

# Conifer encroachment increases foliar moisture content in a northwestern California oak woodland

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## ABSTRACT

**Background.** Foliar moisture content influences crown fire ignition and behaviour. Some spatial variation in foliar moisture is attributable to differences in stand conditions but evidence describing this role is lacking or contradicting. **Aims.** To examine the role of stand conditions on tree physiology and foliar moisture content in Oregon white oak (*Quercus garryana*) and Douglas-fir (*Pseudotsuga menziesii*). **Methods.** We monitored foliar moisture content in both species, and tree physiology (stomatal conductance and leaf water potential) in oak, across three stand conditions, including intact stands (unencroached), stands invaded by Douglas-fir (encroached), and thinned stands with Douglas-fir removed. **Key results.** Encroached stands had higher foliar moisture content than intact or thinned stands. Higher stand density was associated with higher foliar moisture content in both species and foliage ages. Encroached stands also had higher midday leaf water potential compared with intact or thinned stands. **Conclusions.** These findings provide strong evidence that stand conditions and thinning treatments can influence foliar moisture content in Oregon white oak ecosystems, with likely implications for other ecosystems. **Implications.** Better understanding of the role of stand conditions on foliar moisture content may contribute to improved spatial and temporal prediction of foliar moisture content and modelling of potential crown fire behaviour.

**Keywords:** fuel moisture, leaf water potential, live fuel moisture, *Pseudotsuga menziesii*, *Quercus garryana*, tree physiology, wildfire, wildland fuels.

## Introduction

Foliar moisture content (i.e. live fuel moisture in trees and shrubs) is a contributing factor in the ignition and behaviour of crown fires in shrublands and forests (Xanthopoulos and Wakimoto 1993; Dimitrakopoulos and Papaioannou 2001; Weise *et al.* 2005; Pellizzaro *et al.* 2007; Kuljian and Varner 2010). Higher foliar moisture content dampens ignition and spread due to the high specific heat of water and the energetic need to evaporate water prior to combustion (Simms and Law 1967). Foliar moisture content is included in all crown fire models and fire danger ratings used by managers (Van Wagner 1977; Bradshaw *et al.* 1983; Scott and Reinhardt 2001). Although some have questioned the predictive ability of foliar moisture content under field conditions (Alexander and Cruz 2013), others suggest that observed discrepancies between lab and field studies likely reflect an oversimplified consideration of foliar moisture content (Rossa and Fernandes 2018). Still, studies have clearly identified critical thresholds in foliar moisture content that are highly informative in predicting area burned (Dennison *et al.* 2008; Nolan *et al.* 2016), but see Pimont *et al.* (2019) for a critique of this approach. Future projections indicate warming associated with climate change may contribute to reduced foliar moisture content and longer periods below critical threshold levels (Ma *et al.* 2021). These circumstances suggest that consideration of foliar moisture content can be a useful part of the fuels and fire management process (Keyes 2006).

Foliar moisture content within and among species is known to substantially vary temporally and spatially. Temporal fluctuation in foliar moisture content occurs at

diel, seasonal, and interannual scales (Jameson 1966; Van Wagner 1967; Agee *et al.* 2002; Keyes 2006). Spatial variation in foliar moisture content reflects differences in species composition, environmental gradients, and their interactions (Yebra *et al.* 2008; Krix and Murray 2018; Nolan *et al.* 2018). The mechanistic drivers contributing to this variation are still being refined, but likely reflect the interactive influence of climate, edaphic conditions, plant traits, and vegetation structure. Early research by fire scientists primarily treated live fuel moisture as dead fuels with typically higher fuel moisture content, but plant physiologists have long known that water and carbon flows and storage are dynamic (Kozłowski and Clausen 1965), with important implications to plant flammability and fire behaviour (Jolly *et al.* 2014; Krix and Murray 2018). Advances in understanding and predicting foliar moisture content will inevitably require integration of knowledge and approaches across ecophysiology and fire science disciplines, especially under warming and drying conditions (Jolly and Johnson 2018; Nolan *et al.* 2020).

Previous research has identified that variations in foliar moisture content among species are attributable to trait differences that correspond to water and carbon acquisition and regulation strategies. Deeper-rooted species with more reliable access to water resources can be decoupled from site conditions and thus maintain higher foliar moisture content (Brown *et al.* 2022). Plant–water relations (i.e. leaf water potential, transpiration) can also influence foliar moisture content both within and among species (Nolan *et al.* 2018; Pivovarov *et al.* 2019). Differences in foliar moisture content between species have been associated with leaf traits, such as leaf mass area (Krix and Murray 2018).

