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1 **Title:** Physiological drought responses improve predictions of live fuel moisture dynamics in
2 a Mediterranean forest

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16

17 **Key words**

18 Wildfire, drought code, KBDI, fire ecophysiology, turgor loss point, resprouting

19 **Abstract**

20 The moisture content of live fuels is an important determinant of forest flammability. Current
21 approaches for modelling live fuel moisture content typically focus on the use of drought
22 indices. However, these have mixed success partly because of species-specific differences in
23 drought responses. Here we seek to understand the physiological mechanisms driving
24 changes in live fuel moisture content, and to investigate the potential for incorporating plant
25 physiological traits into live fuel moisture models. We measured the dynamics of leaf
26 moisture content, access to water resources (through stable isotope analyses) and
27 physiological traits (including leaf water potential, stomatal conductance, and cellular
28 osmotic and elastic adjustments) across a fire season in a Mediterranean mixed forest in
29 Catalonia, NE Spain. We found that differences in both seasonal variation and minimum
30 values of live fuel moisture content were a function of access to water resources and plant
31 physiological traits. Specifically, those species with the lowest minimum moisture content
32 and largest seasonal variation in moisture (*Cistus albidus*: 49-137 % and *Rosmarinus*
33 *officinalis*: 47-144 %) were most reliant on shallow soil water and had the lowest values of
34 predawn leaf water potential. Species with the smallest variation in live fuel moisture content
35 (*Pinus nigra*: 96-116 % and *Quercus ilex*: 56-91 %) exhibited isohydric behaviour (little
36 variation in midday leaf water potential, and relatively tight regulation of stomata in response
37 to soil drying). Of the traits measured, predawn leaf water potential provided the strongest
38 predictor of live fuel moisture content ($R^2 = 0.63$, AIC = 249), outperforming two commonly
39 used drought indices (both with $R^2 = 0.49$, AIC = 258). This is the first study to explicitly link
40 fuel moisture with plant physiology and our findings demonstrate the potential and
41 importance of incorporating ecophysiological plant traits to investigating seasonal changes in
42 fuel moisture and, more broadly, forest flammability.

44 **1 Introduction**

45 The moisture content of fuels is a major determinant of fire ignition and rate of spread
46 (Bradstock, 2010; Sullivan, 2009). Fuel moisture content is particularly important in driving
47 wildfires in forest ecosystems where fuel loads do not limit fire activity, except for
48 immediately following large disturbances such as fire (Bradstock, 2010). Thus, monitoring
49 and forecasting fuel moisture content is vitally important for undertaking wildfire risk
50 assessments, assessing conditions for prescribed burns, and modelling fire behaviour (Nolan
51 et al., 2016; Sullivan, 2009).

52 Forest fuels consist of both dead and live plant material. Dead fuels, particularly fine
53 fuels (with a diameter <25.4 mm), respond rapidly to atmospheric conditions and can be
54 modelled from inputs such as temperature, humidity or vapour pressure deficit (Matthews,
55 2013; Resco de Dios et al., 2015). In contrast, live fuel moisture content (LFMC) can be
56 much more difficult to model because moisture content is a function of plant physiological
57 and structural traits, which can differ markedly across species (Jolly and Johnson, 2018;
58 Karavani et al., 2018). For example, some tree and shrub species from Mediterranean
59 environments exhibit little seasonal variation in LFMC, while the LFMC of other co-
60 occurring species can vary by as much as a factor of 6 (Pellizzaro et al., 2007; Soler Martin et
61 al., 2017; Viegas et al., 2001). Current approaches for estimating LFMC focus on either
62 modelling moisture content from drought indices, or modelling moisture content with
63 remotely sensed data (Viegas et al., 2001; Yebra et al., 2013). However, drought indices can
64 be difficult to apply because they do not capture the differing responses to drought across co-
65 occurring species, and current remote sensing approaches cannot be used for forecasting
66 LFMC. An eco-physiological approach to investigating LFMC dynamics may overcome
67 these limitations and lead to improved modelling (Jolly and Johnson, 2018).

68 There are at least three different but mutually inter-related physiological processes
69 that might explain why leaf moisture varies differentially across species. One of them is
70 access to water resources, a function of rooting patterns and water availability in the soil
71 profile that, in turn, appears to be related to the post-fire regeneration strategy. For example,
72 species that can resprout following high intensity fire typically have greater allocation to
73 roots and deeper root systems than species lacking this capacity (Bell et al., 1996; Verdu,
74 2000). As a consequence, resprouting species often maintain greater water supply to foliage
75 during dry periods than obligate seeding species (which are fire-killed but regenerate via
76 seed) (Saura-Mas and Lloret, 2007).

77 The second physiological mechanism potentially explaining inter-specific differences
78 in leaf moisture are dynamics in leaf water potential (Ψ_{leaf}). The relationship between Ψ_{leaf}
79 and moisture status is typically characterised by a curvilinear relationship between Ψ_{leaf} and
80 relative water content (Tyree and Hammel, 1972), with relative water content exhibiting a
81 perfect relationship with LFMC (i.e. R^2 of 1). Ψ_{leaf} is largely controlled by stomatal
82 sensitivity to water stress. Traditionally, plants exhibiting little seasonal variation in midday
83 water potential are classified as isohydric, while those with large fluctuations in water
84 potential are classified as anisohydric (Klein, 2014; Tardieu and Simonneau, 1998).
85 Differences in Ψ_{leaf} regulation strategies are generally attributed to differing degrees of
86 stomatal regulation (Martínez-Vilalta and Garcia-Forner, 2016). Following stomatal closure,
87 Ψ_{leaf} can continue to decline due to stomatal leakiness and cuticular conductance (Blackman
88 et al., 2016, Martin-StPaul et al., 2017a).

89 The relationship between Ψ_{leaf} and relative water content (and thus LFMC) can
90 change through time due to osmotic adjustment (Sinclair et al., 1985). Thus, the third
91 mechanism potentially explaining inter-specific differences in live fuel moisture content are
92 the series of osmotic and elastic adjustments that take place in cells, which lead to differences

93 in turgor loss point and water storage capacities. As relative water content declines, the
94 inverse of Ψ_{leaf} declines following a curvilinear function until the point at which cell turgor is
95 lost (the ‘turgor loss point’, Ψ_{TLP} ; Tyree and Hammel (1972)). Below the Ψ_{TLP} , the inverse of
96 Ψ_{leaf} potential declines linearly with further declines in relative water content (Tyree and
97 Hammel, 1972). Thus, the Ψ_{TLP} , is a key parameter affecting the relationship between leaf
98 moisture status and Ψ_{leaf} . As drought stress increases, the turgor loss point may be altered by
99 (i) increasing the concentration of solutes in the vacuole to increase π , the osmotic potential
100 at full turgor; (ii) increasing the elasticity of the cell walls to avoid collapse under turgor loss
101 (decrease of ϵ , the elasticity modulus); or (iii) redistributing the symplastic water outside of
102 the cell walls towards apoplastic water (Bartlett et al., 2012). The point at which cell turgor is
103 lost (the ‘turgor loss point’, Ψ_{TLP}) is an important eco-physiological parameter and is co-
104 ordinated with declines in stomatal conductance of 50% (Brodribb and Holbrook, 2003).
105 There is also increasing evidence that the turgor loss point is co-ordinated with access to soil
106 water resources, being higher (less negative) in species with greater access to water (Bartlett
107 et al., 2012). ϵ and π are both related to changes in LFMC although the latter is considered
108 the main driver of Ψ_{TLP} , and, consequently, more related to drought tolerance (Bartlett et al.,
109 2012).

110 Although there is a clear physiological basis for access to water resources, water
111 potential, stomatal regulation and osmotic and elastic adjustments in controlling LFMC
112 dynamics, there has been little research explicitly examining these relationships. On the one
113 hand, as Jolly and Johnson (2018) noted, fire scientists have traditionally considered live
114 fuels as “very wet dead fuels and nothing more”. On the other hand, plant physiologists have
115 more often focused on water potential and variations in moisture content have been explored
116 to a lesser extent. We argue that linking plant physiology with LFMC dynamics is important

117 because a mechanistic understanding of leaf moisture dynamics may lead to enhanced LFMC
118 forecasting capabilities.

