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# Functional Ecology

## Effects of plant hydraulic traits on the flammability of live fine canopy fuels

Scarff<sup>1,2</sup>, F. R., Lenz<sup>2</sup>, T., Richards<sup>2,3</sup>, A. E., Zanne<sup>4</sup>, A. E., Wright<sup>2</sup>, I. J. , and Westoby<sup>2</sup>, M.

<sup>1</sup> Corresponding author. 12 Halse Cres Melville, WA 6156 Australia.  
fiona.scarff.4@gmail.com

<sup>2</sup> Department of Biological Sciences, Macquarie University, NSW 2109 Sydney Australia.

<sup>3</sup> Current address: CSIRO Land and Water, 564 Vanderlin Drive, Berrimah, Northern Territory 0822, Australia.

<sup>4</sup> Current address: Department of Biological Sciences, George Washington University, Washington, DC 20052, USA.

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### Authors' contributions

FRS and MW conceived the idea of using hydraulic trait data to model ignition time in live fuels;  
methodology was designed by FRS (for modelling moisture content and ignition time) and by TL, IJW and AEZ (for measuring hydraulic traits);  
TL, AER and IJW collected the data;  
FRS, TL and AER analysed the data;  
FRS led the writing of the manuscript.  
All authors contributed critically to the drafts and gave final approval for publication.

### Data availability

Supporting data are archived in the Dryad Digital Repository (Scarff *et al.* 2021), available at <https://doi.org/10.5061/dryad.6hdr7sr00>. Previously archived material relating to hydraulic physiology of twigs can be found at <http://doi.org/10.5061/dryad.hm482> (Richards *et al.* 2014).

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DR FIONA RANI SCARFF (Orcid ID : 0000-0003-0039-3871)

DR IAN WRIGHT (Orcid ID : 0000-0001-8338-9143)

PROFESSOR MARK WESTOBY (Orcid ID : 0000-0001-7690-4530)

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## Effects of plant hydraulic traits on the flammability of live fine canopy fuels

### Abstract

1. Plant species vary in how they regulate moisture and this has implications for their flammability during wildfires. We explored how fuel moisture is shaped by variation within six hydraulic traits: saturated moisture content, cell wall rigidity, cell solute potential, symplastic water fraction and tissue capacitance.
2. Using pressure-volume curves, we measured these hydraulic traits in twigs and distal shoots (*i.e.* twigs + leaves) in 62 plant species across four wooded communities in south-eastern Australia. Moisture content of fine fuels was then estimated for circumstances typical of fire weather. These projections were made assuming that under the hot, dry, windy conditions typical of large wildfires, leaves and fine twigs would function at internal water pressures close to wilting point (*i.e.* turgor loss point, TLP). The effect of different moisture contents at TLP on ignition time was then modelled using a fully mechanistic, finite element model of biomass ignition based on standard principles of physical chemistry.
3. We also measured predawn water potential, an indication of plant access to soil water that is influenced by root architecture. These data were used to model how root traits influence fuel moisture and ignition time.
4. Most variation among species in fuel moisture under fire weather conditions arose from differences in saturated moisture content (3.4–3.6-fold variation). Twig capacitance was

also an important driver of fuel moisture under these weather conditions (1.9–2.2-fold variation in moisture content). A suite of other leaf and root traits influencing how much shoots dry out as they approach wilting point each contributed 1.0–1.6-fold variation in projected fuel moisture during fire weather. Fuel moisture variation in turn drove variation in flammability by modifying predicted ignition time.

5. Two main life-history types in fire-prone habitats are obligate seeders and resprouters. There were no significant differences between these species-groups in estimated fuel moisture during fire weather, nor in any measured hydraulic traits.
6. Live fuel moisture is an important determinant of wildfire activity. Our data show that variation in tissue saturated moisture content amongst co-occurring species represents an important ecological store of variation in flammability in the study communities.

### **Keywords**

Live fuel moisture content, fuel modelling, turgor loss point, pressure-volume curve, capacitance, flammability, ignition time, wildfire.

### **Introduction**

Wildfire has pervasive effects on the structure and species composition of plant communities and at a global scale contributes substantially to atmospheric carbon fluxes (Bond & Midgely 1995; De Bano, Neary & Ffolliot 1998; Randerson *et al.* 2005). Plant material burns most readily when dry and, in many vegetation types prone to crown fire, there is little dead fuel in the canopies of trees or shrubs. In these situations, combustion of crowns depends on the burning of live fuels. Fuel moisture then reflects a spectrum of plant strategies for managing water balance in the face of shifting soil and atmospheric conditions (Ackerley 2004; Skelton, West & Dawson 2015).

Understanding these dynamics requires a link to be drawn between fire science and plant hydraulic ecophysiology (Jolly & Johnson 2018; Nolan *et al.* 2020). Developing this link offers the opportunity to predict fuel moisture, and its relationship with wildfire, across species, at large scales and in respect of novel climatic circumstances (Nolan *et al.* 2020).

### ***Influence of live fuel moisture on fire***

Evidence for whether live fuel moisture influences fire varies with scale and the response variable under consideration. At the level of physical chemistry, water in live fuels is expected to impede combustion. Moisture absorbs energy in its heating and vaporisation that could otherwise have contributed to heating solid fuels (Drysdale 1998; Sullivan 2017). More gradual heating favours decomposition pathways that lead to charring, rather than producing tars that can burn in a flame (Nelson 2001). Inside the flame, vaporised moisture also dilutes reactions and increases thermal capacity, causing the flame to cool (Grant & Drysdale 1997). In addition, there is an effect on flame emissivity (Sullivan 2017). The influence of moisture on ignition times of live fuels is well established in laboratory experiments (White & Zipperer 2010).

Evidence supporting an effect on spread rates in field-scale experimental burns has, however, been lacking (Alexander & Cruz 2013). This dearth has led to discussion about whether live fuel moisture is simply not an important predictor (of spread rate) in fires at that scale, or whether the power to detect these effects in costly field experiments is constrained by sample size, the range of moisture contents investigated and temporal correlation of live and dead fuel moistures (Alexander & Cruz 2013; Pimont *et al.* 2019). Another perspective is that low fuel moisture is a necessary but not sufficient condition for rapid fire spread (Nolan *et al.* 2020). Meanwhile, recent progress in remote sensing of vegetation moisture has furnished mounting evidence of the importance of live fuel moisture in determining burned area at a landscape or regional scale (Yebera *et al.* 2013; Pimont *et al.* 2019). This relationship with landscape- and regional-scale fire activity is supported by comparison of wildfire records with databased field measurements of live fuel moisture (Martin-StPaul *et al.* 2018a; 2018b). Burned area would appear implicitly related to spread rates, since wildfires burn in a finite time-window confined by suitable weather and the speed of any firefighting response (Flannigan *et al.* 2009; Martin-StPaul *et al.* 2018a).

Reconciling different strands of evidence, Rossa and Fernandes (2018) showed that empirical prediction of field spread rates can work well without using live fuel moisture as an input, so long as it remains within the range observed during model development. However they warn that under circumstances of drought, there is a risk of grave underprediction of fire spread if live fuel moistures are neglected. As the intensity and speed of onset of droughts is expected to increase with climate change (Trenberth *et al.* 2014), a better understanding of the dynamics of live fuel moisture is needed.

### ***Plants' response to drying***

The degree to which plants dry out under fire weather conditions varies among species (Etlinger & Beall 2004; Saura-Mas & Lloret 2007). Their moisture status depends on a suite of functional traits, ranging from characteristics of leaf cells through stem tissues to whole plant architecture (Nolan *et al.* 2020). To predict the moisture content of live fuels, it will be necessary to understand how widely these different traits vary, and which exert the strongest influence over plant water status.