Foliar moisture content within a species can vary due to tree- and stand-level factors (Ruffault *et al.* 2022). Tree-level factors such as leaf morphology and tree size (i.e. diameter and height), as well as their corresponding effects on leaf area and rooting depth, likely contribute to variation in foliar moisture content. Tree-level influences on foliar moisture content are also modified by stand-level factors, including stand structure and composition, and their effects on microclimate and soil moisture availability. However, the limited available evidence on the role of stand-level factors on foliar moisture content is seemingly contradictory or dependent on local context (Soler Martin *et al.* 2017; Krix and Murray 2018).

Based on previous research findings and ecophysiological reasoning, there are three conceivable outcomes in the relationship between stand density (e.g. stand basal area) and foliar moisture content. Some evidence suggests that stand density, and more directly stand-level leaf area index, would be negatively associated with foliar moisture content. Prior studies have shown that higher density stands were associated with greater water stress as measured by leaf water potential (McDowell *et al.* 2006; Moreno and Cubera 2008), a circumstance that may explain observed decreases in foliar moisture content with higher stand density (McNamara *et al.* 2019). Conversely, reducing competition through

thinning treatments can increase soil moisture availability and throughfall precipitation, contributing to increased diameter growth (Devine and Harrington 2006, 2013; Gould *et al.* 2011; Sohn *et al.* 2016), with presumable increases in foliar moisture content.

Stand density could also be unrelated to foliar moisture content in some species due in part to plant water regulation strategies. Many species regulate water storage and loss through numerous mechanisms, such as stomatal control, osmotic potential, and modulus elasticity, among others (Pallardy 2008). Thus, changes in stand density may not result in a strong influence on foliar moisture content due to internal physiological regulation. Observations of relatively static foliar moisture content over time have been observed in some species (Viegas *et al.* 2001; Pellizzaro *et al.* 2007), and in one study, foliar moisture content did not differ between thinned and unthinned stands (Soler Martin *et al.* 2017).

A third possible relationship is that foliar moisture content could be positively associated with stand density. In more open or recently thinned stands, higher wind speeds and greater penetration of solar radiation can lead to increased transpiration and evaporative water loss compared with higher density stands (Lagergren *et al.* 2008; Brooks and Mitchell 2011). Furthermore, the larger leaf area of more open-growing trees, and greater soil exposure in more open (lower leaf area index) stands, can increase stand-level transpiration and evaporation that may negatively affect soil water availability (Ruffault *et al.* 2022) and reduce foliar moisture content. Greater overstorey cover associated with higher density stands in more humid environments can reduce surface temperature and increase relative humidity under the canopy (Kane 2021), leading to increased leaf water potential compared with lower density stands due to greater soil moisture availability and higher predawn water potential (Goff 2021). These findings are consistent with observed differences in foliar moisture content between sheltered (higher density stands) and exposed (lower density stands) habitats in a fire-prone landscape of southeastern Australia (Krix and Murray 2018). There is also the possibility that positive, negative, and neutral relationships between plant water stress and foliar moisture content can occur within a given stand, depending on interactions between climate and stand conditions. Differences in the directional effect of plant water stress and foliar moisture content may reflect shifts along a curvilinear relationship (Tyree and Hammel 1972).

Oregon white oak ecosystems provide a framework to examine the role of stand density on tree physiology and seasonal patterns of foliar moisture content. Many Oregon white oak woodlands have substantial encroachment from Douglas-fir (*Pseudotsuga menziesii*) and other conifers from adjacent forests due to the prolonged absence of fire (Agee 1993; Tveten and Fonda 1999). Oregon white oak woodlands and associated prairies have declined by as much as 30% from their historical extent in some areas due to

**Table 1.** Mean ( $\pm 1$  standard error) topographic and stand characteristics by stand condition in an Oregon white oak (*Quercus garryana*) ecosystem of northwestern California (adapted from Kane 2021).

Stand condition	Elevation m	Slope °	Aspect °	Basal area m <sup>2</sup> ha <sup>-1</sup>	Tree density no. ha <sup>-1</sup>
Intact	799 (8.4)	20 (1.1)	168 (21.6)	25 (5.7)	244 (59)
High encroached	777 (9.3)	25 (4.1)	203 (25.5)	58 (2.5)	775 (77)
Thinned	771 (7.8)	22 (0.9)	166 (16.4)	26 (12.9)	510 (129)

encroachment (Fritschle 2008; Knight *et al.* 2020). Low-intensity prescribed fire is a commonly used method to maintain and improve conditions (Underwood *et al.* 2003; Hamman *et al.* 2011). However, prescribed fire can be insufficient in killing invading Douglas-fir (Engber and Varner 2012), partly due to reduced herbaceous fuel loads and higher dead surface fuel moisture that lowers fire intensity in encroached stands (Engber *et al.* 2011). In these instances, managers often opt to remove Douglas-fir by thinning or girdling treatments to improve oak vigour and restore oak woodlands (Devine and Harrington 2013; Kane *et al.* 2019). Removal of Douglas-fir can better facilitate prescribed fire by increasing temperature and vapour pressure deficit (Devine and Harrington 2007; Kane 2021) that aids in reducing dead surface fuel moisture content compared with encroached stands (Engber *et al.* 2011; Kane 2021). However, research on the impacts of conifer encroachment and removal on foliar moisture content have not been examined.