119 Here we seek to understand, for the first time to our knowledge, what are the
120 physiological mechanisms driving changes in LFMC in a Mediterranean forest. We focused
121 our study in Catalonia (NE Spain), a region where forest fires are common. This study is
122 novel because it attempts to bridge research on the relationships between forest fire
123 dynamics, typically focused on fuel moisture content, and drought stress physiology, which
124 has traditionally focused on understanding variation in plant water potential and drought
125 responses. We address two key research questions: (1) what drives differences in LFMC
126 dynamics in co-occurring species? and (2) can plant physiological traits lead to superior
127 performance for models of live fuel moisture content? Regarding the first question, we sought
128 to disentangle the relative roles of (i) access to water resources, (ii) stomatal sensitivity to
129 water stress; and (iii) osmotic and elastic adjustments that take place in cells as drivers of
130 inter-specific differences in LFMC. Although we expected these processes would explain a
131 large portion of the variance in LFMC, we note that this study is not comprehensive and
132 additional factors such as stem capacitance or cuticular conductance (Blackman et al., 2016),
133 among other factors, could also play a role in controlling fuel moisture content. Regarding the
134 second question, we hypothesized that physiologically-based models of LFMC would
135 outperform currently employed drought indices, which ignore divergence in ecophysiological
136 responses under drought among coexisting species.

137

138 **2. Methods**

139 **2.1 Study area**

140 The experiment was conducted at the Natural Park of Poblet in Tarragona, NE Spain (41° 21'
141 6.4728'' latitude and 1° 2' 5.7496'' longitude). The climate is Mediterranean with a mean
142 annual temperature of 13.2 °C and a mean annual precipitation of 600 mm (Bonet et al.,
143 2012). The soil is loamy-sandy, is well drained and originates from decomposed granite
144 (Bonet et al., 2012). The study was conducted on an East-facing slope at an altitude of 700
145 m.a.s.l. The site was deforested during the 19-20th century to obtain firewood and other
146 products and the current stand is the result of forest regrowth during the last few decades. The
147 dominant tree species in the area are different oak (*Quercus ilex*, *Q. faginea*) and pine (*Pinus*
148 *nigra*, *P. sylvestris*) species. The understory is dominated by *Cistus* spp., *Arbutus unedo*,
149 *Ruscus aculeatus*, *Viburnum tinus*, *Cytisus scoparius*, *Erica arborea*, and *Rosmarinus*
150 *officinalis*, among others. Meteorological data were obtained from the closest meteorological
151 station available from the Catalan Service of Meteorology, which was about 5 km from the
152 plots.

153 In this study we chose to focus on: *Pinus nigra* (obligate seeding tree), *Quercus ilex*
154 (resprouting tree), *Arbutus unedo* (resprouting shrub), *Cistus albidus* (obligate seeding
155 shrub), *Erica arborea* (resprouting shrub), and *Rosmarinus officinalis* (obligate seeding
156 shrub) (Table 1). The site is an open forest, meaning that shrub species exposed to full
157 sunlight and not shaded by the trees. We chose these species for two reasons. First, we
158 wanted the same number of seeders and of resprouters. Second, we chose species that, based
159 on previous work, we expected to show contrasting fuel moisture dynamics (Table 1). More
160 specifically, we expected that LFMC in *P. nigra* and *Q. ilex* would be relatively constant
161 through the season, that LFMC in *C. albidus* and in *R. officinalis* would show a sharp decline
162 during the summer drought, and that *A. unedo* and *E. arborea* would show intermediate
163 patterns (Pellizzaro et al., 2007; Viegas et al., 2001).

164 **Table 1.** Overview of study species, including life-form, ecological response to disturbance, and range of live fuel moisture content (LFMC) observed in previous studies and
 165 observed in this study.

	Trees		Shrubs			
Species	<i>P. nigra</i>	<i>Q. ilex</i>	<i>A. unedo</i>	<i>C. albidus</i>	<i>E. arborea</i>	<i>R. officinalis</i>
Ecological response to disturbance	Obligate seeder	Resprouter	Resprouter	Obligate seeder	Resprouter	Obligate seeder
Range in LFMC (%) from previous studies	NA 87-145 for <i>Pinus brutia</i> ¹ ~105-155 for <i>Pinus halepensis</i> ²	54-95 ³	74-144 ³	35-134 ³	42-111 ³	35-136 ³
Range in LFMC (%), this study	96-116	56-91	91-148	49-137	62-128	47-144

166 ¹Study over one fire season in Mediterranean region of Crete, Greece (Dimitrskopoulos and Bemmerzouk, 2003).

167 ²Study over one fire season in Mediterranean NE Spain, values estimated from Fig. 2 in Viegas et al. (2001).

168 ³95% range in LFMC over 20 years of measurements in Mediterranean France (Duché et al., 2017; Martin-StPaul et al., 2018).

169

170 **2.2 Fuel moisture dynamics**

171 All fuel moisture measurements were undertaken over one full fire season, from late spring
172 (May) to early autumn (September) in 2017. Live fuel was sampled to characterise the
173 moisture content of the crown and shrub strata, in addition to characterising the moisture
174 content of each of the study species. LFMC samples were collected in the early afternoon
175 (between 12:00h and 15:30h local time) when diurnal LFMC was expected to be at a
176 minimum. Live fuel was collected by destructively sampling live foliage and small stems (\leq
177 3mm). For each strata and for each species fuel was collected in each of five tins, with 10-20
178 g of dry fuel per tin. Fuel fresh weight was measured then samples oven-dried at 105°C for
179 48 hours and fuel weight measured again. LFMC was calculated as:

$$180 \text{ LFMC} = \frac{F_W - D_W}{D_W} \times 100 \quad (1)$$

181 where F_W and D_W indicate fresh and dry weight, respectively.

182 In total, seven measurements of LFMC were undertaken that were separated by 2-3
183 weeks, with the exception of the second measurement which occurred shortly after the first
184 measurement following rain. During this period, LFMC exhibited a similar range to that
185 observed in previous studies, notably, this includes a 20+ year study from Mediterranean
186 France (Table 1).

187

188 **2.3 Plant physiology measurements**

189 Plant physiology measurements, including access to water resources, leaf water potential and
190 stomatal conductance, were measured within a three-day window corresponding to the LFMC
191 measurements. During each campaign meteorological conditions were similar and there was
192 no rainfall. Due to rain following the first LFMC measurements, there are no physiology

193 measurements associated with that time period. The exception to this is the measurement of
194 osmotic and elastic adjustments (through the pressure-volume curve method) which was
195 timed to capture key periods of fuel moisture: at the end of a wet period (27th July), during a
196 dry period (31st August), and at the end of a very dry period (21st September).

197

198 **2.3.1 Access to water resources**

199 Stable isotope analyses of xylem water, soil water and groundwater ($\delta^{18}\text{O}$ and $\delta^2\text{H}$) were
200 undertaken to study plant access to different water sources along the soil profile. Branch
201 samples were collected from each of five plants per species at the same time as LFMC
202 samples. Five replicate soil samples were collected at 0-10 cm ('shallow' soil water) and 10-
203 25 cm ('deep' soil water). Additionally, we also sampled groundwater from a well nearby.
204 Samples were taken at around noon, immediately kept inside glass tubes that were sealed
205 with paraffin and frozen with dry ice in coolers. Once in the lab, samples were stored in a
206 freezer (-4 °C) until analysis. Plant samples were obtained from non-evaporated branch
207 tissues and bark and phloem were removed in the field prior to sample storage.

208 Water extraction was performed by cryogenic vacuum distillation (Dawson and
209 Ehleringer, 1993) at the Department of Crop and Forest Sciences, Universitat de Lleida
210 (Spain). We placed the sample tubes in a heated silicone oil bath (120 °C) connected to a
211 vacuum system ($\sim 10^{-2}$ mbar) in series with the collector tubes, where the sample water was
212 trapped by liquid N_2 . After the extractions (2h for soil and 1.5h for xylem), we transferred the
213 trapped water into 2 ml vials that were stored at 4 °C until analysis. We tested that water
214 extraction was complete by weighing the samples immediately after distillation and then
215 again after oven-drying at 60 °C for 24 h. Over 90% of all samples gained $\sim 1\%$ weight during

216 drying, indicating that water extraction had been effective as they were dry enough to
217 rehydrate.

218 The isotope composition of the water samples was analyzed by Cavity Ring-Down
219 Spectroscopy (CRDS) in a Picarro L2120-i isotopic water analyzer (Picarro Inc., Sunnyvale,
220 CA, USA) at the Serveis Científico-Tècnics from the Universitat de Lleida (Lleida, Spain).
221 The samples were vaporized (in the Picarro A0211 vaporizer) and then passed through the
222 analyzer. We injected six replicates of 1 μl into the vaporizer, and used the last three for
223 calculations, as they showed homogeneous values that were independent from previous
224 samples (average within-sample standard deviation was 0.16‰ for $\delta^{18}\text{O}$ and 0.67‰ for $\delta^2\text{H}$).
225 We repeatedly analyzed four reference water samples and quantified the precision of the
226 L2120-i at 0.10‰ and 0.40‰, for $\delta^{18}\text{O}$ and $\delta^2\text{H}$, respectively. We express isotope
227 composition in per mil notation $\delta^{18}\text{O}$ and $\delta^2\text{H}$ relative to Vienna Standard Mean Ocean
228 Water. Residual organic compounds in the distilled water can interfere with the analysis of
229 plant and soil samples using CRDS, and we applied a post-processing correction as described
230 in (Martin-Gomez et al., 2015).

