the models had a slightly lower R^2 and larger RMSE when using T_{air} instead of VPD, SWC_{total} instead of $SWC_{shallow}$, and LMA instead of SLA. Including Ψ_{leaf} did not improve model performance either (presumably because of the strong correlation with shallow and deep SWC; Figures S.4 and S.5), so Ψ_{leaf} were discarded as well. Thus, we trained the final models using VPD, SLA, $SWC_{shallow}$ and CO_2 treatment with 500 decision trees and 3 ($n-1$) variables to possibly split at each node. Variable importance was assessed with the 'VIP' package (Greenwell & Boehmke, 2020) using the 'impurity' mode. Since Random Forest is an ensemble learning method based on many independent classification and regression trees, each run produces slightly different outcomes. Hence, we set the seed to '1234' to generate reproducible model runs for our reported metrics (R^2 and RMSE), and have included a sensitivity analysis that compares the R^2 and associated RMSE for 1000 randomly selected seeds in the appendix (Figure S.6). We then compared how our predictions of LFMC from the statistical biophysical model compare against predictions of LFMC based on a satellite model (see Section 2.6) and from established relationships between Ψ_{leaf} and LFMC from pressure–volume curves (see Section 2.7).

2.6 | Predictions of live fuel moisture content from a satellite model

We used reflectance data from Sentinel 2A and Sentinel 2B satellites to calculate LFMC (herein referred to as satellite model).

Sentinel 2 data were obtained from Digital Earth Australia (DEA), which provides analysis-ready data that have been corrected for position, terrain, radiometry, atmosphere and sun-sensor geometry (Dhu et al., 2017). We selected the satellite images that contained the EucFACE rings and were closest in time to each LFMC observation with a maximum time-lapse of ±10 days. We use methods developed by Rozas-Larrondo et al. (2021) to compute LFMC using the Sentinel-2 data. The methodology comprises a Random Forest Regressor that establishes a relationship between seven Sentinel-2 reflectance bands and estimated LFMC values derived from MODIS (Yebra et al., 2018). Rozas-Larrondo et al. (2021)'s methodology is under operationalisation by Geoscience Australia and the code is publicly available on Github(https://github.com/ANU-WALD/sentinel2_fmc). Once LFMC was computed, the values for a given ring were extracted from each scene using the average value of a 2×2 pixel kernel located at the centre of each ring (Figure S.7). A 2×2 window was used to reduce the potential noise due to residual atmospheric effects and georeferencing errors and because it matches with the size of the rings (25 m diameter). Note that the satellite model will provide a plot-integrated estimate of LFMC across each ring, which includes a mixture of overstorey and understorey species due to the spatial resolution of the windows. Since our direct observations of LFMC are only sourced from *E. tereticornis* in the overstorey, this will likely increase the bias when comparing tree-based observations of LFMC with plot-based predictions from the satellite model.

2.7 | Predictions of live fuel moisture content from pressure–volume curves

We further assessed whether seasonal observations of LFMC could be predicted from Ψ_{leaf} using pressure–volume curves (*p–v* curves; Nolan et al., 2020). *p–v* curves describe changes in relative leaf water content with Ψ_{leaf} on a dehydrating cut shoot (Tyree & Hammel, 1972) but can also characterize changes in LFMC with Ψ_{leaf} (Nolan et al., 2020). We generated *p–v* curves at EucFACE on one to two leaves per tree, from a total of 26 trees, collected during drought (June and October 2018) and during a wet summer (January 2022). Each leaf was rehydrated to saturation before shoots were dehydrated on a bench while Ψ_{leaf} and leaf mass were measured periodically (ranging from every few minutes when leaves were close to full turgor to >1 h when leaves were approaching very low water potentials). We used a Scholander-type pressure chamber for Ψ_{leaf} measurements. Once the *p–v* curves were completed, leaves were oven-dried for 48 h at 105°C to obtain the dry weight, and LFMC was calculated for each measurement during the dry-down period following Equation (2). In a study at the adjacent Cumberland Plain flux tower site (≈1.5 km from the study site), Nolan et al. (2022) found that the linear model of LFMC and Ψ_{leaf} outperformed the two-phase relationship that uses separate fits for above/below the TLP when using *p–v* curves to predict seasonal variation in LFMC. We also assessed both the two-phase model and a simpler linear

model to predict LFMC as a function of Ψ_{leaf} for *E. tereticornis* at EucFACE. Applying the approach in Nolan et al. (2022) to our *p–v* curves, we calculated LFMC from field observations of Ψ_{leaf} using the following equations:

$$\text{LFMC}_{linear} = \left(8.71 \Psi_{leaf}\right) + 118.6. \tag{3}$$

$$\text{LFMC}_{aboveTLP} = \left(3.91 \Psi_{leaf}\right) + 114.9. \tag{4}$$

$$\text{LFMC}_{belowTLP} = \left(\left(\frac{-1}{\Psi_{leaf}}\right) - 0.0283\right) / 0.0038. \tag{5}$$