The aim of this case study was to characterise the seasonal patterns of foliar moisture content of Oregon white oak and Douglas-fir under varying stand conditions in northwestern California. Specifically, the objectives of the research were to: (1) determine the influence of Douglas-fir encroachment and removal on seasonal changes in foliar moisture content; and (2) compare the effect of stand density on tree physiology (leaf water potential and stomatal conductance) and foliar moisture content across stand conditions. Based on field observations and prior related research at the study site, our hypothesis for this study was that encroached stands would have higher foliar moisture content in Oregon white oak and Douglas-fir, and that this trend would be driven by denser stands having higher leaf water potential and lower stomatal conductance. Results of this study will provide much-needed information about the influence of stand density and tree physiology on foliar moisture content that can better assist in predicting foliar moisture content and modelling of potential crown fire behaviour.

## Methods

### Study site and experimental design

Our study was conducted in Kneeland, California, USA at the Mountain View site (40.71°N 123.90°W) on the Yager

Creek tract of Humboldt Redwood Company. The climate at the study site is characterised as mediterranean, with a maritime influence that experiences coastal summer fog. Between June and November, temperature ranges between 10.1 and 25.4°C, and precipitation ranges between 169 and 664 mm, based on the 30-year mean climate (1989–2018) for the study site (PRISM Climate Group 2020). Based on the Kneeland remote automated weather station data that is located about 2 km from the study site (40.72°N 123.93°W), mean monthly temperatures ranged from 11.2 to 21.9°C (mean 16.6°C), minimum relative humidity ranged from 7 to 86% (mean 42%), and precipitation totalled 252 mm (64% of the 30-year mean) from June to November 2018.

The bedrock of the study site is of sedimentary and meta-sedimentary origin and is part of the Franciscan Complex in the Coast Range Province. Shallow, fine loamy alfisol soils in the Elkcamp series and fine mixed mollisol soils in the Kinman series characterise the site. Prior observations at the study site did not detect differences in soil texture and water holding capacity between encroached and intact stands (S. Marshall, unpubl. data). The elevation of the site ranged between 680 and 820 m, with moderately steep southern (from southeast to southwest) slopes ranging from 19 to 35°. Fire has not been recorded at the site since 1900 (CALFIRE 2020), although the site was prescribed burned the year following data collection of the current study in 2019. Prior to fire exclusion and forced removal of Indigenous communities from the region, fire return interval within the study area was estimated to be between 6 and 10 years (LANDFIRE 2020).

Intact Oregon white oak woodlands with limited Douglas-fir encroachment are generally more common along the mid-to upper-slope portions of the site. Oak woodlands with encroachment are generally more prevalent in lower slope positions that are adjacent to Douglas-fir forests. Oregon white oak and Douglas-fir were the dominant two species, but California black oak (*Q. kelloggii*) and Pacific madrone (*Arbutus menziesii*) were also present. We intentionally minimised the potential influences of topographic differences among stand conditions by selecting sites with overlapping elevation, aspect, and slope position (Table 1). Based on a previous study at the same site, tree age did not differ among stand conditions (Schriver *et al.* 2018). Most Oregon white oak and California black oak occurred between 1850 and 1900, while almost all Douglas-fir established after 1950.

Thinning and harvest treatments were implemented at the site in 2017 using a combination of variable-retention harvesting and group-selection harvesting approaches. Treatments primarily focused on the removal of Douglas-fir trees >25 cm diameter at breast height (DBH; 1.37 m). Retention of some Douglas-fir that were growing intertwined within the crowns of large oak trees was necessary to limit damage to oaks and potential injury to operators.

Our experimental design for the study included sampling a total of nine plots – three plots for each stand condition (intact, high encroached, and thinned). The intact woodland and high encroached plots were randomly selected as part of a previous study (Schriver *et al.* 2018). Intact stands represent relatively open oak woodland stands that had limited or no encroachment by Douglas-fir. Yet, these stands may have slightly increased in oak density over the years due to reduced fire frequency (Fritschle 2008; Schriver *et al.* 2018). High encroached stands contained moderate-to-large Douglas-fir that partially overtopped the oaks. We intentionally selected thinned plots that were located close to heavily encroached stands and had clear evidence of Douglas-fir removal. All plots contained at least three oaks greater than 15 cm DBH within a 10 m radius of plot centre. Within each plot, we identified each species and measured the DBH of all trees within 10 m (area = 78.5 m<sup>2</sup>) of plot centre. From these data, we calculated stand basal area and tree density for each plot and stand condition. As intended, stand structure varied by stand condition ( $F_{2,7} = 5.2$ ,  $P = 0.048$ ; Table 1). Encroached stands had higher tree density and mean basal area compared with intact and thinned stands. Variation in stand basal area in thinned stands was higher than intact or encroached stands because one plot was not as heavily thinned due to the inability to remove some Douglas-fir that had crowns intertwining with oaks.