231

232 **2.3.2 Leaf water potential and stomatal conductance**

233 Leaf water potential (Ψ_{leaf}) and stomatal conductance (g_s) were measured on each of five
234 plants per species per campaign. On each sampling day, Ψ_{leaf} was measured at pre-dawn and
235 midday, which typically represent minimum and maximum periods of diurnal water potential
236 respectively. Leaves for Ψ_{leaf} were cut and then immediately sealed in a plastic bag inside a
237 cooler until measurements, which were performed within less than 15 minutes from
238 collection using a Scholander-type pressure chamber (PMS Instruments, Corvallis, OR,

239 USA). Stomatal conductance measurements were performed using a steady state porometer
240 (SC-1, Decagon Devices Inc, Pullman, WA, USA) in fully-expanded sun-facing leaves.

241

242 **2.3.3 Osmotic and elastic adjustments (pressure-volume curves)**

243 Pressure-volume curves were performed following Sack et al. (2011) on three plants per
244 species. **Shoots** were saturated before bench dehydration, and we sequentially measured Ψ_{leaf}
245 and leaf weight during dehydration. We calculated relative water content (RWC) as:

$$246 \text{ RWC} = \frac{F_W - D_W}{T_W - D_W} \times 100 \quad (2)$$

247 where F_W , D_W and T_W are the fresh, dry and turgid leaf weights respectively. RWC was
248 plotted against $1/\Psi_{\text{leaf}}$ and we calculated Ψ_{TLP} (osmotic potential at turgor loss point, where
249 the curve transitions from the linear to the curved portion), π (osmotic potential at maximum
250 turgor, the absolute inverse of y-intercept of the linear part of the curve), ε (the elasticity
251 modulus, the slope of the curve above Ψ_{TLP}) and saturated LFMC (calculated from the
252 intercept of the mass of leaf water with Ψ_{leaf} , and leaf dry mass). Saturated LFMC is more
253 commonly referred to as saturated water content and expressed as a proportion between 0-1,
254 for consistency, we refer to it here as saturated LFMC and present it in the same units (i.e.
255 %).

256

257 **2.4 Analyses**

258 All statistical analyses were undertaken in R 3.4.1. (R Development Core Team, 2017). The
259 relative contributions of source water to xylem water were assessed using a Bayesian isotope
260 mixing model. Simulations of contributions of source water (groundwater, shallow soil water,
261 deep soil water) to xylem water were generated using Markov chain Monte Carlo methods,

262 using the SIAR package (Parnell and Jackson, 2013) following Barbeta et al. (2015). We ran
263 500 000 iterations, and discarded the first 50 000. The mean contribution of each water
264 source was then calculated for each species and each sampling time. Differences in the
265 relative contributions of source water were then assessed using a two-factor ANOVA, with
266 sampling date and species as factors plus their interaction, and Tukey's honest significant
267 difference post-hoc tests.

268 Differences in LFMC, contributions of source water, predawn and midday Ψ_{leaf} , g_s
269 and pressure-volume curve parameters (Ψ_{TLP} , π , ε and saturated LFMC) between species were
270 assessed using a two-factor ANOVA, with sampling date and species as factors (plus their
271 interaction). Data were checked for normality and homogeneity of variance. If significant
272 differences were found, Tukey's honest significant difference *post-hoc* tests were performed.
273 Note, a repeated measures ANOVA was not considered appropriate as different plants were
274 selected during each sampling campaign (Quinn and Keough, 2002).

275 Relative similarities between the six species in LFMC dynamics and physiological
276 traits were assessed through a principal component analysis. The following traits were
277 included: minimum LFMC (measured on 5 September, 2017) and variation in LFMC over
278 time; the relative contributions of shallow soil water, deep soil water and groundwater to
279 xylem water at the time of minimum LFMC; predawn and midday Ψ_{leaf} and g_s at the time of
280 minimum LFMC; and each of the pressure-volume curve parameters during the time of
281 minimum LFMC. All trait data were scaled to have unit variance prior to the analysis.

282 To assess which of the plant physiological traits measured at the same time as LFMC
283 (i.e. all traits excluding the pressure-volume curves parameters) could be used to model
284 LFMC, we undertook a correlation analysis between all traits and LFMC across sampling
285 dates. Correlations were undertaken with species-level averages from each sampling period,
286 and Pearson's correlation coefficient (" R ") calculated. Traits which had a significant

287 correlation ($p < 0.05$) were then selected for multiple linear regression with LFMC. To avoid
288 problems with collinearity, for those traits which had a significant correlation with each other
289 ($R > 0.5$), the trait with the lower correlation with LFMC was excluded from the regression.
290 We also modelled LFMC as a function of drought indices commonly used for fuel moisture
291 and fire behaviour predictions: the Keetch-Byram drought index (KBDI; Keetch and Byram,
292 1968) and the drought code (DC) in the Canadian Forest Fire Weather Index system (Van
293 Wagner, 1987). We compared the performance of each of the LFMC models using Akaike's
294 information criterion (AIC) (Akaike, 1974).

295

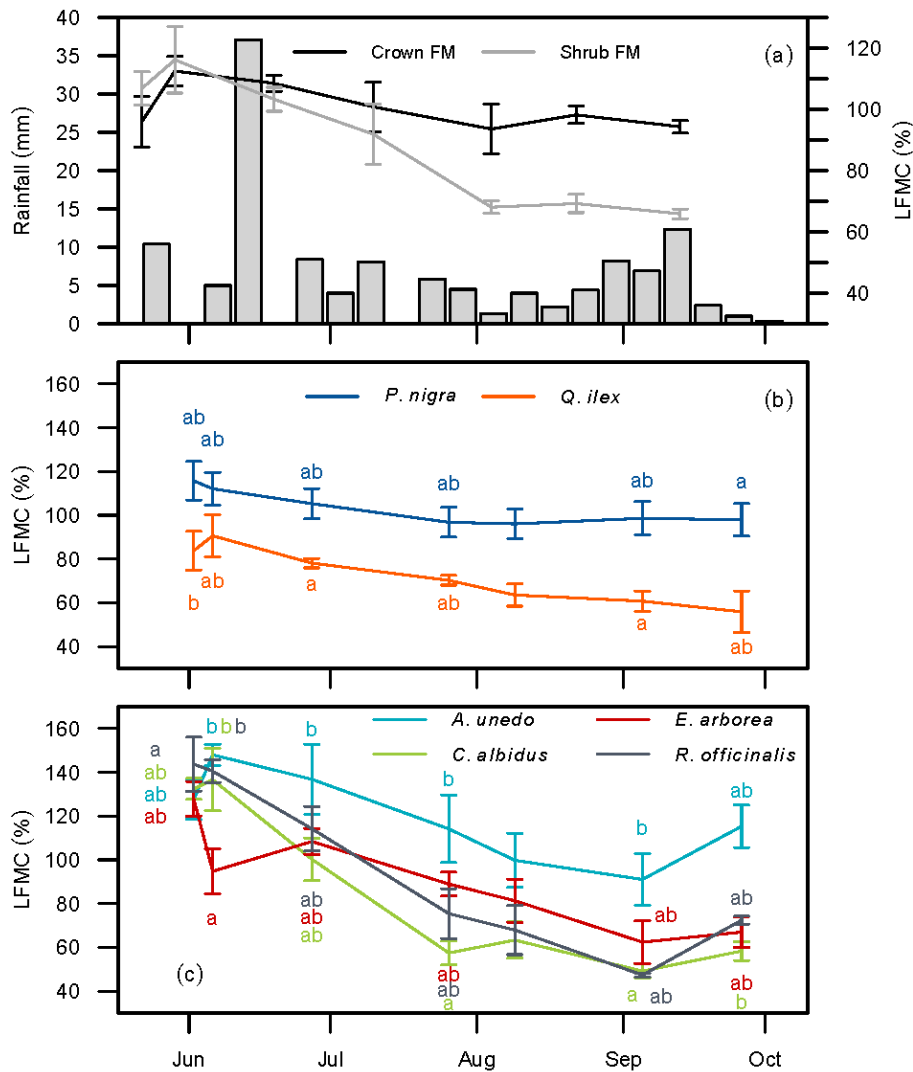
296 **3. Results**

297 **3.1 Fuel moisture dynamics**

298 LFMC in tree crown and shrub strata were highest at the start of summer, and lowest in late
299 summer and into early autumn (Fig. 1a). There were significant differences in LFMC
300 between species, with a significant interaction found between species and sampling date ($F_{30,}$
301 $_{166} = 2.8, p < 0.001$, Fig. 1b-c). Over time, *A. unedo* either had similar or significantly higher
302 LFMC than all other species ($p < 0.05$), ranging from 91-148%. The second highest LFMC
303 values were generally observed in *P. nigra*, ranging from 96-116%. The lowest LFMC was
304 observed in *Q. ilex* (56-91%), *C. albidus* (49-137%), *E. arborea* (62-128%) and *R. officinalis*
305 (47-144%).