Since we found no significant effect of CO_2 treatment on Ψ_{leaf} or LFMC (see Section 3.1), we combined the leaves from all trees to establish the relationships with Equations (3)–(5).

3 | RESULTS

3.1 | Leaf traits vary seasonally but not with atmospheric CO_2

All examined leaf traits displayed clear seasonal variability (Figure 1), but we found no significant effect of CO_2 treatment on Ψ_{leaf}, SLA or LFMC when season was included as a factor (*p*-values >0.1 for all analyses). Predawn and midday Ψ_{leaf} were lowest in the drier months (spring and winter) and increased in the wetter months (summer and autumn; Figure S.8). SLA and LFMC were lowest in spring and highest in summer, and both variables showed little variation between the remaining seasons.

3.2 | Soil water content controls variation in predawn Ψ_{leaf}

Predawn Ψ_{leaf} decreased from −0.1 MPa during high SWC to −1.9 MPa when the SWC was lowest in the shallow layer (Figure 2a) and the full profile (Figure 2b). The total SWC within the full profile alone explained 69%–76% of variability in predawn Ψ_{leaf} for eCO_2 and aCO_2 treatments, which was reduced to 65% and 70% (for eCO_2 and aCO_2, respectively) when restricting the total SWC to the shallow layer (Figure 2a). In contrast, midday Ψ_{leaf} decreased less strongly with decreasing SWC (between −1.2 and −2.8 MPa), and SWC alone was only able to explain up to 43% of variation in midday Ψ_{leaf} with no notable difference when including the full profile over the shallow layer.

3.3 | Specific leaf area is the single most important predictor of live fuel moisture content