## Data collection

Foliar moisture samples were haphazardly collected monthly from three trees of Oregon white oak and Douglas-fir in the co-dominant or dominant canopy position within the 10 m radius of each plot to account for spatial variability at the plot level. DBH for all trees sampled for foliar moisture content ranged between 19.0 and 36.2 cm, and did not differ among stand conditions ( $P > 0.246$ ). However, the crown base heights of Oregon white oaks were substantially lower in intact stands (~2–6 m) than in encroached and thinned stands (~6–12 m). Sampling of foliage was conducted every month from June until November in 2018, using pole pruners to cut one or two branches from the lower one-third of the crown. We separately collected new foliage (formed in 2018) of both Douglas-fir and Oregon white oak and old foliage ( $\geq 2$  years old) in Douglas-fir only. Because Oregon white oak is deciduous, only new foliage was collected. All sampling occurred on sunny or lightly overcast days between 1100 and 1500 hours. The collection time of each sample

was recorded on the sample bag. Each samples had an average live leaf dry mass of approximately 10 g (s.e. = 0.28 g). Collected samples were separately placed in a prelabelled and preweighed sealable plastic bag. Bags were then placed in a cooler, and were immediately weighed with the plastic bag to 0.01 g on an analytical balance upon arrival at the Cal Poly Humboldt Fire Lab in Arcata, California, USA. Foliage samples were removed from the plastic bag, placed into separate paper bags, and oven-dried for at least 3 days at 60°C. Higher drying temperatures have been suggested (Matthews 2010), but we intentionally selected a lower drying temperature to limit volatile mass loss with the trade-off of retaining some (~1–3%) cellular bound moisture. Each sample was removed from the paper bag and weighed after drying. We calculated percentage of foliar moisture content for each sample by subtracting the wet weight from the dry weight, dividing by the dry weight, and multiplying by 100.

On 25 August 2018, we measured leaf water potential and stomatal conductance of ten Oregon white oak trees within each of five stand conditions: (1) intact (no Douglas-fir encroachment); (2) moderate encroached without thinning; (3) moderate encroached with thinning; (4) high encroached without thinning; and (5) high encroached with thinning. Sampling on this date was chosen because we knew soil moisture would be around its lowest and wildfires most commonly expected. Moderate encroached plots were still dominated by Oregon white oak, but contained some Douglas-fir in the canopy. For each sampled tree, leaf water potential was measured at predawn (0200–0500 hours) and at midday (1030–1400 hours) using a pressure chamber (Model 600, PMS Instruments, Corvallis, OR, USA), and stomatal conductance was measured using a leaf porometer (SC-1, Decagon Devices Inc., Pullman, WA, USA). All samples were collected from the lower crown using a pole pruner, with midday samples taken from fully illuminated portions of the crown when possible. Once a small branch was pruned from the crown, three to five leaf water potential measurements were taken from different sub-branchlets and averaged into one value. Three stomatal conductance measurements were taken at midday from different leaves and averaged into one value. For each midday water potential sample, a subset of the sample was used to calculate foliar moisture content.

## Data analysis

We used a linear mixed effect modelling approach using the `lmer` function in the `lme4` package (Bates *et al.* 2015) in the R statistical environment (version 4.0.2, R Development Core Team 2022). This approach was used to determine if foliar moisture content significantly varied by foliage age (new and old foliage), species (Oregon white oak and Douglas-fir foliage), stand condition (intact, high encroached, and thinned), and time (June through November). Foliar moisture content values were log transformed to meet the normality and equal