306 Both tree species exhibited the smallest seasonal variation in LFMC values (35% for
307 *Q. ilex* and 20% for *P. nigra*). The shrubs all exhibited much larger variation in seasonal
308 LFMC, particularly *R. officinalis* (97%). These differences between shrub and tree species
309 resulted in crown LFMC exhibiting lower seasonal variation (94-113%) than shrub LFMC
310 (66-116%). We note that the 20-year database from Southern France (Duché et al. 2017) was

311 able to capture slightly lower LFMC values for the shrubs (~10% lower). This difference may
 312 be driven by more extreme conditions being captured in the 20-year dataset, and/or by
 313 differences in drying procedure (Matthews, 2010). At any rate, our sampling was able to
 314 capture a substantial portion of the variation in LFMC that has been previously documented
 315 to occur in these species (Table 1).

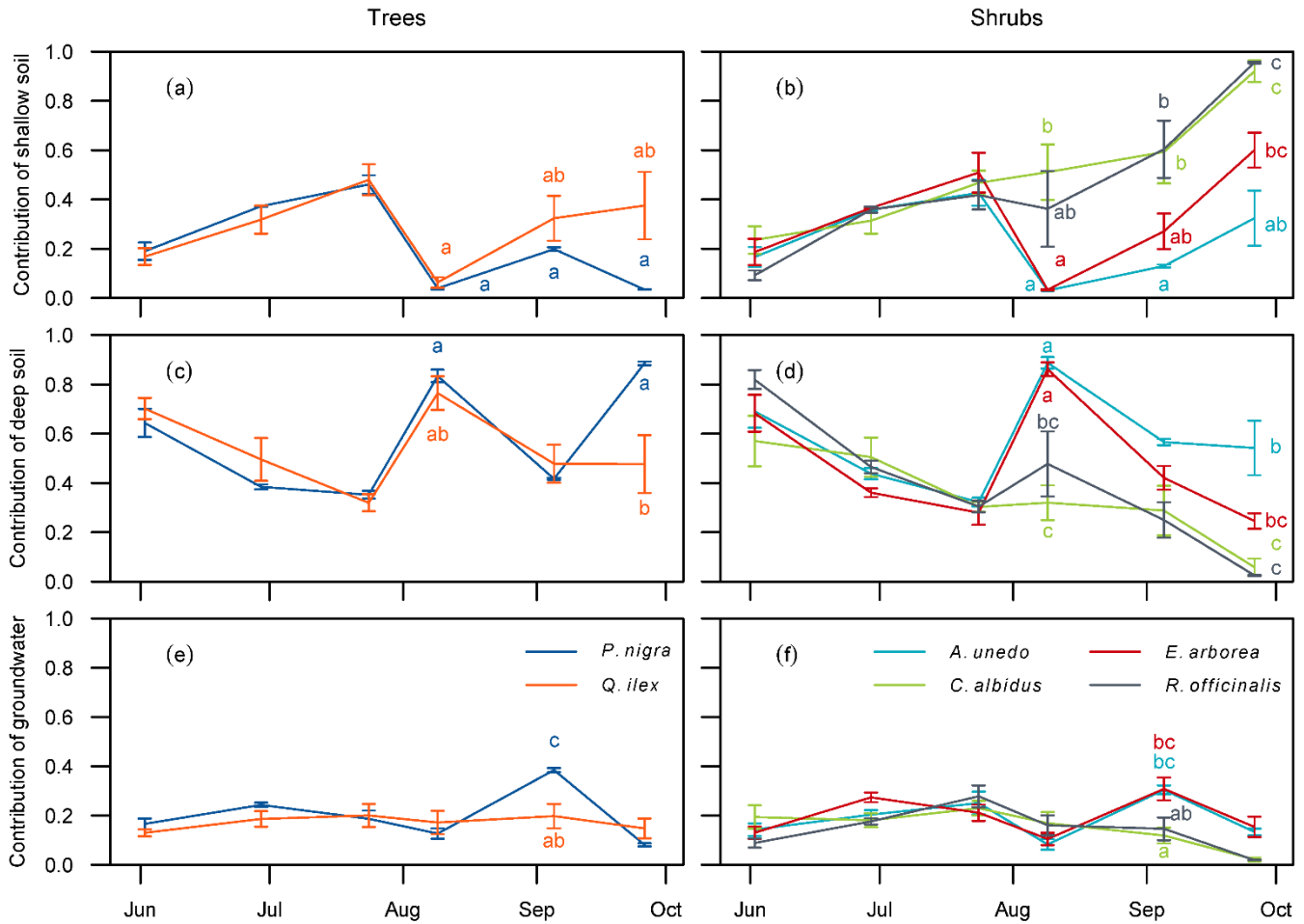


316
 317 **Fig. 1.** (a) Weekly rainfall and temporal trends in composite live fuel moisture content (LFMC) of trees and
 318 shrubs (b) LFMC of individual tree species and (c) LFMC of individual shrub species, ± 1 SE. For (b) and (c)
 319 differing letters above a sampling date indicate significant differences among species, for that sampling date (p
 320 < 0.05). Note, these significant differences refer to all six species sampled.

321

322 3.2 Access to water resources

323 Shallow and deep soil layers were the largest contributors of source water to plants, with
324 significant differences among species and over time (Fig. 2). There was a significant
325 interaction between species and sampling date for shallow soil water ($F_{25, 145} = 6.2, p$
326 <0.001), deep soil water ($F_{25, 145} = 7.2, p <0.001$) and groundwater ($F_{25, 145} = 3.4, p <0.001$).
327 Differences between species were only observed in late summer to early spring (August-
328 September), where there was a trend of increasing use of shallow soil water, in particular for
329 the shrubs *C. albidus* and *R. officinalis*, where shallow soil water contributed 92% and 96%
330 respectively to xylem water in late September (Fig. 2b). This is in contrast to *P. nigra*, where
331 shallow soil water only contributed 3% to xylem water during this period (Fig. 2a). Uptake of
332 groundwater resources was highest in early September, particularly for *P. nigra* (38%), *A.*
333 *unedo* (30%) and *E. arborea* (31%).



335 **Fig. 2.** Mean contributions of (a-b) shallow soil water, (c-d) deep soil water and (e-f) groundwater to plant
 336 xylem water, ± 1 SE. Differing letters above a sampling date indicate significant differences among species for
 337 that sampling date ($p < 0.05$). Note that these significant differences refer to all six species sampled.