LFMC varied between 80% and 160% for the duration of the experiment (Figure 3), which included the peak of the drought and a subsequent re-wetting period. In contrast, shallow SWC varied more
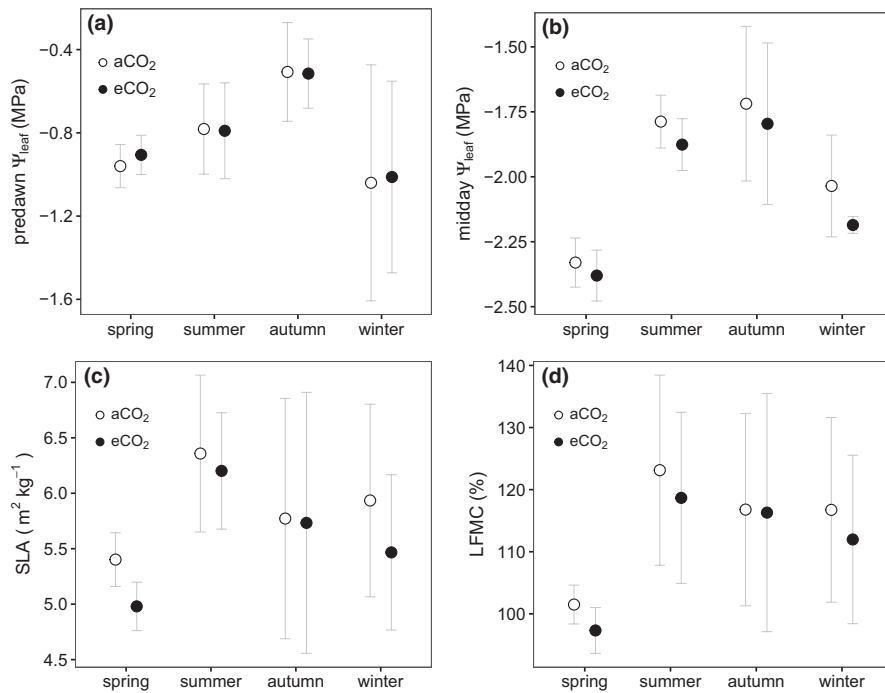
FIGURE 1 Seasonal variability (means ± SE) of predawn and midday leaf water potentials (Ψ_{leaf} in MPa; top row), specific leaf area (SLA in $m^2\,kg^{-1}$; panel c) and live fuel moisture content (LFMC in %; panel d) for ambient (aCO_2; open symbols) and elevated (eCO_2; closed symbols) CO_2 treatments.
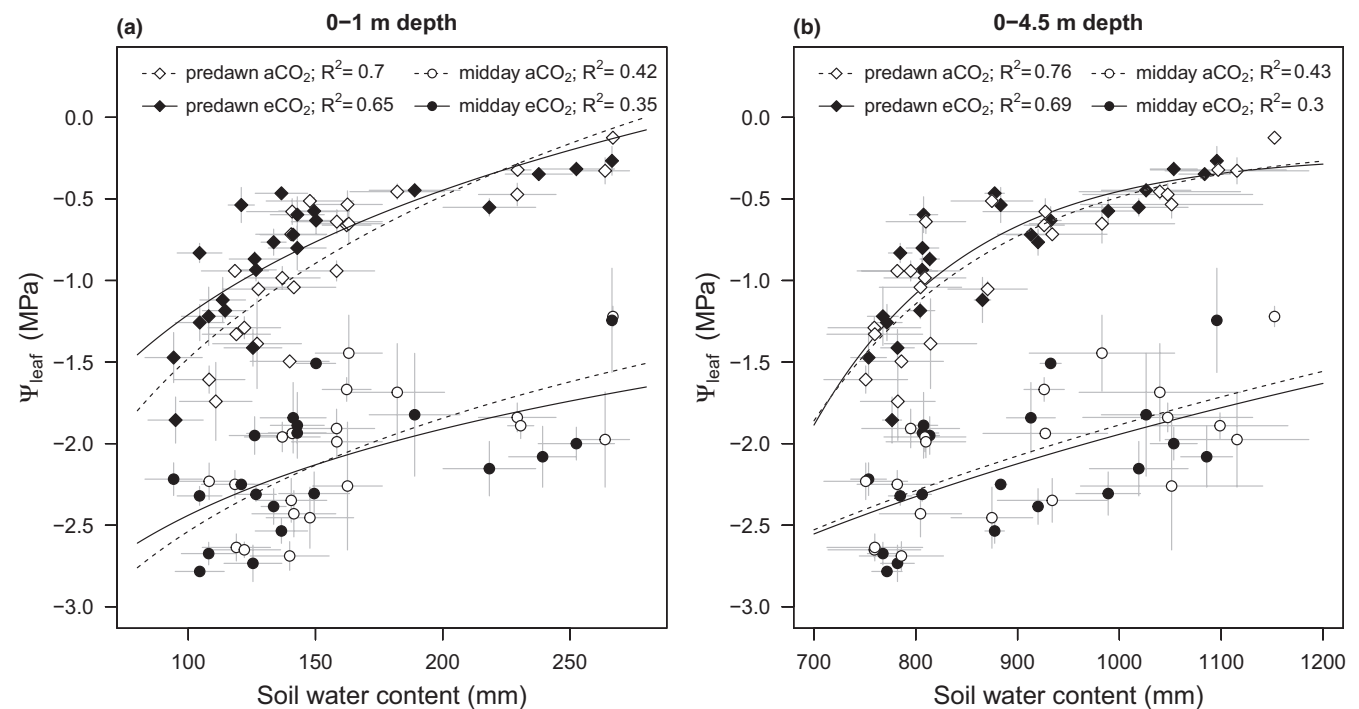

FIGURE 2 Relationship between leaf water potentials (Ψ_{leaf} in MPa) and soil water content (SWC in mm) for ambient (aCO_2; open symbols) and elevated (eCO_2; closed symbols) CO_2 treatments for the shallow layer (0–1 m depth; panel a) and the full profile (0–4.5 m depth; panel b). Shown are means ± SE, and predawn (midday) measurements are symbolized by rhombus (circles).

than twofold (between 94 and 230 mm; Figure 3a) and SLA ranged from 3.9 to 5.8 $m^2\,kg^{-1}$ for the corresponding observation dates (Figure 3b). The variation in SWC explained up to 41% of the variation in predawn LFMC, which decreased to 22% for midday LFMC. Yet, SLA alone was able to explain between 82% of midday LFMC in aCO_2 treatments and 98% of predawn LFMC in eCO_2 treatments (Figure 3b). The range of observed SLA and LFMC values was greater

under eCO_2 than aCO_2 concentrations due to lower LFMC in eCO_2 treatments during particularly dry conditions (Figure 3a).