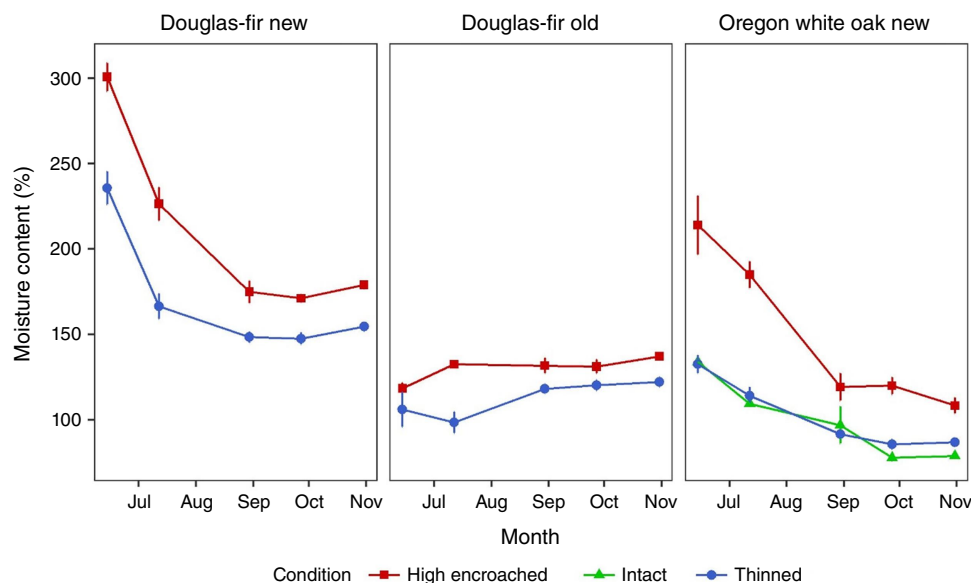
variance assumptions of residuals in each analysis. The random effect structure of the mixed effects models included a random intercept term for each unique plot. All candidate models included the fixed effect of time. Additional models included foliage age, species, or stand condition, and an additive model with foliage age, species, and stand condition. All candidate models were evaluated for multicollinearity using the `vif` function in the package `car` (Fox and Weisberg 2019). Explanatory variables with variance inflation factors  $>4$  were excluded from the top models (Hair *et al.* 2018). Model selection was determined based on the lowest Akaike information criterion (AIC) value, and in cases where the top models were within 2 AIC, the model with the fewest parameters was selected (Burnham and Anderson 1998). We report the significance of each variable considered using Type III analysis of variance. To examine the effects of stand condition on foliar moisture content, linear regression modelling was used to compare mean foliar moisture content by foliage age, foliage species, total stand basal area, and stand condition of each of the nine plots. A linear regression modelling approach was also used to examine the relationship between Oregon white oak tree physiology (midday and predawn leaf water potential, stomatal conductance). We also used a linear mixed effect modelling approach as described above to examine if foliar moisture content in Oregon white oak was significantly related to leaf water potential (midday and predawn), stomatal conductance, stand condition (intact, moderate encroached, and high encroached), and thinning treatment (thinned or unthinned).

## Results

### Stand influences on foliar moisture content

An additive model including time, species, foliage age, and stand condition best explained variation in foliar moisture content (Fig. 1). Species explained the most variation in mean foliar moisture content over the duration of the study ( $F = 251.2$ ,  $P < 0.0001$ ), with Douglas-fir foliage having 39% more foliar moisture content than Oregon white oak foliage. Foliage age also explained much of the variation in foliar moisture content ( $F = 237.2$ ,  $P < 0.0001$ ), with new foliage having 25% more foliar moisture content than old foliage. Foliar moisture content was also strongly associated with time ( $F = 122.9$ ,  $P < 0.0001$ ). Generally, foliar moisture content of new leaves was highest in June and decreased through late September. Older Douglas-fir needles tended to increase slightly in foliar moisture content over time. Stand conditions differed in foliar moisture content ( $F = 61.2$ ,  $P < 0.0001$ ). Mean foliar moisture content across all foliage ages and species over the duration of the study was about 65 and 35% higher in encroached stands than in intact ( $P < 0.0001$ ) and thinned stands ( $P = 0.0012$ ), respectively. Mean oak foliar moisture content was 2.6% higher in intact stands compared with thinned stands, but were not statistically different ( $P = 0.3945$ ).

An additive model of foliage age, species, and stand basal area were related to mean seasonal foliar moisture content (Fig. 2). Species explained the most variation in foliar moisture content ( $F = 64.1$ ,  $P < 0.0001$ ). Foliage age explained



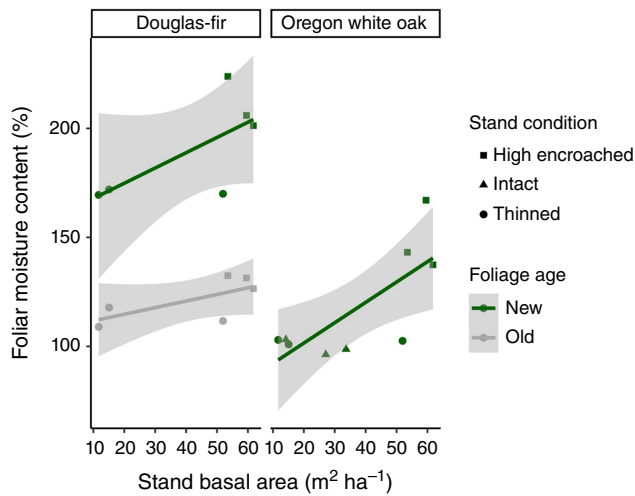
**Fig. 1.** Changes in observed foliar moisture content (mean  $\pm$  1 standard error) by species (Oregon white oak and Douglas-fir), foliage age (new and old), and stand condition (high encroached, intact, and thinned) from June through November 2018 for an oak woodland site in northwestern California, USA. Lines provide broad seasonal trends and do not consider known hourly and daily variation.