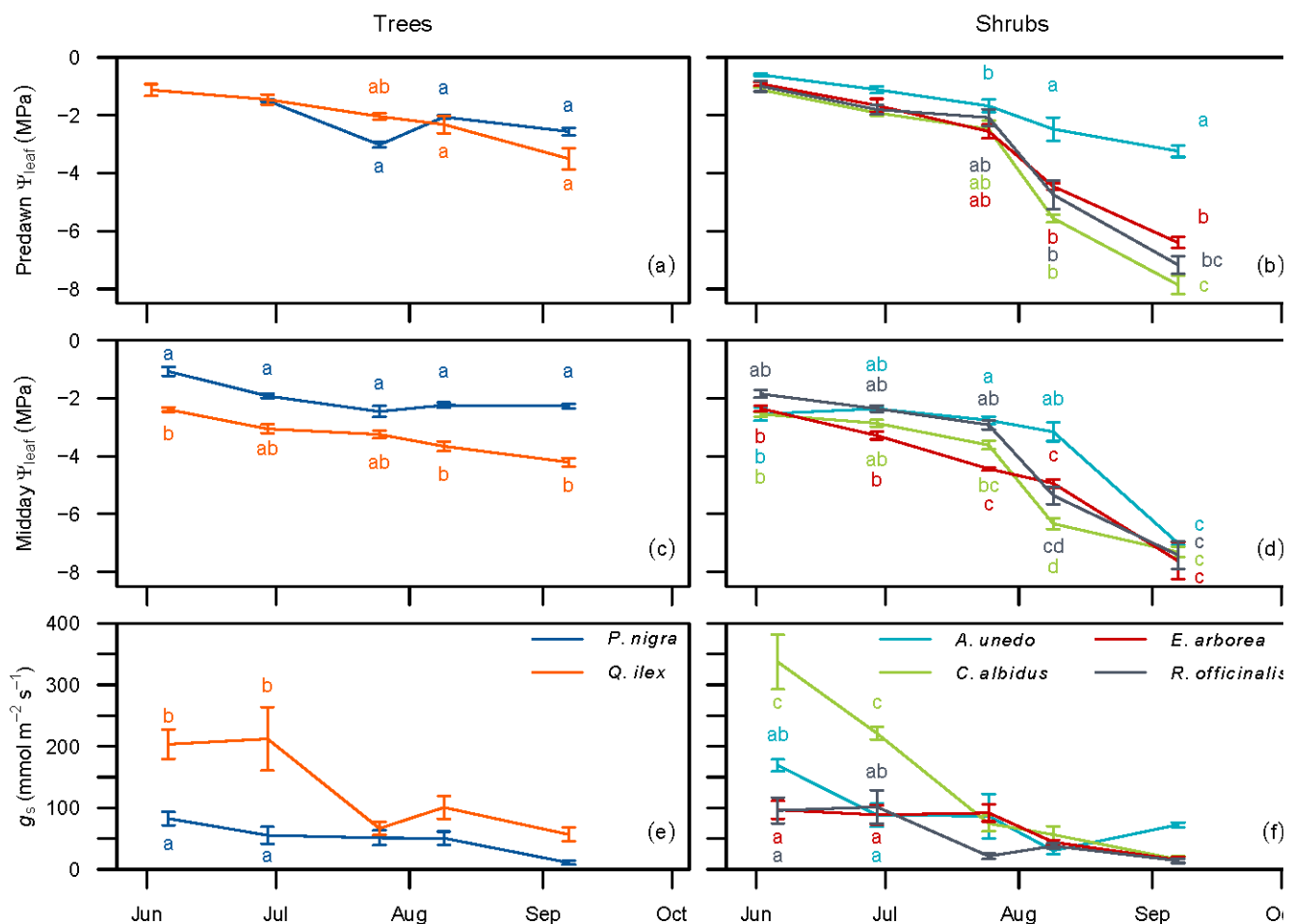
338

339 3.3 Leaf water potential and stomatal conductance

340 There were significant interactions between species and sampling date for predawn Ψ_{leaf} ($F_{19, 106} = 18.8, p < 0.001$),
 341 midday Ψ_{leaf} ($F_{20, 115} = 20.7, p < 0.001$) and g_s ($F_{20, 129} = 5.7, p < 0.001$).

342 Over time, the largest declines in predawn and midday Ψ_{leaf} were exhibited in the shrubs,
 343 compared to the trees (Fig. 3 a-d). Within the shrubs, there were no significant differences in
 344 minimum values of midday Ψ_{leaf} observed during the driest period (early September: -7.01 to
 345 -7.62 MPa). At this time, midday Ψ_{leaf} in *Q. ilex* was significantly higher (-4.21 MPa), and

346 midday Ψ_{leaf} in *P. nigra* was also significantly higher (-2.27 MPa). Despite these differences
 347 in Ψ_{leaf} , during this dry period there were no significant differences in g_s (Fig. 3e-f). There
 348 were however, differences in g_s during wet periods, with the largest g_s observed in one of the
 349 shrub species (*C. albidus*: 337.1 mmol m⁻² s⁻¹). Instrument malfunction prevented us from
 350 conducting water potential and stomatal conductance measurements during the last sampling
 351 period. Because the last sampling period occurred after the onset of the fall rains, with the
 352 consequent rise in saturated LFMFC for some species (see next section), it was not considered
 353 critical.



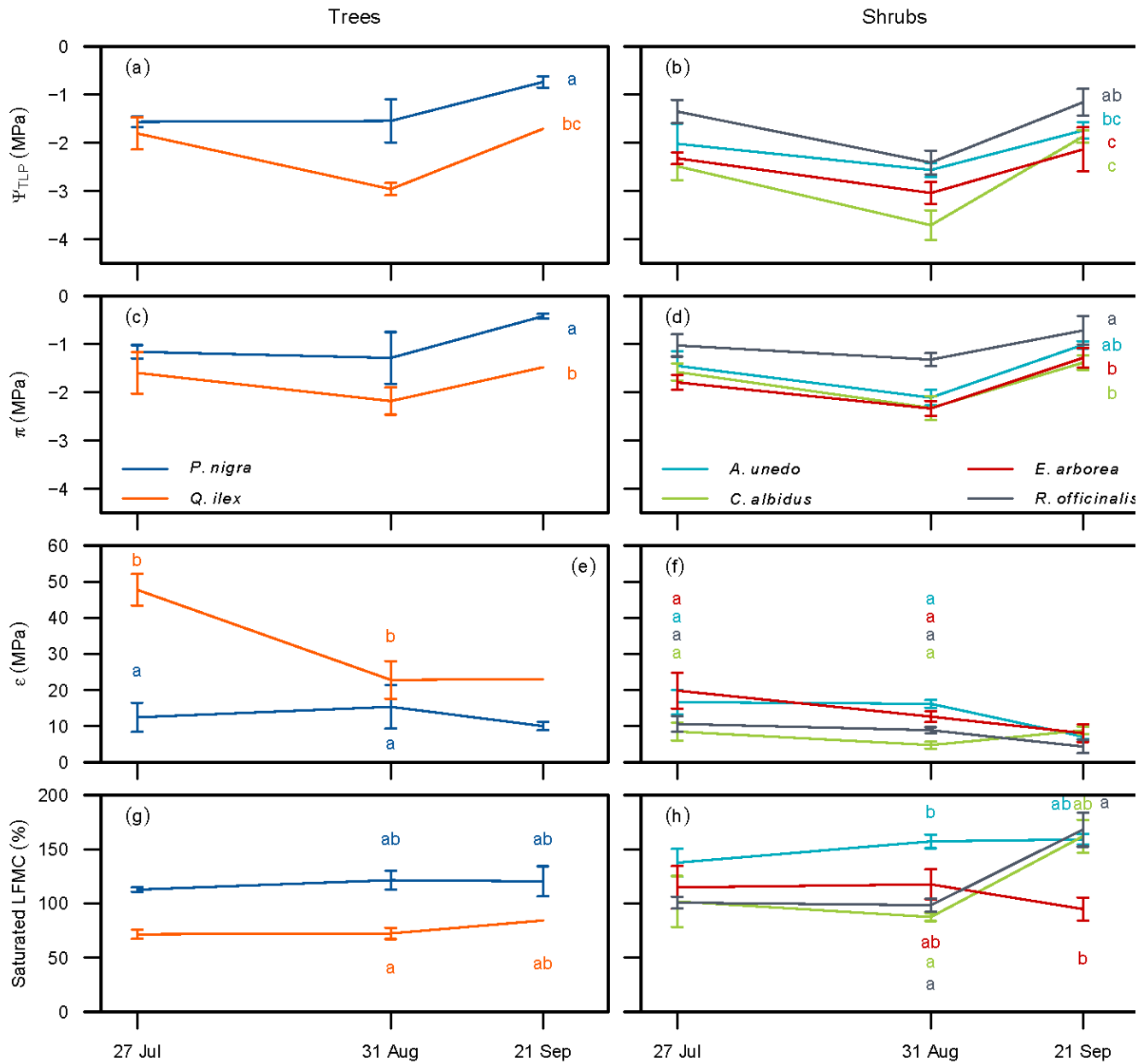
354
 355 **Fig. 3.** Mean predawn leaf water potential (Ψ_{leaf}) (a-b), midday Ψ_{leaf} (c-d) and stomatal conductance (g_s), ± 1 SE.
 356 Differing letters above a sampling date indicate significant differences among species, for that sampling date (p
 357 < 0.05). Note, these significant differences refer to all six species sampled.

358

359 **3.4 Osmotic and elastic adjustments (pressure-volume curves)**

360 There was a significant difference in Ψ_{TLP} among species ($F_{5,31} = 10.2, p < 0.001$) and over
361 time ($F_{2,31} = 24.1, p < 0.001$), with no interaction between species and time ($F_{10,31} = 1.0, p$
362 $= 0.482$). Across all sampling dates, the species with the highest Ψ_{TLP} were *P. nigra* (-1.6 to -
363 0.7 MPa) and *R. officinalis* (-2.4 to -1.2 MPa), and the species with the lowest Ψ_{TLP} were *C.*
364 *albidus* (-3.7 to -1.9 MPa) and *E. arborea* (-3.0 to -2.1 MPa; Figure 4a-b). Similarly, there
365 was a significant difference in π among species ($F_{5,31} = 6.8, p < 0.001$) and over time ($F_{2,31} =$
366 $17.6, p < 0.001$), with no interaction between species and time ($F_{10,31} = 0.4, p = 0.954$). Across
367 all sampling dates, the species with the highest π were *P. nigra* (-1.3 to -0.4 MPa) and *R.*
368 *officinalis* (-1.3 to -0.7 MPa), and the species with the lowest π were *C. albidus*, *E. arborea*
369 and *Q. ilex* (-2.3 to -1.3 MPa; Figure 4c-d).