When combining plant traits, hydrological status and atmospheric variables into a biophysical model (Figure 4) we were able to explain 89% of variability in predawn LFMC (RMSE = 6.67) and 76% of variability in midday LFMC (RMSE = 5.81) when using only shallow SWC, VPD, SLA and CO_2 treatment. Adding Ψ_{leaf}, or replacing
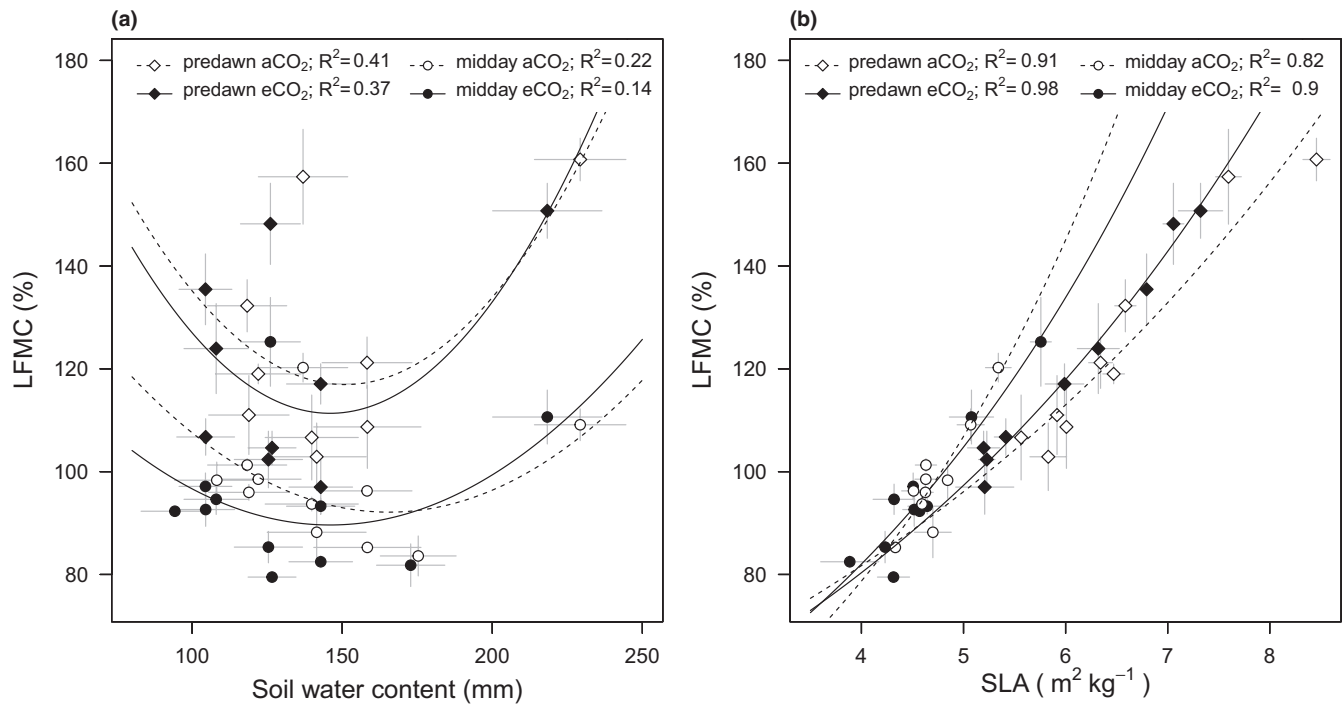
(a)

(b)

FIGURE 3 Relationship between live fuel moisture content (LFMC in %) and soil water content from 0 to 1 m depth (in mm; panel a) or specific leaf area (SLA in $m^2 kg^{-1}$; panel b) for ambient (aCO_2; open symbols) and elevated (eCO_2; closed symbols) CO_2 treatments. Shown are means ± SE, and predawn (midday) measurements are symbolized by rhombus (circles).