The intensity and rate of spread of wildfires are driven by fine fuels, which comprise leaves and twigs up to about 6 mm thick (Morvan & Dupuy 2004). When plants have good access to soil water and atmospheric conditions are mild, the live leaves and twigs are fully turgid. Their moisture content at full turgor varies among species (Shipley *et al.* 2005). Under drought conditions, which can tend to precede extensive wildfires (Bradstock *et al.* 2014), the availability of soil water to many plants declines. The moisture content of live fine fuels is then additionally influenced by species' investment in rooting architecture and access to soil moisture. With the onset of hot, dry, windy conditions associated with fire weather, shoots continue to dry out.

The movement of water from the soil into roots, up the stem and out the leaves as vapour, is driven by gradients in the potential energy of water at different points along this path. These differences are expressed as water potentials, measured in MPa (Nelson 2001). Shoot water potential is influenced by three cellular-level leaf traits: cell wall elasticity, the osmotic potential associated with cell solutes, and the proportion of tissue water contained inside vs. outside the plasma membrane (Koide *et al.* 1989). The physiological theory behind how these traits modify tissue moisture, and how they can be measured, is set out in detail in Fig 1. Briefly, certain characteristics allow a plant to continue transpiring under desiccating conditions. This is possible for species with rigid cell walls, high cell solute concentrations or a tendency to maintain cell wall moisture even as vacuoles and cytoplasm dehydrate. In such species, the shoots dry out more before their cells lose turgor and stomata close.

These considerations relating to live cells in leaves are less important in twigs where there can be substantial dead tissue. Twigs have a variable capacity to store water; this hydraulic capacitance largely determines their moisture content at a given water potential (Koide *et al.* 1989).

### ***Study aims***

Here we explored how interspecific variation in hydraulic traits influences fuel moisture content and ignition time in wildfires. Most of the total land area that burns in wildfires is affected by *large* fires, reflecting the frequency distribution of wildfire size which follows a Pareto distribution (Schoenberg, Peng & Woods 2003). We assume that under the harsh weather conditions associated with large fires, plants are approaching stomatal closure. This corresponds approximately with the turgor loss point (TLP, Brodribb & Holbrook 2003), also known as wilting point (see Fig 1). The fuel moisture content ( $\text{g H}_2\text{O g}^{-1}$  dry mass) for leaves at TLP,  $\text{MC}_{\text{TLP}}$ , can be obtained from four parameters (Fig 1): their saturated moisture content  $\text{MC}_{100}$ , the fraction  $W_S$  of total moisture content contained within the symplastic compartment (=cytoplasm + vacuoles), the osmotic potential of their solutes at full turgor  $\text{SP}_0$ , and cell wall elasticity  $\epsilon$ . In addition to measuring these parameters empirically, we also set out to partition the contribution of each parameter to live fuel moisture during fire weather, based on well-established theoretical relations among these physical quantities (Koide *et al.* 1989, Box 1).

The aim of this study was to examine how much each of the above traits varies across species, and through the use of a mechanistic model of fuel combustion, to express that variability in terms of changes in ignition time. First, the contribution of each trait to leaf or twig moisture was defined based on established equations of plant hydraulics (see Methods, Eqs 1 and 2). We then examined hydraulic traits in 62 species growing in four fire-prone Australian sites stratified by rainfall and soil texture (Lenz, Wright & Westoby 2006; Richards *et al.* 2014). Taking the range in each trait among species, we calculated the associated shift in leaf moisture content. The range of moisture contents was translated into shifts in ignition time for a leaf or twig exposed to a flame front, using a physical chemistry-based numerical model of leaf ignition.

## **Materials and Methods**

### ***Theoretical treatment of fine fuel moisture***

The functional ramifications of plant traits are often explored by means of correlations. However, we wished to compute how variation in plant hydraulic traits mechanistically forces changes in plant moisture and ignition time during prime wildfire conditions. The traits investigated were: saturated moisture content  $MC_{100}$ , leaf cell wall rigidity  $\varepsilon$ , leaf cell solute potential  $SP_0$ , leaf symplastic water fraction  $W_S$  and stem tissue capacitance  $\bar{C}$ . We re-arranged two classic equations relating turgor pressure to water content, to partition the effect of these traits on fuel moisture during fire weather ( $MC_{TLP}$ ). Eq 1 governs water content in leaves and fine distal shoots. Eq 2 governs water content in twigs. (See Appendix 1 for derivation).

[Eq 1]

$$MC_{TLP} = MC_{100} \left( 1 + \frac{SP_0 W_S}{\varepsilon} \right)$$

[Eq 2]

$$MC_{TLP} = MC_{100} (1 + \psi_{TLP} \bar{C})$$

The quantities on the right sides of Eqs 1 and 2 vary across species. From these relations, it is possible to calculate how strongly that variation drives differences in fuel moisture content under typical fire weather when plants are wilting (*i.e.*  $MC_{TLP}$ ). The methods for these calculations are set out in Appendix 1.

We also tested whether there were systematic differences in these traits according to post-fire regeneration strategy – see Appendix 3 for methods and results.

### **Study sites**

Hydraulic traits were sampled from species at four sites in coastal and inland New South Wales, Australia (Table 1) representing a contrast in rainfall (1220 vs 387 mm  $y^{-1}$ ) and soil type (clay-rich vs sands). All sites lie within 1° of latitude, have a common mean annual temperature of 17.5°C and relatively aseasonal rainfall (Wright, Reich & Westoby 2001; Wright, Westoby & Reich 2002). Fires can occur at any time of year but summer is the peak fire period (Anon 2003; Anon 2006).



At each site 16 to 18 woody evergreen non-climbing taxa were sampled for leaf hydraulic traits, for a total of 62 species from 7 families (Lenz, Wright & Westoby 2006). Species were randomly chosen from previously-compiled species lists at the high-rainfall sites. At the less diverse low-rainfall sites only species with >4 individuals were sampled. Further details of study sites and species-selection criteria are available in Wright, Reich and Westoby (2001), Wright, Westoby and Reich (2002) and Lenz, Wright and Westoby (2006). A subset of 6–8 species were sampled at each site for stem hydraulic traits, covering 30 species overall (Richards *et al.* 2014).

### ***Physiological measurements***

Hydraulic trait measurements were made on samples from three and five individuals per species, for fine shoots and twigs respectively. For fine shoots, pressure bomb measurements were used to construct a pressure-volume curve (Tyree & Hammel 1972), from which  $\epsilon$ ,  $SP_0$ ,  $W_s$ ,  $\psi_{TLP}$ ,  $MC_{100}$  and  $MC_{TLP}$  were estimated (see Fig 1). For twigs, psychrometer measurements were used to construct a cumulative water release curve, allowing estimation of  $MC_{100}$  and  $\bar{C}$ . Full details on field and laboratory techniques and on calculation methods are provided by Lenz, Wright and Westoby (2006) for fine shoots and Richards *et al.* (2014) for twigs.

Conventionally, capacitance and modulus of elasticity are commonly estimated as a slope of these curves close to full hydration. Because we were interested in the influence of these traits on water loss to TLP, we instead computed them as slopes on the chord between full saturation and turgor loss point. (Note that Richards *et al.* (2014) reported capacitances calculated across the ‘native operating range’ between predawn and midday water potentials; the measurements presented here differ from the original study in that respect).

To obtain a measure of plant access to soil water that can be compared among species within a site, measurements were made of predawn and midday shoot water potentials (Lenz, Wright & Westoby 2006). One replicate shoot was collected from each of five individuals for each species, and the balance pressure was measured in a pressure chamber. Predawn water potential  $\psi_{PD}$  is a measure of access to soil water, integrating both root traits and local soil characteristics. Midday water potential  $\psi_{MD}$  is a measure of plant water status during the hottest time of day and can be used to estimate midday moisture content.