370 There were significant interactions between species and sampling date for ϵ ($F_{10,31} =$
371 $2.8, p = 0.014$). Among species, the largest ϵ was observed in *Q. ilex* during the wet sampling
372 period (July 27: 47.7 MPa), ϵ then declined (to 22.8 MPa; Fig. 4e-f). **The values of ϵ for *Q.***
373 ***ilex* in late July were abnormally high for unknown reasons.** There were no further
374 differences in ϵ among species at any sampling time. There were significant interactions
375 between species and sampling date for saturated LFMC ($F_{10,31} = 3.1, p = 0.007$; Figure 4g-h).
376 The largest saturated LFMC tended to occur in *A. unedo* (138-159%) and *P. nigra* (113-
377 122%), with the lowest values in *Q. ilex* (72-84%) and *E. arborea* (95-118%). The remaining
378 two species showed relatively large seasonal variations in saturated LFMC: 88-162% for *C.*
379 *albidus* and 98-168% for *R. officinalis*, **with saturated LFMC increasing significantly**
380 **following spring rain in early September.**



381

382 **Fig. 4.** Mean turgor loss point (Ψ , a-b), osmotic potential at full turgor (π , c-d), bulk modulus of elasticity (ϵ , e-f)

383 and LFMC at saturation (g-h), ± 1 SE. Where there are letters above points (e-f), these indicate significant

384 differences between species for a given date. Where there are letters to the right (a-d), these indicate

385 significant differences between species across all sampling dates.

386

387

388

389 3.5 Principal component analysis

390 Two principal component axes accounted for the majority of the variation among species,
391 with axis one accounting for 57.3% and axis two accounting for 20.8% (Table 2). Axis one
392 had strong loadings for most of the 12 traits included in the analysis, except for π and g_s . The
393 strongest loadings for axis one were for predawn Ψ_{leaf} , the relative contribution of shallow soil
394 water to xylem water, minimum LFMC and seasonal variation in LFMC. For axis two, the
395 strongest loadings were for π , g_s and Ψ_{TLP} . Axis three (which contributed to 13.9% of
396 variance) had strong loadings for saturated LFMC, midday Ψ_{leaf} and ϵ . Along axis one *P.*
397 *nigra* was most dissimilar to *C. albidus* and *R. officinalis*, while along axis two, *P. nigra* was
398 most dissimilar to *A. unedo* and *Q. ilex* (Fig. 5).

399

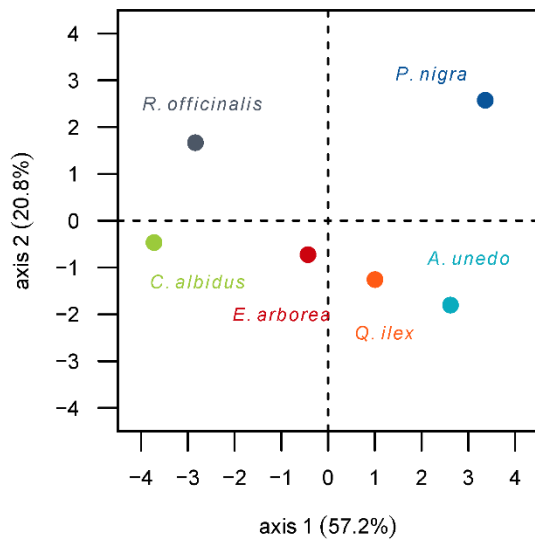
400 **Table 2.** Loading scores (correlations) of traits in the principal component analysis among six species. Traits are
 401 arranged in descending order of their loading on component 1.
 402 Abbreviations: Ψ_{leaf} (leaf water potential), LFMC (live fuel moisture content), ϵ (bulk modulus of elasticity), Ψ_{TLP}
 403 (turgor loss point), g_s (stomatal conductance), π (osmotic potential at full turgor).

Variable	Component 1 (57.3% of variance)	Component 2 (20.8% of variance)	Component 3 (13.9% of variance)
Predawn Ψ_{leaf}	-0.37	0.00	-0.15
Contribution of shallow soil water	0.36	0.15	-0.14
Minimum LFMC	-0.34	0.08	0.28
Variation in LFMC	0.34	-0.06	0.29
Contribution of groundwater	-0.33	0.11	0.24
Contribution of deep soil water	-0.32	-0.35	0.03
ϵ	-0.29	-0.17	-0.38
Ψ_{TLP}	-0.26	0.43	0.08
Midday Ψ_{leaf}	-0.26	0.28	-0.42
Saturated LFMC	-0.21	-0.06	0.63
g_s	-0.18	-0.46	-0.07
π	-0.07	0.57	0.03

404

405

406



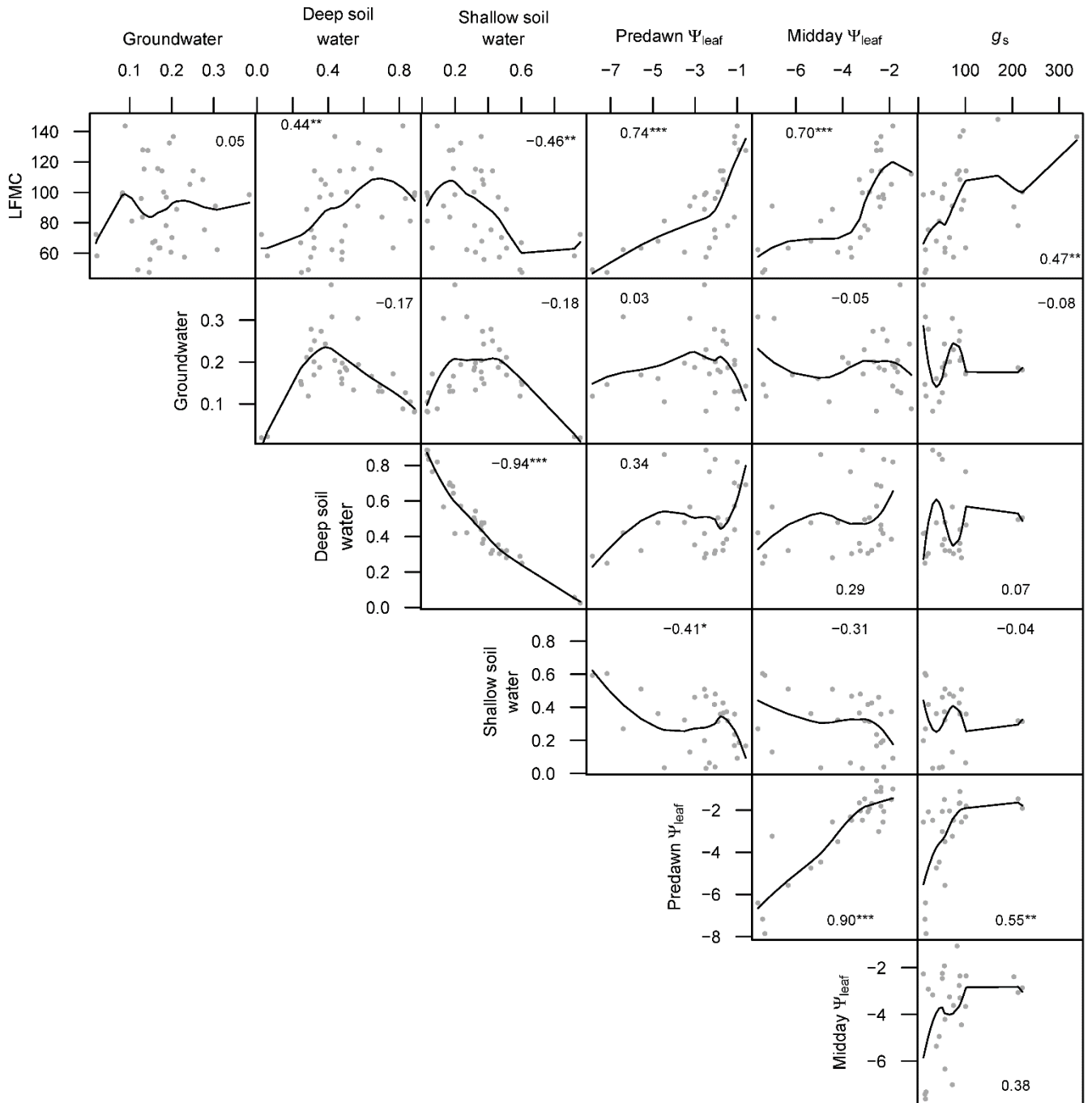
407

408 **Fig. 5.** Principal component analysis of twelve traits, incorporating live fuel moisture content, access to water,
409 and ecophysiological traits for six species.