VPD with T_{air}, $SWC_{shallow}$ with SWC_{total}, and SLA with LMA did not increase the percent of variance explained by the model, and neither did combining predawn and midday observations into one model ($R^2 = 0.89$ and RMSE = 6.76; Figure S.9). The single most important variable to explain variation in predawn and midday LFMC was SLA, with much reduced variable importance for VPD (33% for predawn and 32% for midday LFMC) and SWC (5% for predawn and 11% for midday LFMC) compared with SLA (Figure 4b). Excluding SLA from the models substantially reduced the percent of variance explained by all models (full model: $R^2 = 0.61$ and RMSE = 12.87; Figure S.10, predawn model: $R^2 = 0.71$ and RMSE = 10.89 and midday model: $R^2 = 0.59$ and RMSE = 7.58; Figure S.11), and VPD became the most important variable to explain the variability of LFMC in all models. CO_2 treatment was of negligible importance in all models (<5% compared with most important variable; Figure 4 and Figures S.9–S.11).

3.4 | Model comparison for predicting midday live fuel moisture content

When comparing observations of midday LFMC at EucFACE against predictions using the random forest model and the published models (two p–v curve models; Nolan et al., 2022 and a satellite model; Yebra et al., 2018), the random forest model outperformed the published models (Figure 5 and Table S.1). Thereafter, the linear p–v curve model had slightly lower mean absolute error, root mean square error and model bias than the two-phase p–v curve model, but both models had an overall narrow prediction range that was

unable to capture the high and low range of LFMC observations. Despite slightly higher bias metrics for the satellite model, the satellite model was able to capture a greater range of LFMC observations than the p–v curve models. Yet the satellite model tended to underpredict LFMC, particularly when LFMC was low. Overall, the random forest model had only a marginally positive bias (0.9%–1.4%), while the satellite model and the p–v curve model had a larger bias but in opposite directions (11.2% to 18.1% and −0.3% to −7.6%, respectively). Furthermore, the p–v curve models performed slightly better for ambient than elevated CO_2 treatments, whereas the satellite model performed better for elevated than ambient CO_2 treatments. Differences in model performance between treatments were only marginal for the random forest model.

4 | DISCUSSION

Our study highlights that incorporating dynamic variation in SLA in combination with hydraulic and atmospheric variables substantially improves predictions of LFMC during sustained drought periods. SLA was the single most important predictor of LFMC during the observation period. Ultimately, the combination of leaf traits with hydrological and atmospheric variables could explain up to 89% of variability in temporal LFMC dynamics. Due to the importance of leaf traits for predicting LFMC at our study site, the biophysical model clearly outperformed existing approaches to model LFMC that do not take dynamic transformations of leaf traits into account. VPD was the second most important variable after SLA for
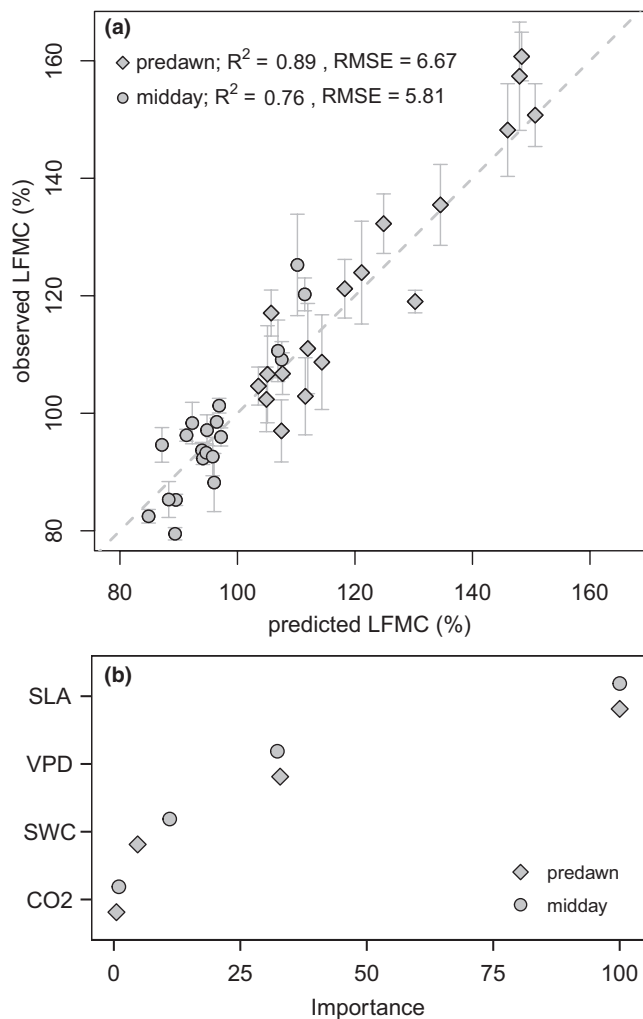
FIGURE 4 Predictions vs. observations (means ± SE) of live fuel moisture content (LFMC in %; panel a) and variable importance scaled to the most important variable in descending order (panel b) for the predawn and midday models. Assessed variables include specific leaf area (SLA in $m^2\,kg^{-1}$), vapour pressure deficit (VPD in kPa), soil water content within the 0–1 m layer (SWC in mm) and CO_2 treatment (ambient vs. elevated CO_2). Predawn (midday) measurements are symbolized by rhombus (circles).