### ***Effect of predawn water potentials on aerial fuels***

The calculations in Appendix 1 capture how characteristics of the distal parts of shoots influence their moistness during fire weather. The moisture content of aerial live fuels is also influenced by plants' access to soil water, reflecting investment in deep or extensive root systems as well as microsite. We calculated the effect of varying access to soil water on the moisture content of species' fine fuels at midday (see Appendix 2 for details).

### ***Numerical model of leaf ignition***

To determine the effect of trait variation on ignition times, a numerical model of leaf ignition was used to estimate ignition times associated with the projected range in moisture contents during fire weather as calculated above. The model is fully specified, together with all parameter values, by Scarff, Gray and Westoby (2012). Briefly, it is a finite element model that represents the physical chemistry of combustion at many points through a leaf or twig cross-section. There are no empirical constants; the only parameters are verifiable measures of material properties such as conductivity and specific heat. As the model tracks heating and fuel decomposition using relations from both physics and chemistry, it falls into the category of 'fully physical' models reviewed by Sullivan (2009). Atmospheric mixing effects are neglected, placing our approach amongst the 'fuel-driven' models described by Mell *et al.* (2007). The model predicts how the combustion of the leaf proceeds through time, tracking the temperature and the amount of cellulose, water and char. Evaporation of water and thermal decomposition of dry mass are governed by Arrhenius kinetics. Ignition occurs when the supply of flammable vapours to the nascent flame reaches a critical value. Heating of the leaf or twig is governed by the rate of heat supply to the fuel surface from an external source, and by conduction through the thickness of the fuel item.

For the present exercise we set up the boundary conditions to mimic heating of a fuel item placed 2.5m above ground level, 2.5m in horizontal distance from a 5 m-tall, 50 m-wide, linear flame front burning on a 40°C day under windless conditions and on level terrain. The leaves and twigs were assumed to be composed of pure cellulose plus water. Here cellulose serves as a convenient proxy for more complex plant chemistry; although other compounds such as lignin and hemicellulose are also present, little pyrolysis occurs below 200°C (Fisher *et al.* 2002). Leaves were represented as flat plates of finite thickness but infinite area; i.e. heat could only be transferred through the faces of the leaf lamina, not its edges. One side of the plate was able to

view the flame, the other side viewed only the ambient environment. Leaf thickness was based on species means recorded by Wright, Westoby and Reich (2002). Twigs were represented as square prisms of infinite length, with one face able to view the flame. Values for leaf density, twig density and leaf thickness were based on species means averaged across all sites ( $440 \text{ kg m}^{-3}$ ,  $705 \text{ kg m}^{-3}$ ,  $0.44 \text{ mm}$ ). Twig thickness was set to  $3 \text{ mm}$ . In a minor elaboration of the original model (Scarff, Gray & Westoby 2012), thermal conductivity of the fuel item was allowed to vary dynamically based on moisture content, according to a relation provided by Siau (1984).

As a validation exercise, the model was also set up to imitate the conditions of a published laboratory ignition experiment in which fresh leaves were plunged individually into a  $400^\circ\text{C}$  muffle furnace with a spark ignition pilot, and the time to ignition recorded (Gill & Moore 1996). For this purpose, only species with essentially flat leaf structures were modelled, amounting to 44 species.

### ***Statistical methods***

In addressing the question of where fires can occur and how they can spread, it is useful to consider how variation in fuel moisture is distributed. Our sampling design allows variation to be decomposed into regional-scale differences, associated with rainfall gradients; landscape-scale shifts, associated with edaphic transitions; and fine-scale patchiness, associated with species growing interspersed in mixed stands. For this purpose, we reprised an earlier exploration of variance structure in the moisture content data (Lenz, Wright & Westoby 2006). This analysis was recast to enable scrutiny of questions of wildfire occurrence and spread (vs plant hydraulic strategy examined in the earlier work) and expanded to include measurements of twigs. The percentage variance explained by contrasts in rainfall, soil type and differences among co-occurring species was computed based on a  $2 \times 2$  factorial ANOVA with the first two variables as fixed effects (Hammer, Harper & Ryan 2001; Triola, Triola & Roy 2018). Effect size was calculated using the parameter omega squared ( $\omega^2$ ) with regard to its lack of bias and good performance with data exhibiting heteroscedasticity and mild to moderate departures from normality (Troncoso Skidmore & Thompson 2013; Yigit & Mendes 2018). Since  $\omega^2$  is an unbiased estimator of effect size, negative values are possible; these were rounded up to zero.

To explore how different hydraulic traits contribute to fuel moisture content at TLP, we used the (non-statistical) methods set out in Appendix 1. Correlations or regressions relating these variables are not generally discussed here, since the purpose of this paper is instead to furnish a mechanistic understanding of how variation in different hydraulic traits determines fine fuel moisture content. (Various regressions from the distal shoot data set were examined by Lenz, Wright and Westoby (2006)). Nonetheless two correlations are reported to illustrate how solute potential is correlated with moisture content at TLP, not through any direct mechanistic effect, but via a shared correlation with a third variable. Since the data exhibited a notable degree of skewness and kurtosis, the Spearman's rank correlation was used (Hammer, Harper & Ryan 2001).

## **Results**

### ***Fuel moisture varies widely among species***

Hydraulic traits were estimated across the four sites (Fig 2) in shoots (62 species) and twigs (30 species). (Data in Fig 2 were previously presented by Lenz, Wright and Westoby (2006, Table 1B) and Richards *et al.* (2014, Fig 2a)). There was substantial variation among species in estimated moisture content of distal shoots at turgor loss point TLP (Fig 2a). This measure of live fuel moisture under wildfire conditions varied by 4.0-fold across species, from 0.56 g water per g dry mass up to 2.25 g g<sup>-1</sup>. There was 2.4–3.6-fold variation within sites.

Distal shoots consist of both leaves and fine twigs. Where twigs were studied in isolation, there remained 3.1-fold variation across all species, from 0.23–0.92 g g<sup>-1</sup>, and 1.8–2.7-fold variation within sites (Fig 2b).

### ***Saturated moisture content drives much of this variation***

Of all the hydraulic traits examined, the saturated moisture contents (MC<sub>100</sub>) of distal shoots and twigs were responsible for the largest share of variation in predicted water content in severe fire weather (MC<sub>TLP</sub>). Saturated moisture content ranged from 0.70–2.5 g g<sup>-1</sup> of distal shoot dry mass, a 3.6-fold variation which implies an equivalent, 3.6-fold influence on water content at TLP (Figs 2c, 3). In twigs, saturated moisture content ranged from 0.47–1.6 g g<sup>-1</sup> of dry mass, implying a 3.4-fold influence on water content at TLP (Figs 2d, 3).

Twig capacitance was also sufficiently varied as to exert a strong influence on twig moisture content during fire weather. Across all species it varied 3.7-fold (0.078–0.29 MPa<sup>-1</sup>), implying a 1.9–2.2-fold influence on twig water content at TLP, for high- and low-rainfall sites respectively (Fig 3).

The influence of the other measured shoot traits was more modest. Like capacitance, these traits directly influence the amount of water loss from full turgor to TLP. Variation in cell wall elasticity exerted the strongest effect, associated with a 8.3-fold range in water loss. This equates to a 1.3–1.7-fold effect on water content at TLP, for high- and low-rainfall sites respectively (Fig 3). In distal shoots, the symplastic water content and solute potential were each associated with a 1.2 (high rainfall) to 1.4 (low rainfall) -fold effect on water content at TLP (Fig 3). However solute potential was correlated with water content at TLP ( $r_s=0.53$ ,  $p<0.0001$ ) not via its direct effect on water loss, which was relatively small, but because it is correlated with, and directly influences, the moisture content of shoots at full turgor ( $r_s = 0.52$ ,  $p<0.0001$ ).