410

411 3.6 Developing a physiologically based LFMC model

412 Correlation analysis revealed that five of the six continuously measured traits (i.e. excluding
413 pressure-volume curve parameters) were significantly correlated with LFMC ($p < 0.05$; Fig.
414 6). The only trait not significantly correlated with LFMC was the relative contribution of
415 groundwater to xylem water. Of the five traits significantly correlated with LFMC, there was
416 significant collinearity ($R > 0.5$) among many of the traits. Excluding traits with significant
417 collinearity (and retaining the trait with the highest correlation with LFMC) left two traits for
418 developing a physiologically based LFMC model. These were predawn Ψ_{leaf} and the relative
419 contribution of shallow soil water to xylem water.



420

421 **Fig. 6.** Correlation matrix of LFMF and ecophysiological traits measured through time. Stars represent level of
 422 significance of the correlations (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$)

423

424 Linear and multiple linear regressions of these two traits against LFMF resulted in
 425 significant models for all combinations of the traits ($p < 0.05$, Table 3). Of these models, the
 426 linear regression of predawn Ψ_{leaf} (log-10 transformed) had the lowest AIC (249) and highest

427 adj. R^2 (0.63; Fig. 7a). Linear regression of the drought indices (KBDI and the drought code)
 428 against LFMC resulted in a poorer fit than the leaf water potential model (Table 3; AIC = 258
 429 and adj. $R^2 = 0.49$ for both models; Fig. 7b-c).

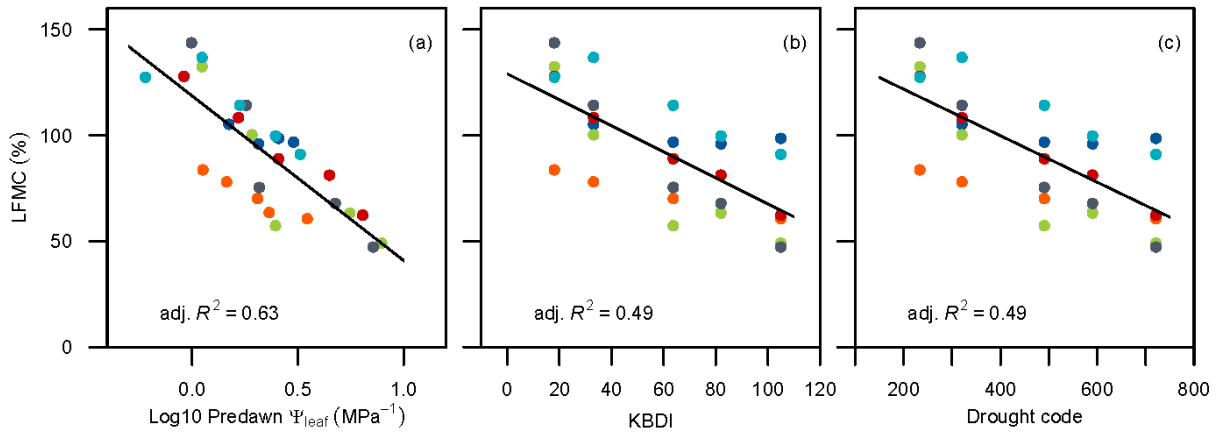
430

431 **Table 3.** Summary of LFMC models developed using physiological traits and drought indices (the Keetch-Byram
 432 Drought Index, KBDI, and the drought code in the Canadian Forest Fire Weather Index system).

Model	adj. R^2	P	AIC
LFMC = 118.76 -77.86 log ₁₀ (- Ψ_{leaf})	0.63	<0.001	249
LFMC = 122.68 -73.80 log ₁₀ (- Ψ_{leaf}) -17.58(shallow soil water)	0.62	<0.001	250
LFMC = 108.27 -54.89(shallow soil water)	0.19	0.005	335
LFMC = 125.08 -0.61(KBDI)	0.49	<0.001	258
LFMC = 143.82 -0.11(Drought code)	0.49	<0.001	258

433

434



435

436 **Fig. 7.** Linear regression of seasonal live fuel moisture content (LFMC) as a function of (a) predawn leaf water
 437 potential (Ψ_{leaf}), (b) the Keetch-Byram drought index (KBDI) and (c) the drought code in the Canadian Forest
 438 Fire Weather Index system. Different colours represent different species, as in previous figures. Data represent
 439 mean values of five plants at each of five sampling times.

440

441 **4. Discussion**

442 Both seasonal variation and minimum values of LFMC were clearly a function of plant
 443 physiology in this Mediterranean forest ecosystem. We observed that (i) those species with
 444 the lowest minimum LFMC and largest seasonal variation in LFMC (*C. albidus* and *R.*
 445 *officinalis*) were most reliant on shallow soil water (Fig. 2) and had the lowest values of
 446 predawn Ψ_{leaf} (Fig. 3); and (ii) species with the smallest variation in LFMC (*P. nigra* and *Q.*
 447 *ilex*) exhibited relatively less variation in Ψ_{leaf} than co-occurring species (Fig. 4). Of the
 448 physiological traits measured, predawn Ψ_{leaf} provided the strongest predictor of LFMC,
 449 outperforming two drought indices commonly used in LFMC modelling (Table 3, Fig. 7). **We**
 450 **have known for decades that Ψ_{leaf} and RWC are strongly related within one species**
 451 **(Scholander et al. 1965), but with important differences occurring across species (Bartlett et**
 452 **al. 2012, Ramírez et al. 2012). It is thus remarkable that a single regression line between**
 453 **predawn Ψ_{leaf} and LFMC across six different species, belonging to highly contrasting**

454 functional and phylogenetic groups, already improved LFMC predictions beyond current
455 approaches based on fire danger indices. Further research will be necessary to understand the
456 generality of this claim, and we expect additional improvements in prediction may occur after
457 considering species-specific responses. Overall, our findings demonstrate the importance of
458 plant traits in driving LFMC dynamics and the potential for incorporating an eco-
459 physiological approach to investigating forest flammability and live fuel moisture content.

460

461 **4.1 What drives differences in live fuel moisture content dynamics in co-occurring** 462 **species?**

463 There are three inter-related physiological processes that we hypothesised would contribute
464 to varying LFMC dynamics in co-occurring species: (i) differential access to soil water pools,
465 (ii) stomatal sensitivity to water stress; and (iii) osmotic and elastic adjustments that take
466 place in cells, leading to different water storage capacities. Our results provide support for all
467 three hypotheses, which we now discuss in detail.

468 The pattern of access to soil water resources was similar across plant species until
469 August, but important differences arose after that date. For the obligate seeding shrub species,
470 *C. albidus* and *R. officinalis*, there was greater reliance on shallow soil moisture during
471 periods of water stress compared to tree species (Fig. 2). We note that the apparent increasing
472 reliance of shrubs on shallow soil water towards the end of the dry season, may be an artefact
473 of isotopic enrichment due to declines in transpiration, and may not represent increased
474 access to shallow soil water (Martin-Gomez et al., 2017). However, the large seasonal
475 variability in LFMC and predawn Ψ_{leaf} observed in the shrub species is consistent with a large
476 reliance on shallow soil water. Further, these results are consistent with previous LFMC
477 observations in the Mediterranean Basin, where shrubs were observed to be more responsive

478 to seasonal dryness than trees (Viegas et al., 2001). For the tree species studied here, there
479 was relatively little seasonal variation in LFMC and this was coincident with a relatively
480 larger dependence on deep soil water. Finally, the resprouting shrub species, *A. unedo* and *E.*
481 *arborea*, showed a dependence on shallow and deep water intermediate between that of the
482 obligate seeder shrubs and the trees. The resprouting shrubs also exhibited an intermediate
483 level of seasonal variation in LFMC (Fig. 2).