predicting predawn and midday LFMC, highlighting the critical role of atmospheric moisture demand in controlling instantaneous LFMC and associated wildfire risk. Contrary to our hypotheses, elevated atmospheric CO_2 concentrations did not exert any significant influence on Ψ_{leaf}, SLA or LFMC dynamics. Nonetheless, eCO_2 concentrations may complicate wildfire risk predictions by extending the range in SLA and LFMC during particularly wet or dry periods.

4.1 | Why does specific leaf area exert such strong control on live fuel moisture content?

Our study highlights the importance of leaf phenology and plant physiological adjustments in response to water stress for instantaneous predictions of predawn and midday LFMC in this mature
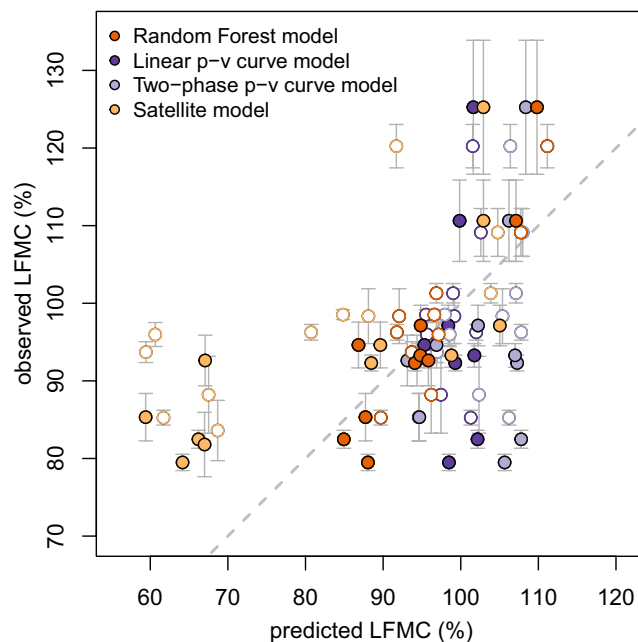

FIGURE 5 Predictions of midday live fuel moisture content (LFMC in %) versus observations using the Random Forest model (red circles), two models based on *p–v* curves (light and dark purple circles) and the satellite model (yellow circles) at the EucFACE site for ambient (open circles) and elevated (closed circles) CO_2 treatments. Shown are means ± SE, and the dashed line indicates the 1:1 relationship between observations and predictions.

eucalypt woodland. SLA indicates the leaf-level construction cost of light interception, making it a key trait that influences leaf life span and plant growth, and an important indicator of species fitness in their environment (Falster et al., 2018; Gutschick & Wiegel, 1988; Poorter et al., 2009; Wright et al., 2004). Efforts are ongoing to understand the physiological processes that regulate the spatiotemporal variation of SLA (Wujeska-Klause et al., 2019b).

Environmental conditions exert strong controls on SLA, particularly radiation, atmospheric conditions (CO_2 concentrations and air temperature) and nutrient and water availability (Poorter et al., 2009). Crous et al. (2021) demonstrated that shade resulted in 13% lower LMA in lower vs. upper canopy leaves at the EucFACE experiment, and we observed 25% higher SLA during predawn sampling times compared with midday (Figure S.2). This could be related to sampling from different canopy positions (see Section 2.2) or the ageing process of mature leaves. Leaf age affects the photosynthetic capacity of *E. tereticornis* (Wujeska-Klause et al., 2019a), which likely contributed to seasonal and annual variation in SLA (Figure S.2; Figure 1). Moreover, fewer leaves might have emerged during the drought (Griebel et al., 2022), leading to extended life spans of mature leaves that further exaggerated the overall range in SLA.