#### ***High moisture content delays ignition***

Validation of the physical chemistry-based model of leaf combustion against the leaf ignition experiment (Gill & Moore 1996) showed excellent fit (Fig 4a;  $r^2=0.81$ ). Experimental ignition times (circles, Fig 4b) increased strongly with moisture content. Thick and thin leaves diverged in ignition time as moisture content increased (compare light and dark circles). The model predictions (light and dark triangles, Fig 4b) accurately captured the difference in slope at the edges of the data cloud, corresponding to fuel particles of differing thickness.

#### ***Ignition time most affected by variation in saturated moisture content***

Applying this ignition model to the 62 species examined in the present study, the range in shoot moisture at TLP across all species corresponded to a 2.8-fold range in ignition time of an individual vertical leaf exposed to a wide 5 m-tall flame front at a distance of 2.5 m. For twigs, predicted ignition time varied 2.3-fold.

Saturated moisture content ( $MC_{100}$ ) was the trait that most influenced modelled ignition time (Fig 5). The range in saturated moisture content was associated with ranges in ignition time through factors of 2.4 – 2.5 (leaves) and 2.4 – 2.7 (twigs). Twig capacitance ( $\bar{C}$ ) also exerted a strong

influence, with predicted ignition times ranging 1.8-fold. The range in other individual hydraulic traits across all species was associated with a 1.2 to 1.4-fold range in ignition time (Fig 5).

### ***Root traits exert modest effects on live fuel moisture***

These effects of leaf and twig traits on fuel moisture content apply to a scenario of severe fire weather in which high temperatures, low humidity and high winds drive plants to TLP. Under milder conditions, plant investment in rooting architecture could also influence leaf and twig moisture by providing better access to soil water. Predawn water potential ( $\psi_{PD}$ ), a measure of root access to soil water, varied within sites by up to 3.6 MPa at the low-rainfall sites and up to 0.80 MPa at the high-rainfall sites. Within both low- and high-rainfall sites, this amounted to a 4.6-fold variation in  $\psi_{PD}$  (Fig 3).

This range in  $\psi_{PD}$  across species translated to very modest shifts in midday water potential at high-rainfall sites (1.04-fold shift for distal shoots, 1.07-fold for twigs; Fig 3). At the drier sites, it corresponded to a 1.6-fold shift in distal shoot moisture content at midday (Fig 3), leading to a 1.4-fold variation in predicted ignition time (Fig 5). The effect of root traits on twig moisture at dry sites was difficult to estimate accurately, because for 28% of samples the most negative midday water potentials lay beyond the measured capacitance curve. Whereas there was a theoretical basis for extrapolating the curve in the case of distal shoots (Appendix 2), no equivalent procedure was available for twigs. The remaining samples provide a conservative estimate, indicating a 1.16-fold shift in midday water content (Fig 3), and a 1.1-fold variation in modelled ignition time (Fig 5).

### ***Fuel moisture varies mostly within sites***

Most variation in  $MC_{TLP}$  occurred within sites rather than among them, reflecting differences between co-occurring species. Fires spreading across soil boundaries at the landscape scale would likely encounter little difference in fuel moisture relative to the variation within vegetation stands (Table 2, Fig 2). At the regional scale, twigs and distal shoots were drier in more arid inland locations (mean moisture at TLP, twigs = 0.587 g g<sup>-1</sup> (high rain) vs 0.408 g g<sup>-1</sup> (low rain); distal shoots = 1.19 g g<sup>-1</sup> (high rain) vs 1.00 g g<sup>-1</sup> (low rain). Comparisons of shoot  $MC_{TLP}$  by site were reported by Lenz, Wright and Westoby (2006).

## **Discussion**

### ***Building better fuel models***

Plant species vary widely in flammability, enough to alter fire regimes (D'Antonio & Vitousek 1992; Brooks *et al.* 2004). Capturing the functional traits behind species differences in flammability is essential in moving from case studies of the flammability of particular species to a more generalised predictive capacity. Such an approach is especially desirable in the context of climate change projections where the incidence of fires and area burnt are expected to change (Moritz *et al.* 2012; Bistinas *et al.* 2014; , but see Hantson *et al.* 2016). Climatic factors bearing upon the hydraulic regulation of plants, such as the incidence or severity of drought and fire weather, are also expected to shift (Flannigan *et al.* 2009; Cary *et al.* 2012; Trenberth *et al.* 2014). These changing circumstances call for mechanistic rather than empirical models, and have driven a recent effort to bring about a marriage of plant ecophysiology with fire and live fuel modelling (Jolly & Johnson 2018; Martin-StPaul *et al.* 2018b; Nolan *et al.* 2020). Our data go to the question of how best to develop the representation in fuel models of species differences in live fuel moisture content.

In this study of four woody plant communities, there was considerable variation among species in live moisture content of fine fuels modelled under typical bushfire conditions. Within species, large changes in moisture content were predicted between mild and harsh conditions of soil moisture and evaporative demand. These are familiar patterns consistent with previous experience of fuel moisture (Weise *et al.* 2005; Pellizzaro *et al.* 2007; Chuvieco *et al.* 2009). A key new insight from the present work is that differences among species in how much their shoots dry out were relatively small. Our study makes it clear that species differences in live fuel moisture during conditions conducive to large fires were mainly determined by differences in the starting point, i.e. the saturated moisture content, rather than by differences in the subsequent extent of water loss in the face of dry soils and hot, dry, windy weather. The other hydraulic traits we examined influence either the water potential that plants run down to or the amount of water loss associated with reaching a given water potential. Of these, sapwood capacitance is the next most important trait in driving species variation in moisture content during fire weather. The remaining traits appear to play a relatively minor role in this regard. Nonetheless they represent the sensitivity of live fuel availability to progressively more extreme weather events.

This new information means that a large portion of ecophysiological variation in plant moisture can be incorporated into live fuel models with the addition of a single variable. Saturated moisture content ( $MC_{100}$ ) is easily and quickly measured without specialist equipment. Expressed as leaf dry matter content ( $=1-MC_{100}/100$ ), it is widely reported in ecological and ecophysiological databases (e.g. 214, 513 observations on 6,786 species, Kattge *et al.* (2011)). On the basis of our findings, it appears the logical place to begin in developing more sophisticated fuel models that accommodate the diversity of plant hydraulic strategy. However, we note that in some environments, saturated moisture content can vary within a species through a fire season, reflecting shooting phenology (e.g. Nolan *et al.* 2018). Whereas in this study we took a snapshot of 62 species across a short period of time, ecophysiological models of live fuel moisture will need to incorporate seasonal and stand-age variability in hydraulic traits. Nolan *et al.* (2020) have shown how measurements of plant hydraulic traits could be assembled into a physiological model of live fuel moisture content. As well as enabling the prediction of live fuel moisture, modelling plant water relations also offers the opportunity to predict canopy die-off in drought, and the accompanying accession of newly senesced foliage into the litter layer (Nolan *et al.* 2020).

An investigation of hydraulic trait variation similar to our study examined the live fuel moisture of six species in Mediterranean forest in Catalonia (Nolan *et al.* 2018). Live fuel moisture content was best predicted across a fire season by predawn water potential. Fuel moisture predictions based on this single ecophysiological parameter were better than ones based on soil drought indices, which are commonly computed in fuel modelling (Nolan *et al.* 2018; Ruffault *et al.* 2018). These results suggest that there is scope for improving live fuel models by including ecophysiological characteristics. Predawn water potential did not strongly drive fuel moisture content in our own study, but we note that there is no contradiction between our results and those of Nolan and colleagues. They sought to predict live fuel moisture throughout a five-month period, including at times when the vegetation was likely too wet to burn widely. In contrast, we did not attempt to sample a seasonal decline in fuel moisture. Instead we sought to predict live fuel moisture at turgor loss point, reasoning that it is under these conditions that the largest fires, contributing the greatest area burned, are likely to occur. Thus, the Catalonian study addresses the question of when and where fires might occur, whereas our study considers how fuel moistures might vary among species in the circumstances under which most burning does occur.