substantial variation in foliar moisture content ( $F = 53.1$ ,  $P < 0.0001$ ), with new foliage having higher foliar moisture content than old foliage. Stand basal area was positively related with foliar moisture content ( $F = 14.3$ ,  $P = 0.0015$ ), but the strength of this relationship varied by foliage type, and an interaction between the two terms was not more

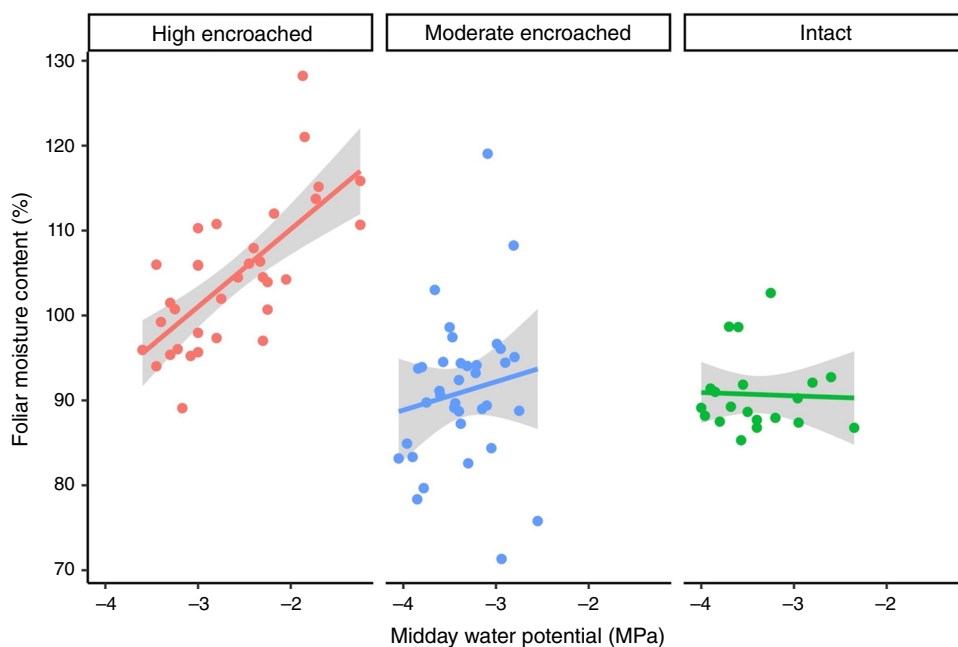
informative. Although based on univariate analysis, Oregon white oak foliar moisture content had a better relationship with stand basal area ( $R^2 = 0.56$ ,  $P = 0.02$ ) compared with relationships with either new or old Douglas-fir foliage ( $R^2 < 0.47$ ,  $P > 0.13$ ).

### Tree physiology influences on foliar moisture content

Leaf water potential was strongly related to Oregon white oak foliar moisture content, but the strength of this relationship varied with stand condition (Fig. 3). The most informative model included midday leaf water potential, stand condition, and an interaction term. Foliar moisture content across all stand conditions was better associated with midday leaf water potential ( $P < 0.0001$ ) than predawn leaf water potential ( $P = 0.12$ ). Stand condition ( $F = 7.5$ ,  $P = 0.001$ ), and the interaction of stand condition with midday leaf water potential ( $F = 4.7$ ,  $P = 0.01$ ), exerted the strongest influence on foliar moisture content. Midday leaf water potential as a factor by itself was not quite significant ( $F = 3.0$ ,  $P = 0.08$ ) but was still included in the most informative model. Based on univariate analysis for each stand condition, high encroached stands had the strongest relationship between midday leaf water potential and foliar moisture content ( $R^2 = 0.49$ ,  $P < 0.0001$ ) compared with moderate encroached or intact stands ( $R^2 < 0.02$ ,  $P > 0.398$ ). Stomatal conductance and thinning treatment were not considered to be informative in the top model. Mean midday water potential among all stands examined was also strongly positively associated with stand basal area at the plot level ( $R^2 = 0.96$ ,  $P = 0.0037$ ).



**Fig. 2.** Comparison of mean foliar moisture content collected from June to November 2018 at an oak woodland site in northwestern California, USA by species (Douglas-fir and Oregon white oak), foliage age (new and old), and stand condition (high encroached, intact, and thinned). Grey shading represents 95% confidence intervals. Based on univariate analysis, Oregon white oak foliar moisture content had a better relationship with stand basal area ( $R^2 = 0.56$ ,  $P = 0.02$ ) compared with relationships between stand basal area and new or old Douglas-fir ( $R^2 < 0.47$ ,  $P > 0.13$ ).