Our study clearly identified the importance of SLA, and thus of variation in tissue dry matter content, for controlling temporal variation in LFMC dynamics in a temperate eucalypt forest (Figure S.3). This strong correlation is not surprising given that SLA and LFMC both incorporate leaf dry weights in the denominator (see Equations 1 and

2). We expect SLA to remain an important predictor for LFMC dynamics in other ecosystems, as Jolly et al. (2014) illustrated that phenological changes in leaf dry mass were a stronger predictor of seasonal LFMC dynamics than changes in leaf water content for *Pinus contorta*. Furthermore, Brown et al. (2022) highlighted that biomass fluctuations were most important for predicting LFMC in a deep-rooted species (*Pseudotsuga menziesii*), whereas changes in SWC were more important than SLA for shallow-rooted species. In addition, Nolan et al. (2022) highlighted the correlation between SLA and maximum LFMC of 16 species in Australian forests across a large climatic gradient and identified much larger variability in SLA between species (≈3.5–8 $m^2 kg^{-1}$) compared with the temporal variability of midday SLA within our examined species (3.9–5.8 $m^2 kg^{-1}$). This suggests that the wider range of variation in SLA across species and aridity gradients will ultimately determine the upper limits of landscape-scale variability in LFMC.

SLA and LMA are widely measured traits that are commonly available in plant trait databases such as AusTraits (Falster et al., 2021), TRY (Kattge et al., 2020), or GLOPNET (Reich et al., 2007), whereas LFMC is a trait not nearly as common (GlobeLFMC database; Yebra et al., 2019). Thus, the high correlation of SLA with LFMC holds great promise for using widely measured traits to overcome gaps in direct observations of LFMC by either linking repeat sampling of SLA to instantaneous LFMC or by using species-specific and/or community means of SLA to determine maximum LFMC and, thus, the upper limit of landscape-scale variability in LFMC. Furthermore, our model comparison suggests that including plant traits and atmospheric variables has great potential to improve existing models for predicting spatiotemporal variation in LFMC, irrespective of whether these models are based on hydrological variables such as soil moisture (Vinodkumar et al., 2021), meteorological drought indices (Pellizzaro et al., 2007; Ruffault et al., 2018; Viegas et al., 2001), process-based models (Balaguer-Romano et al., 2022) or optical remote sensing (Caccamo et al., 2011; Nolan et al., 2016; Yebra et al., 2013, 2018).

4.2 | How will climate change influence wildfire risk?

Globally, temperatures are rising at unprecedented speed, triggering an increase in the number, duration, and intensity of heatwaves and droughts likely to occur in this century (Hoegh-Guldberg et al., 2018; Perkins-Kirkpatrick & Lewis, 2020). The general warming trend has been accompanied by accelerated rises in VPD, which is a direct measure of atmospheric demand for water and a key driver for ecosystem functioning and plant mortality (Bauman et al., 2022; Grossiord et al., 2020; McDowell et al., 2022; Novick et al., 2016). In our model, VPD was the most important variable after SLA and explained between 22% (full model) and 33% (predawn or midday model) of the remaining variability in LFMC. This, along with VPD becoming the most important variable when omitting SLA (Section 3.3), suggests that VPD was more important for predicting predawn and midday LFMC than SWC. The relationship between VPD and burn area increased in vegetation that is sensitive to water

limitation (Rao et al., 2022), which could explain the critical role of VPD in reducing LFMC at our site during the drought. Moreover, Balch et al. (2022) highlighted the importance of night-time VPD for sustaining active fire when flammability fails to cease at night. In our model, the scaled variable importance of VPD increased by 50% when predicting predawn LFMC compared with the full model (Figure S.9), aligning with a number of recent studies that highlight the commonly underestimated importance of VPD for global wildfire risk (Balch et al., 2022; Chiodi et al., 2021; Clarke et al., 2022; Rao et al., 2022). Since VPD is an important predictor of the moisture content of both dead fuels (Ray et al., 2010; Resco de Dios et al., 2015; Resco de Dios et al., 2021) and live fuels (this study), our finding of the combined importance of VPD and SLA provides a physiological basis for the relationship between burn area and VPD that is increasingly observed globally.