### ***Plant hydraulic traits exert a strong influence on fire behaviour***

If a case is to be made for building plant hydraulic function into fuel models, it is important first to assess how much it alters the activity of real fires. To address this question, differences in moisture content across species can be compared with observed live fuel moisture contents in wildfires.

In the chaparral of southern California, monthly burned area increased by ~23-fold across a ~1.6-fold increase in live fuel moisture values from 140%–90%, reaching a ceiling across the range 90%–55% (Schoenberg *et al.* 2003). In central Spain, fluctuation in live fuel moisture through time was related to fire occurrence, fire size and burned areas in grassland, shrubland and oak forest (Chuvieco *et al.* 2009). Approximately 2-fold variation in live fuel moisture in *Cistus* and *Rosmarinus* shrubs was associated with ~25-fold increase in the number of fires, and ~15-fold increase in burned area. In Iberian shrubland, the likelihood of fire in any given square km fell ~5-fold across an approximate doubling of fuel moisture from around 60% to 120% (Jurdao, Chuvieco & Arevalillo 2012, Fig 8).

In the present study, predicted moisture content of distal shoots at wilting point ( $MC_{TLP}$ ) varied 4-fold across all species, driven substantially by a 3.6-fold variation in saturated moisture content. For contrast, the large ranges in fire activity reviewed above were associated with a 2-fold range of fuel moisture within each study. Some of the species variation we report occurred among sites or rainfall zones, but the greater component was derived from differences among species growing alongside one another within our sites. Differences in hydraulic regulation amongst co-occurring species are large enough to exert a powerful influence on fire behaviour. They represent a substantial ecological store of variation in flammability.

### ***Directions in pyroecophysiology***

The great challenge for pyroecophysiology will be developing methods for making fire behaviour predictions at stand, landscape and continental scales based on inputs measured at much smaller scales (e.g. leaves, individual plants). Flammability and fuel load of surface fuel beds have now been successfully predicted based on chemical and structural traits of individual leaves (Grootemaat *et al.* 2015; Grootemaat *et al.* 2017). Prediction of vertical propagation of fire at stand scale has recently been greatly improved by incorporating traits of leaves and shoot architecture in a biophysical, mechanistic model (Zylstra *et al.* 2016). Models for the mechanistic

prediction of plant water status from physiological traits include the recent work of Nolan *et al.* (2020) and Martin-StPaul, Delzon and Cochard (2017). Their mechanistic, physiology-based approaches offer the opportunity to transcend species- and location- specific calibration of fuel moisture relationships in the context of an evolving climate.

### ***Impact of drought on this study***

The field work for the present study was conducted during southeastern Australia's Millennium Drought (2001-2009), at that time the driest period since 1900 on some measures (van Dijk *et al.* 2013). In this context, drought-induced xylem embolisms may have influenced our measurements of predawn water potential (Perez-Harguindeguy *et al.* 2013). The suitability of plant hydraulic data from a drought period, for predicting fuel moisture during wildfires, varies among our sites. Drought is a risk factor for fire at the wetter sites. By contrast, fires in the drier sites are made less likely by drought, which prevents the development of dense stands of annual grasses that provide fuel continuity (Bradstock *et al.* 2014). These stands are a feature of exceptionally wet years and develop only on heavy-textured soils and not at sandy sites. Nonetheless the increased landscape permeability to fire associated with dense annual grasses means that communities on sandy soil are still more likely to burn in wetter years, because of fires spreading into them from adjacent communities on heavy soils (Bradstock 1990).

### ***Conclusions***

Variation across species in hydraulic traits exerts a substantial influence on the ignitability of live woody fuels under the conditions likely to prevail during wildfires. This influence is determined in particular by the moisture content of leaves and fine twigs at full turgor, which directly impacts moisture content in fire weather. Saturated moisture content is easily measured, widely reported and represents a good first candidate for building ecophysiological variation into fuel models. A range of properties of the leaves, stem and roots, which control the amount of water lost as plants wilt, exert a subtler influence. In our study of eastern Australian coastal and semi-arid sites with strong contrasts in soil texture, most variation in fuel moisture resided amongst species growing intermingled within mixed stands, rather than among rainfall zones or soil types.

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### **Supplementary material**

Appendix 1 – Algebraic treatment of fine fuel moisture

Appendix 2 – Influence of access to soil water on aerial fuels

Appendix 3 – No influence of regeneration strategy on hydraulic traits

### **Data availability**

Supporting data are archived in the Dryad Digital Repository (Scarff *et al.* 2021), available at <https://doi.org/10.5061/dryad.6hdr7sr00>. Previously archived material relating to hydraulic physiology of twigs can be found at <http://doi.org/10.5061/dryad.hm482> (Richards *et al.* 2014).

## Figures

**Fig 1.** An example of a pressure-volume curve, showing how different hydraulic traits can be estimated. Cell diagrams illustrate how cell turgor changes at key points along the curve. Moisture content of live shoots varies with their water potential ( $\psi$ ). In fully saturated cells (I) osmotic pressure from the cell solutes pushing the cell membrane outward is exactly balanced by the inward hydrostatic pressure imposed by cell walls. As moisture is lost, the elastic cell walls deform inward (II). Beyond turgor loss point (TLP), the cell membranes shrink away from the cell walls (III) and cell solutes become progressively more concentrated. The symplastic compartment of the cell, bounded by the cell membrane, becomes steadily smaller. The relationship between tissue water content and  $\psi$  is thus controlled first by changes in hydrostatic pressure from cell walls and later by changes in cell solute potential. TLP marks the transition between these two regimes. Cell diagrams after Mader and Windelspecht (2017, Fig. 4.7); graph after Lenz, Wright and Westoby (2006).

**Fig. 2.** Hydraulic traits in distal shoots and twigs across four sites stratified by rainfall and soil texture (Lenz, Wright & Westoby 2006; Richards *et al.* 2014). Each point is a species mean; horizontal lines show site means.

**Fig. 3.** Modelled moisture content of live fine fuels during fire weather, in response to variability in eight hydraulic traits. Moisture content was calculated at wilting point (TLP, see Appendix 1) for all traits except  $\psi_{PD}$ . The  $\psi_{PD}$  data indicate how variation in rooting investment would influence moisture content under conditions typically too mild to cause wilting: at midday on a winter or spring day (Appendix 2). Each column spans between a wettest and driest projected moisture content, associated with the observed range of values in that trait across species. Black columns show how this trait range would translate into moisture contents at the high rainfall sites; grey columns relate to the low rainfall sites. See Fig 5 for predicted influence on ignition times.

**Fig. 4.** Comparison of ignition time of leaves of 44 species in a muffle furnace (Gill & Moore 1996) with predictions of the numeric model. **(a)** Observed ignition times compare favourably with values predicted from species moisture content, leaf thickness and tissue density. **(b)** Ignition

times increase with moisture content, and the slope of that relationship is steeper as leaves become thicker (darker symbols). The model predictions (triangles) capture both relationships accurately.

**Fig. 5.** Changes in ignition time driven by species variation in eight hydraulic traits. Left panel shows modelled leaf ignition times based on traits measured in distal shoots. Right panel shows modelled twig ignition times based on twig traits (refer to right axis). Each column spans between a fastest and slowest ignition time, associated with the observed range of values in that trait across species. Black columns show how this trait range would translate into ignition times at the high rainfall sites; grey columns relate to the low rainfall sites. Ignition times were modelled for a leaf or twig positioned 2.5m above ground level, 2.5m horizontally from a 5m flame front 50m wide. See Fig 1 for more details about each trait.