484 The time at which water extraction patterns began to diverge across species (August)
485 was coincident with marked declines in predawn Ψ_{leaf} . Those species which exhibited a large
486 degree of variation in LFMC (shrubs), also exhibited a large degree of variation in Ψ_{leaf} .
487 Changes in water availability also triggered differences in g_s among species. Across species
488 g_s declined as Ψ_{leaf} declined (Fig. 3), indicating close connection between Ψ_{leaf} and g_s . For *Q.*
489 *ilex*, there were only small declines in Ψ_{leaf} and LFMC following a large decline in g_s (from
490 212 to 57 mmol m⁻² s⁻¹). For the shrubs, large declines in Ψ_{leaf} and LFMC were still
491 observed following g_s approaching zero (from mid-August to September). Continued declines
492 in Ψ_{leaf} may have been due to stomatal leakiness and/or cuticular conductance (Blackman et
493 al., 2016, Martin-StPaul et al., 2017a). During drought periods Ψ_{leaf} is also likely to be
494 affected by xylem cavitation, in addition to stomatal and cuticular conductance. For species
495 with high vulnerability to cavitation, water supply to foliage may be disrupted earlier during
496 drought (Choat et al., 2018), resulting in faster declines in LFMC. However, most species
497 operate close to their hydraulic safety margins and may therefore be at similar risk of
498 cavitation during drought (Choat et al., 2012). This is likely to be the case for the
499 Mediterranean species studied here, with the trees exhibiting higher (less negative) values of
500 minimum Ψ_{leaf} compared to the shrubs (Fig. 3c-d), and also generally exhibiting greater
501 vulnerability to cavitation (Martin-StPaul et al., 2017a; Martin-StPaul et al., 2017b; Lens et

502 al., 2016). Leaf shedding strategies will also affect the moisture content of foliage (Choat et
503 al., 2018) and the occurrence of dead fine fuels.

504 Differences in cell wall elasticity may also account for the different amplitudes of
505 LFMC observed among species. High cell wall elasticity (i.e. low bulk modulus of elasticity)
506 likely plays a role in preventing cell dehydration during drought (Bartlett et al., 2012). This is
507 consistent with our observations of high cell wall elasticity in those species with large
508 seasonal variation in LFMC, and low cell wall elasticity in *Q. ilex*, which had low seasonal
509 variation in LFMC (Fig. 4e-f). The low LFMC observed in *Q. ilex* is likely a function of low
510 saturated LFMC (72-84%), particularly in comparison to *A. unedo* (138-159%), although
511 these differences were not significant. Leaf water storage has not been well studied compared
512 to stem water storage, but is important in maintaining water supply to meet transpiration
513 demand during periods of water stress (Himeno et al., 2017). Thus, the larger saturated
514 LFMC of *A. unedo* foliage may particularly benefit this anisohydric species in maintaining
515 water supply for transpiration during seasonal dry periods, which is not required for the
516 relatively isohydric *Q. ilex*. The significant increase in saturated LFMC for the two obligate
517 seeding shrubs (*C. albidus* and *R. officinalis*) at the end of the dry season (Figure 4h) may
518 have been a consequence of new shoot production. Thus, understanding shoot phenology and
519 the timing of the production of new shoots could also affect LFMC (Fares et al. 2017).

520 The seasonal changes in saturated LFMC observed here (Fig. 4g-h) may also
521 contribute to differing relationships between LFMC and soil moisture content. In a study of
522 Mediterranean Basin species, including four of the species studied here, Viegas et al. (2001)
523 observed a different relationship between LFMC and the drought code during phases of soil
524 wetting and drying. This is consistent with our results of larger saturated LFMC values at the
525 end of the dry season.

526

527 **4.2 Importance of plant functional type and ecological response to disturbance**

528 Among species, the largest differences in LFMC were due to plant functional type,
529 specifically, tree species had less seasonal variation in moisture content compared to shrub
530 species (Fig. 1). Within tree species, ecological response to disturbance, i.e. whether the
531 species was a resprouter or obligate seeder, did not affect seasonal variation in LFMC, with
532 both species exhibiting similarly low variability (20 and 35%). However, within shrub
533 species there was a trend of resprouting species exhibiting less variability (57 and 66%) in
534 LFMC than the obligate seeders (88 and 97%). These differences are consistent with previous
535 observations in the Mediterranean Basin, where relative water content was higher in
536 resprouting species, suggesting greater water supply to resprouters compared to obligate
537 seeders (Saura-Mas and Lloret, 2007). Importantly, these differences in LFMC variability did
538 not translate to significant differences in minimum LFMC between resprouting and obligate
539 seeding shrub species (Fig. 1c).

540

541 **4.3 Can plant physiological traits be incorporated into models of live fuel moisture** 542 **content?**

543 Our results clearly demonstrate that LFMC dynamics are not just a function of rainfall, with
544 plant structural and physiological traits also affecting LFMC. In particular, we found that
545 predawn Ψ_{leaf} provides a strong predictor of LFMC dynamics, **as expected from the tight**
546 **curvilinear relationship between Ψ_{leaf} and relative water content (Tyree and Hammel, 1972).**
547 Predawn Ψ_{leaf} generally reflects differences in root water potential, and hence soil water
548 potential close to the roots (Hinckley et al., 1978). Thus, there is a mechanistic basis for why
549 predawn Ψ_{leaf} would provide a better predictor of LFMC than drought indices, which do not
550 account for gradients in moisture content with depth, and cannot account for differences in

551 rooting depth between co-occurring species. We note that comparing the predictive
552 performance of Ψ_{leaf} against that of drought indices as performed here is not a fair
553 comparison because, while Ψ_{leaf} was measured *in situ*, data for drought indices came from a
554 meteorological station that was 5 km away. However, the correlations that we obtained
555 between drought indices and LFMC are similar to those in other studies where both datasets
556 were collected concurrently (Viegas et al., 2001). Thus, the correlations obtained here
557 between Ψ_{leaf} and LFMC are higher than those obtained between drought indices and LFMC
558 here or elsewhere (Castro et al., 2003; Dimitrskopoulos and Bemmerzouk, 2003; Pellizzaro et
559 al., 2007; Viegas et al., 2001).

560 Pre-dawn Ψ_{leaf} is co-ordinated with many of the plant traits that influence LFMC,
561 including midday Ψ_{leaf} and stomatal conductance (Fig. 6). Thus, we suggest that predawn
562 Ψ_{leaf} may provide improved predictions of LFMC than currently applied drought indices (e.g.
563 the KBDI and drought code). The development of a single model of LFMC as a function of
564 Ψ_{leaf} is desirable, because it avoids the need for species-specific calibration. However,
565 incorporating inter-specific differences has the potential to improve LFMC predictions even
566 further. In the Mediterranean species studied here we found that all species except *Q. ilex*
567 exhibited statistically similar relationships between pre-dawn Ψ_{leaf} and LFMC (see
568 supplementary material). For *Q. ilex* the elevation of this regression was significantly lower,
569 i.e. for a given value of Ψ_{leaf} , LFMC was lower. As previously discussed, the lower LFMC of
570 *Q. ilex* is likely a function of the lower saturated LFMC in this species. Leaf water potential
571 is relatively quick to measure (minutes) in comparison to the time required for empirical
572 LFMC measurements (48 hours), and may thus provide a useful tool for assessing fuel
573 moisture content at small spatial scales, e.g. for management burns. Measuring Ψ_{leaf} at
574 midday is more practical than at predawn, for instance, when one wants to get a quick
575 estimate of LFMC before conducting a prescribed burn. However, for the purpose of

576 regional/continental LFMC modelling, predawn Ψ_{leaf} is desirable because, in principle, it is
577 affected by less parameters than midday water potential and, consequently, it is easier to
578 model.

579 We note that predawn Ψ_{leaf} is not solely a physiological trait *per se*. As noted above, it
580 reflects the availability of water in the rhizosphere in the absence of significant nocturnal
581 transpiration (Hinckley et al., 1978). Consequently, predawn Ψ_{leaf} results from the interaction
582 between soil water availability at different depths and the root profile. The development of
583 regional predictions in LFMC based upon predawn Ψ_{leaf} would thus depend on coupling a
584 soil water balance model with information on rooting depths. There are more simplistic
585 approaches that rely on incorporating climatic variables such as precipitation and potential
586 evapotranspiration (Taylor et al., 2012). Further developments on regional predictions of
587 predawn Ψ_{leaf} should thus be at the forefront of our research efforts to render superior LFMC
588 modelling.

589

590 **4.4 Conclusions**

591 We suggest that incorporating plant physiological parameters into LFMC modelling provides
592 a way forward for improving estimates of LFMC. Here, we demonstrate that a simple
593 parameter, predawn leaf water potential, can provide improved estimates of LFMC that
594 account for the differing responses of co-occurring species to drought. Further investigation
595 of the use of predawn leaf water potential, or other plant traits, in modelling LFMC is
596 warranted. A challenge in developing a universal model of LFMC based on predawn leaf
597 water potential will be accounting for differing rooting patterns between co-occurring
598 species, particularly in ecosystems with deep soils. A further challenge is that not all species

599 maintain an equilibrium between pre-dawn and soil water potential, with solute accumulation
600 in the leaf and nocturnal transpiration modifying this relationship (Donovan et al., 2001).

601

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609

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