**Fig. 3.** Relationship between Oregon white oak midday leaf water potential and foliar moisture content by stand condition (high encroached, moderate encroached, and intact) for 1 day (25 August 2018) at midday within an oak woodland site in northwestern California, USA. Grey shading represents 95% confidence intervals. Based on univariate analysis for each stand condition, high encroached stands had the strongest relationship between midday leaf water potential and foliar moisture content ( $R^2 = 0.49$ ,  $P < 0.0001$ ) compared with this relationship in moderate encroached or intact stands ( $R^2 < 0.02$ ,  $P > 0.398$ ).

## Discussion

Our study demonstrates that seasonal foliar moisture dynamics in a northwestern Oregon white oak ecosystem were related to differences in stand condition and its influence on tree physiology. We found that increased stand density associated with Douglas-fir encroachment resulted in higher midday leaf water potential and higher foliar moisture content than in lower density stands (intact or thinned). Given the inclusion of foliar moisture content in crown fire modelling and fire danger rating systems (e.g. Van Wagner 1977; Bradshaw *et al.* 1983; Scott and Reinhardt 2001), our findings suggest the need to consider the competitive environment (i.e. stand density, leaf area index) when developing predictive models of foliar moisture content, or when assigning foliar moisture content values within crown fire modelling scenarios.

Consistent with our expectations, encroached stands supported higher foliar moisture content in both Douglas-fir and Oregon white oak compared with the more open thinned or intact stands. Our results agree with previous research that found similar differences in foliar moisture content between sheltered and exposed ecosystems in south-eastern Australia (Krix and Murray 2018). Our study advances our understanding because we were able to examine differences in stand density within the same species and site conditions, limiting the potential impacts of some confounding factors. Yet, uncertainty remains as to the direct mechanisms that contributed to the observed differences among stand conditions. We suspect that higher density stands (such as the encroached stands observed within our study) had greater canopy cover, which can reduce the amount of solar radiation that reaches the forest floor, resulting in cooler air temperature and higher relative humidity beneath the canopy (Ma *et al.* 2010; Kane 2021). Additionally, deeper and denser organic soil horizons (i.e. litter and duff) present within encroached stands (Engber *et al.* 2011) may also impede soil drying. These conditions can reduce evaporative losses of soil moisture and increase leaf water potential, contributing to higher foliar moisture content (Nolan *et al.* 2018; Balaguer-Romano *et al.* 2022). Yet, our results run contradictory to observations that increased stand density and greater leaf area index can have negative impacts on plant water status (McDowell *et al.* 2006). This inconsistency may highlight that our findings are limited to woodlands and forests located within less arid climates or under non-drought conditions. A need exists for additional research to examine these relationships under a broader range of annual and regional climate scenarios.

Although our results are supportive of the role of stand basal area modifying soil moisture conditions and their influence on foliar moisture content, there are other potential mechanisms that could explain the observed differences. An alternative possibility is that thinned and intact stands similarly had higher leaf area at the tree-scale that resulted

in lower foliar moisture content compared with encroached stands in both Douglas-fir and Oregon white oak. This may be plausible for Oregon white oak in our study because of their ability to epicormically sprout following thinning treatments (Devine and Harrington 2006); however, we observed similar foliar moisture content differences between thinned and encroached stands for Douglas-fir, a species that is a weak epicormic sprouter (Punches and Puettmann 2018). Similarly, our study had some potentially confounding effects in our comparisons between intact stands and encroached stands because of differences in tree heights and crown characteristics. However, our comparisons between encroached and thinned stands remain robust because of limited tree and crown differences between conditions for both species examined.

Another possible explanation is that intact and thinned stands differed in rooting depth and access to deeper water sources, which were not directly examined in our study. However, a complementary study that examined the depth of water source based on isotopic analysis at the same study site did not find differences between intact and high encroached stands for both Oregon white oak and Douglas-fir (Goff 2021), and thinned stands should not meaningfully differ in water source in either species 1 year after thinning, assuming rooting depth remains somewhat static. Still, future research that more explicitly examines these and other possible mechanisms to explain observed differences in foliar moisture content – and the context (e.g. climate, species, and stand density) in which they may occur – is warranted.