## Tables

**Table 1. Study sites.** The fire intervals required to maintain existing native communities are shown. NB Mallee is a short-statured, multi-stemmed form of eucalypt. References: <sup>1</sup>Anon (2006, Appendix 1) <sup>2</sup>Anon (2003, Table 3).

	Higher rainfall clay-rich soils	Higher rainfall sandy soils	Lower rainfall clay-rich soils	Lower rainfall sandy soils
Latitude,	-33.579,	-33.694,	-32.967,	-32.976,
Longitude	151.292	151.143	146.155	146.146
Vegetation	Closed forest	Low open woodland	Open Woodland	Open shrub mallee
Fire interval	15 – 30y <sup>1</sup>	7 – 30 y <sup>1</sup>	>40 y <sup>2</sup>	15 – >40 y <sup>2</sup>
Most recent fire before study	Wildfire 1993-4; prescribed burn 2005-6	Wildfire 1990-1; prescribed burn 2005-6	Wildfire 1984-5	Wildfire 1977-8

**Table 2.** Percentage variance explained ( $\omega^2$ ) at different spatial scales, with regard to moisture content of fine fuels at turgor loss point. Superscripts indicate results of 2x2 ANOVA (rainfall x soil): ns not significant, \*  $p < 0.05$ , \*\*  $p < 0.01$ . See Lenz *et al* (2006) for a further exploration of partitioning of variance in these variables.

%	Distal shoots	Twigs
Rainfall	6.36*	22.0**
Soil type	0 <sup>ns</sup>	7.16 <sup>ns</sup>
Rain × soil	0 <sup>ns</sup>	1.45 <sup>ns</sup>
Within sites	93.6	69.4

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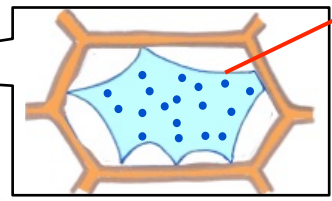
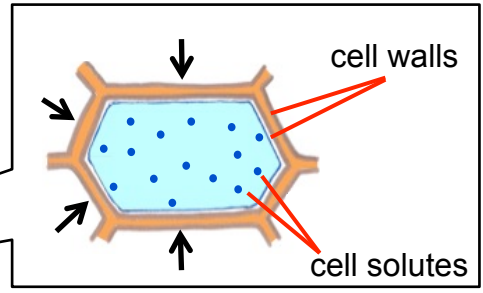
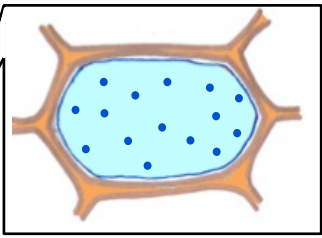
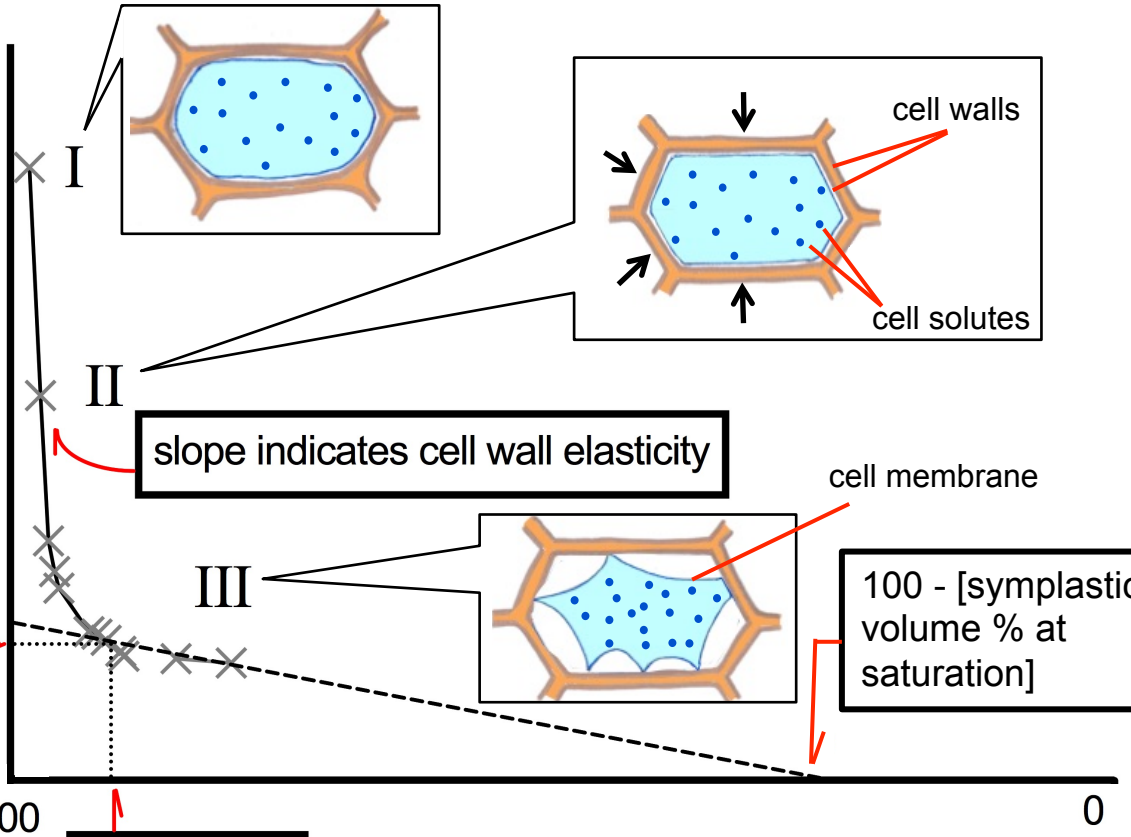
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Pressure<sup>-1</sup>  
(MPa<sup>-1</sup>) ↑