Droughts have been commonly associated with large fire events and severe fire seasons (Canadell et al., 2021; Duane et al., 2021; Keeley & Syphard, 2021; Nolan et al., 2021), especially when severe soil-dryness co-occurs with extreme temperatures (Libonati et al., 2022). The individual and combined likelihood of drought, heat and fire are projected to increase in many regions over the 21st century (Hoegh-Guldberg et al., 2018). Drought stress is hypothesized to be ameliorated by elevated atmospheric CO_2, as increases in photosynthesis along with concurrent decreases in stomatal conductance improve the intrinsic leaf-level plant water use efficiency (De Kauwe et al., 2021; Medlyn et al., 2011). However, we found no significant effect of CO_2 treatments on Ψ_{leaf}, SLA or LFMC. SLA typically decreases under eCO_2 in C3 species (including *Eucalyptus* sp.; Aspinwall et al., 2018; Duane et al., 2021; Poorter et al., 2009), so the missing effect might have been due to insufficient statistical power from the duration of the sampling campaign, or due to phosphorus limitation in the soils at the EucFACE experiment (Crous et al., 2015). The soils of southeastern Australia are typically nutrient-deficient, making it challenging to generalize the absence of a CO_2 response for the examined plant water use and leaf traits to other ecosystems due to complex interactions between CO_2 concentrations and soil nutrient availability (Ochoa-Hueso et al., 2019).

Direct observations of LFMC and leaf traits in response to CO_2 fertilization are rare. Manea et al. (2015) found in a glasshouse study that ignition time was positively correlated to leaf moisture content, and the latter was reduced under eCO_2. This suggests that living fine fuels will be more flammable in future CO_2 concentrations, which was confirmed by shorter ignition times of fuels in elevated than ambient CO_2 concentrations (Manea et al., 2015). A potential explanation for these counter-intuitive observations is that foliar nitrogen content is negatively correlated with leaf flammability (Grootemaat et al., 2015), and leaf nitrogen concentrations were reduced in woody plants grown under eCO_2 at seedlings in the glasshouse study (Manea et al., 2015) and at mature *E. tereticornis* leaves at EucFACE (Wujeska-Klause et al., 2019b). In contrast, lower SLA has been linked to longer ignition times and smoulder duration in Australian evergreen perennial plants (Grootemaat et al., 2015), highlighting the potential for individual leaf traits to influence flammability in

opposing directions. Dynamic vegetation models might provide further insights into fire risk under future climates (Harrison et al., 2021; Kloster & Lasslop, 2017; Rabin et al., 2017), but they do not routinely assess LFMC (Ma et al., 2021). Fortunately, LFMC can be calculated from leaf wet and dry weights, which Ma et al. (2021) capitalized on when using a hydrodynamic vegetation model (FATES-HYDRO) to estimate the influence of LFMC on fire risk under future climates in California's chaparral shrubs. They found that CO_2 fertilization would mitigate fire risk by increasing LFMC by up to 4.8%, but this was not able to offset estimated increases in fire risk due to warming and decreased precipitation.

5 | CONCLUSIONS

Our study provides a physiological basis for the relationship between burn area and VPD that is increasingly observed globally. While we were able to demonstrate the importance of incorporating dynamic variation in plant traits and VPD for predicting LFMC during droughts, elevated atmospheric CO_2 concentrations did not exert any direct influence on the temporal dynamics of plant traits or LFMC. Whether this changes with higher atmospheric CO_2 concentrations or during more prolonged and severe droughts remains unknown. Yet, plant traits, and particularly SLA, are more widely measured than LFMC, holding great promise to bridge the gap between missing direct observations of LFMC and thus to improve existing models that include fuel moisture dynamics into wildfire risk assessments. Moreover, ecological forecasts of LFMC at continental scale might be coming within reach when combining biophysical and satellite-based models of LFMC with near-term or seasonal forecasts of meteorological and hydrological variables, the latter of which have recently been integrated into Australia's national ensemble forecasting system. Such continental-scale assessments and forecasts of LFMC dynamics are of great interest to agencies tasked with operational management of planned burns and wildfires.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data used in the manuscript and its supporting information are stored in our institutional archive and are publicly available here: https://doi.org/10.26183/bf6d-kh20.

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SUPPORTING INFORMATION

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

Appendix S1. Supplementary figures and tables.