



Physiological drought responses improve predictions of live fuel moisture dynamics in a Mediterranean forest



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ABSTRACT

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

1. Introduction

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

Forest fuels consist of both dead and live plant material. Dead fuels, particularly fine fuels (with a diameter < 25.4 mm), respond rapidly to atmospheric conditions and can be modelled from inputs such as

temperature, humidity or vapour pressure deficit (Matthews, 2013; Resco de Dios et al., 2015). In contrast, live fuel moisture content (LFMC) can be much more difficult to model because moisture content is a function of plant physiological and structural traits, which can differ markedly across species (Jolly and Johnson, 2018; Karavani et al., 2018). For example, some tree and shrub species from Mediterranean environments exhibit little seasonal variation in LFMC, while the LFMC of other co-occurring species can vary by as much as a factor of 6 (Pellizzaro et al., 2007; Soler Martin et al., 2017; Viegas et al., 2001). Current approaches for estimating LFMC focus on either modelling moisture content from drought indices, or modelling moisture content with remotely sensed data (Viegas et al., 2001; Yebra et al., 2013). However, drought indices can be difficult to apply because they do not capture the differing responses to drought across co-occurring

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species, and current remote sensing approaches cannot be used for forecasting LFMC. An eco-physiological approach to investigating LFMC dynamics may overcome these limitations and lead to improved modelling (Jolly and Johnson, 2018).

There are at least three different but mutually inter-related physiological processes that might explain why leaf moisture varies differentially across species. One of them is access to water resources, a function of rooting patterns and water availability in the soil profile that, in turn, appears to be related to the post-fire regeneration strategy. For example, species that can resprout following high intensity fire typically have greater allocation to roots and deeper root systems than species lacking this capacity (Bell et al., 1996; Verdu, 2000; del Castillo et al., 2016). As a consequence, resprouting species often maintain greater water supply to foliage during dry periods than obligate seeding species (which are fire-killed but regenerate via seed) (Saura-Mas and Lloret, 2007).

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

The relationship between Ψ_{leaf} and relative water content (and thus LFMC) can change through time due to osmotic adjustment (Sinclair, 1980). Thus, the third mechanism potentially explaining inter-specific differences in live fuel moisture content are the series of osmotic and elastic adjustments that take place in cells, which lead to differences in turgor loss point and water storage capacities. As relative water content declines, the inverse of Ψ_{leaf} declines following a curvilinear function until the point at which cell turgor is lost (the ‘turgor loss point’, Ψ_{TLP} ; Tyree and Hammel (1972)). Below the Ψ_{TLP} , the inverse of Ψ_{leaf} potential declines linearly with further declines in relative water content (Tyree and Hammel, 1972). Thus, the Ψ_{TLP} is a key parameter affecting the relationship between leaf moisture status and Ψ_{leaf} . As drought stress increases, the turgor loss point may be altered by (i) increasing the concentration of solutes in the vacuole to increase π , the osmotic potential at full turgor; (ii) increasing the elasticity of the cell walls to avoid collapse under turgor loss (decrease of ϵ , the elasticity modulus); or (iii) redistributing the symplastic water outside of the cell walls towards apoplastic water (Bartlett et al., 2012). The point at which cell turgor is lost (the ‘turgor loss point’, Ψ_{TLP}) is an important eco-physiological parameter and is co-ordinated with declines in stomatal conductance of 50% (Brodribb and Holbrook, 2003). There is also increasing evidence that the turgor loss point is co-ordinated with access to soil water resources, being higher (less negative) in species with greater access to water (Bartlett et al., 2012). ϵ and π are both related to changes in LFMC although the latter is considered the main driver of Ψ_{TLP} , and, consequently, more related to drought tolerance (Bartlett et al., 2012).

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

extent. We argue that linking plant physiology with LFMC dynamics is important because a mechanistic understanding of leaf moisture dynamics may lead to enhanced LFMC forecasting capabilities.

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

2. Methods

2.1. Study area

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

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

2.2. Fuel moisture dynamics

All fuel moisture measurements were undertaken over one full fire season, from late spring (May) to early autumn (September) in 2017.

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