slope indicates cell wall elasticity

[Solute potential at saturation]<sup>-1</sup>

cell membrane

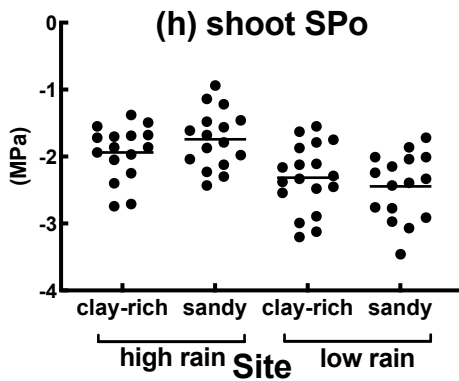
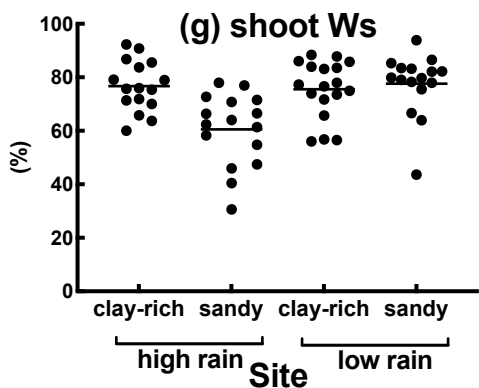
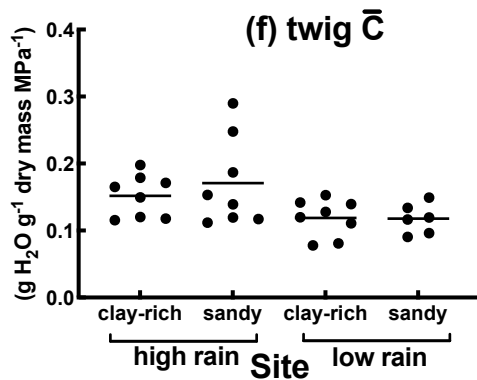
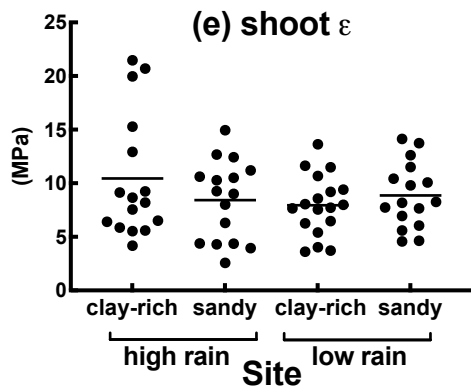
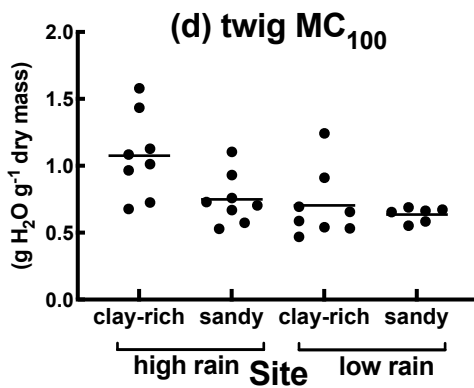
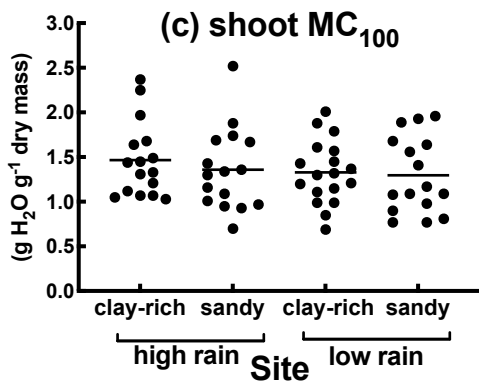
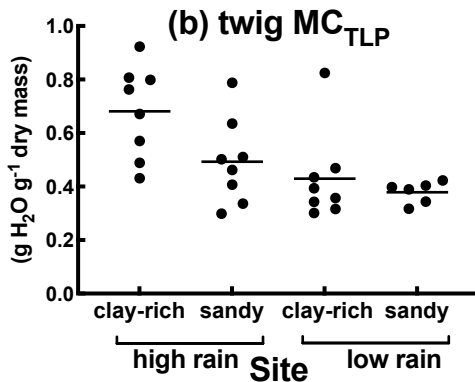
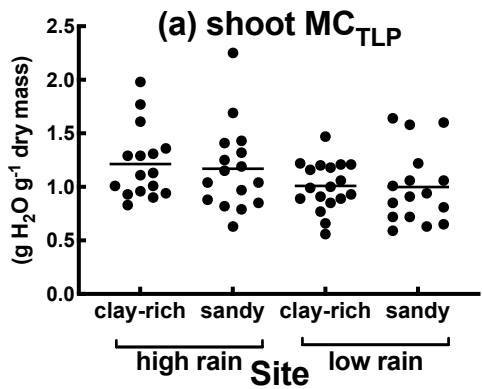
100 - [symplastic volume % at saturation]

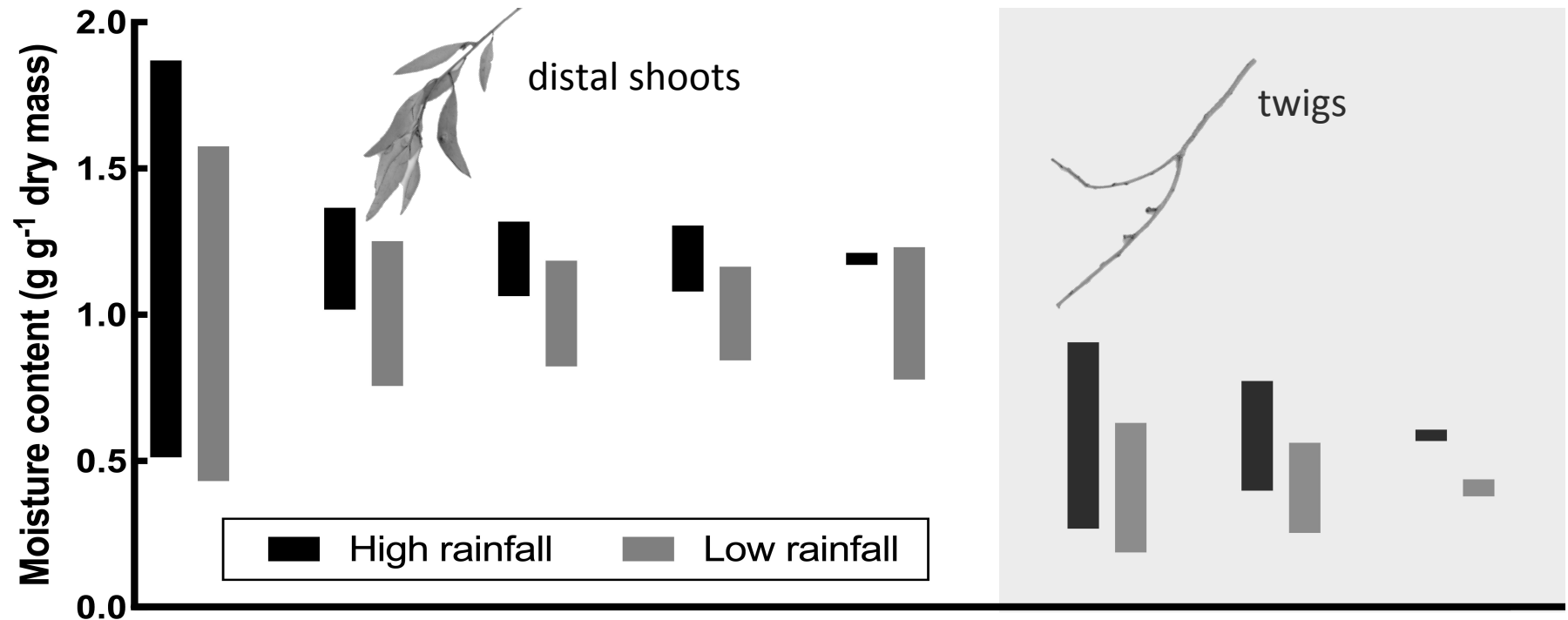
[Turgor loss point]<sup>-1</sup>

Water content at turgor loss point

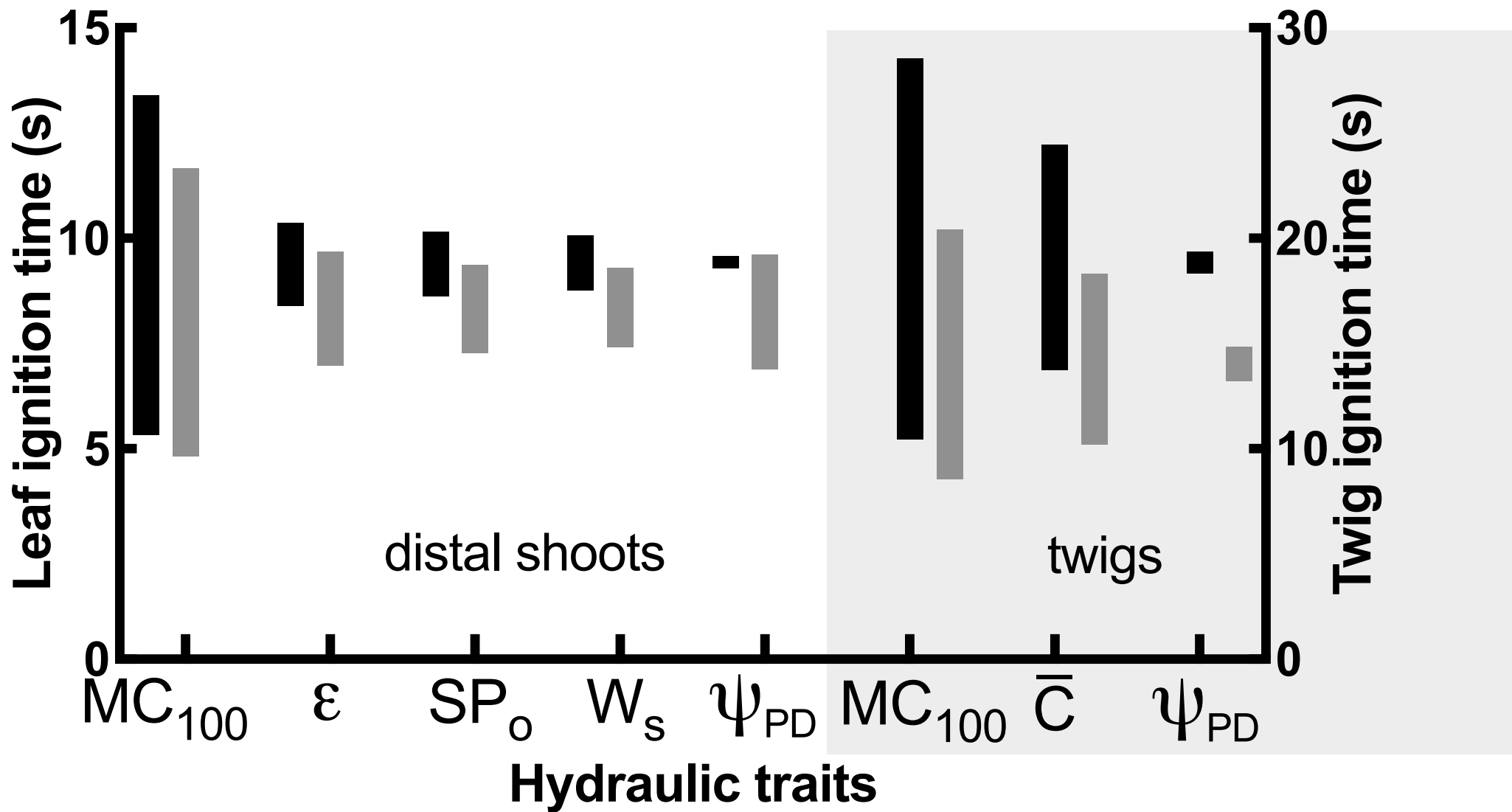
Relative water content (%)



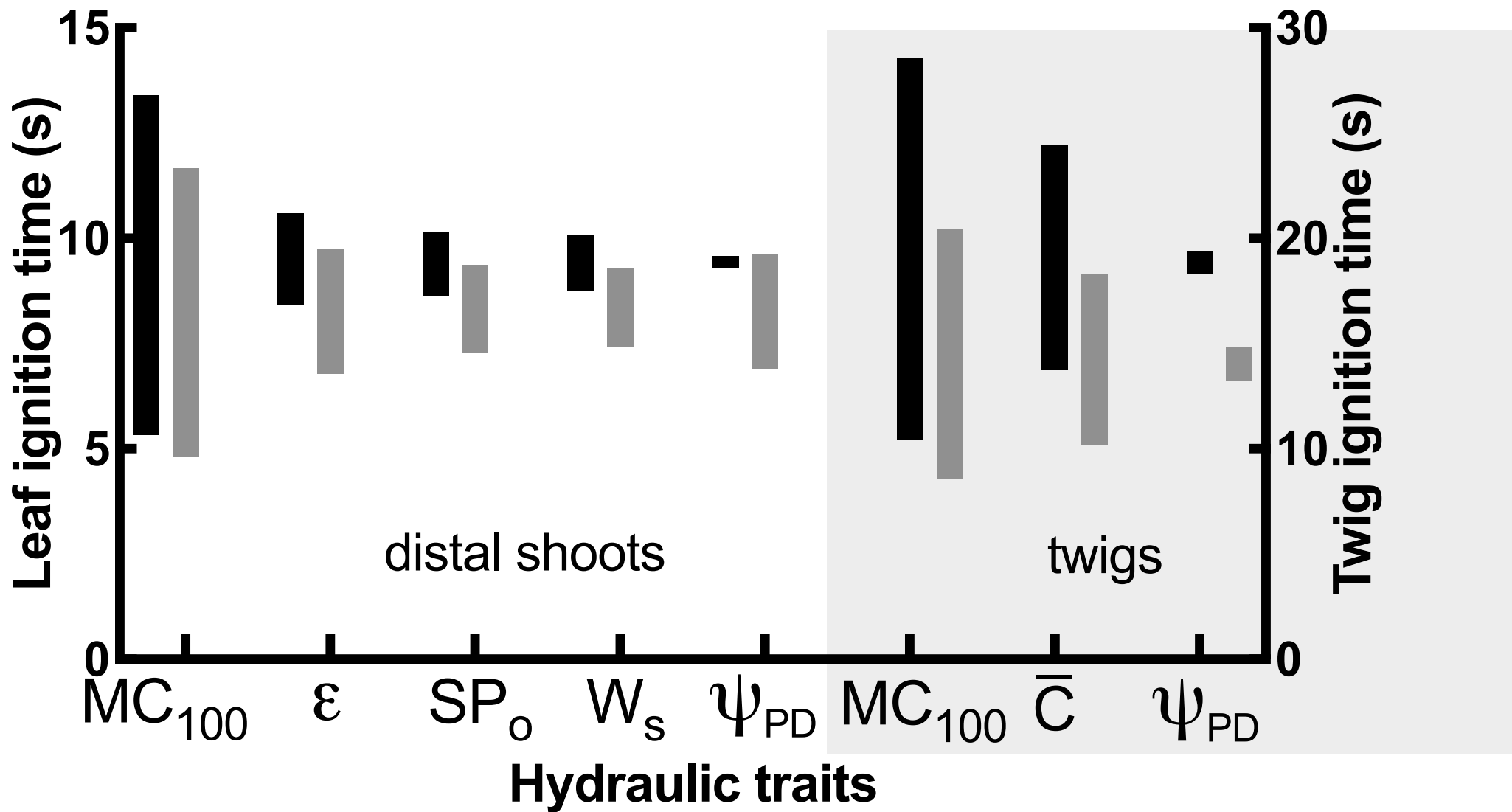




Trait	MC <sub>100</sub>	ε	SP <sub>0</sub>	W <sub>S</sub>	ψ <sub>PD</sub>	MC <sub>100</sub>	$\bar{C}$	ψ <sub>PD</sub>
Full name	Saturated water content	Modulus of elasticity	Solute potential	Symplastic water fraction	Pre-dawn water potential	Saturated water content	Capacitance	Pre-dawn water potential
Trait range	0.689 – 2.51	2.57 – 21.47	-3.46 – -0.937	30.6 – 93.9	Low rain -1.00- -4.56 High rain -0.22- -1.02	0.468 – 1.58	0.0778 – 0.290	Low rain -1.00- -4.56 High rain -0.22- -1.02
Units	g g <sup>-1</sup> dry mass	MPa	MPa	%	MPa	g g <sup>-1</sup> dry mass	g g <sup>-1</sup> MPa <sup>-1</sup>	MPa
max:min trait value	3.6 ×	8.3 ×	3.7 ×	3.1 ×	4.6 ×	3.4 ×	3.7 ×	4.6 ×







Site:  high rainfall  low rainfall