Our results contrasted previous findings that indicated thinning treatments did not influence leaf water potential or foliar moisture content. Where we found lower foliar moisture content in thinned stands compared with encroached stands for both Douglas-fir and Oregon white oak, differences in foliar moisture content between thinned and unthinned stands of maritime pine (*Pinus pinaster*) were not detected (Soler Martin *et al.* 2017). We suspect this discrepancy reflects climatic differences between the two studies. Although both studies have mediterranean climates with pronounced summer dry seasons, our site in northwestern California, USA was likely more moderated due to coastal proximity and the influence of summertime fog. Another possibility is that the duration of thinning effects of foliar moisture content declines over time. Our study was implemented 1 year after thinning, whereas the Soler Martin *et al.* (2017) study was implemented 7 years after thinning. It is possible that the influence of thinning decreases over time because tree species equilibrate foliar moisture content through increased leaf area and compensation of physiological processes (e.g. stomatal control, osmotic potential). The declining influence of thinning has been observed with growth responses in trees (Sohn *et al.* 2016), but further examination of the role of thinning across differing climates and its impact on leaf area, tree physiology, and foliar

moisture content are warranted, with particular attention to how these responses persist or vary with time.

Seasonal patterns of foliar moisture were generally consistent among stand conditions but differed with foliage type. Foliar moisture content of new foliage in Douglas-fir and Oregon white oak was highest in late spring/early summer and steadily decreased over the prolonged dry summer, as has been found in other species (Agee *et al.* 2002). Old Douglas-fir foliage was lowest at the start of the fire season and generally increased over time. However, we recognise that a portion of the observed seasonal changes in foliar moisture content likely coincided with dry mass changes due to leaf phenology (Kozłowski and Clausen 1965; Jolly *et al.* 2014), but these phenological changes were not examined as part of our study.

The effects of species (Douglas-fir and Oregon white oak) on foliar moisture content, independent of foliage age, were persistent in our study, where new Douglas-fir foliage maintained higher foliar moisture content than new Oregon white oak foliage. Differences in foliar moisture content between these two species are expected, given the physiological, phenological, and structural (e.g. root depth) differences between them that relate to plant water use and drought tolerance strategies. It is well known that Oregon white oak is much more drought tolerant than Douglas-fir (Niinemets and Valladares 2006; Beckmann *et al.* 2021). A complementary study conducted at the same site found that Oregon white oak was accessing soil water at deeper soil depths than Douglas-fir (Goff 2021), partially reflecting differences in tree ages between species at our sites (Douglas-fir were around 70 years old whereas Oregon white oak were around 120–170 years old). Interestingly, in our study, Oregon white oak had lower foliar moisture content compared with Douglas-fir, contradicting previous research that has shown shallower rooted species tend to have lower foliar moisture content (Brown *et al.* 2022). It is therefore more likely that our observed differences in foliar moisture content between these two species reflect anatomical, morphological (e.g. leaf mass area), and physiological differences that relate to plant hydraulic strategies (Kelly 2016; Hahm *et al.* 2018; Beckmann *et al.* 2021).

Our observations of foliar moisture content in Douglas-fir ranged between 150 and 300% in new foliage and 100–150% in old foliage between June and November. These values were slightly higher than recorded in a previous study conducted from July to September in Montana, which had values between 120 and 200% and 80 and 120% for new and old Douglas-fir foliage, respectively (Philpot and Mutch 1971). Slight differences in the range of foliar moisture content between studies likely reflect a combination of sample timing and climatic differences between the two sites, with our site in California having relatively milder temperatures during the fire season due in part to coastal proximity. We are unaware of prior studies that have examined foliar moisture content in Oregon white oak. However, foliar moisture

content of deciduous broadleaf tree species in Canada ranged between 130 and 250% from spring to summer (Van Wagner 1967), which were slightly higher than our observations in Oregon white oak (90 and 220%) over the same time period.

We found that differences in Oregon white oak foliar moisture content were associated with tree physiological measures that varied with stand condition. Midday leaf water potential (rather than predawn leaf water potential) was significantly related to foliar moisture content in Oregon white oak leaves, but was contingent on stand condition. Previous studies in other fire-prone ecosystems have found predawn leaf water potential to be better associated with foliar moisture content (Nolan *et al.* 2018). We are uncertain why foliar moisture content was better related to midday leaf water potential and only in the high encroached stands of our study. The stronger role of midday leaf water potential in high encroached stands may indicate that foliar moisture content is more responsive to diel changes in stand microclimate conditions than previously appreciated, but a deeper examination is necessary. Additionally, we only examined leaf water potential among stands on 1 day, and it is possible that this relationship may shift under wetter or drier conditions within or among years.

In our study, we found that tree- and stand-level factors can influence foliar moisture content within an Oregon white oak ecosystem of northern California. Our findings provide further validation of previous calls to better integrate ecophysiological approaches and concepts to understand foliar moisture content dynamics (Jolly and Johnson 2018; Nolan *et al.* 2020). Improved estimates of foliar moisture content and the role of stand conditions can also provide managers and fire behaviour analysts with better assumed values for modelling potential crown fire behaviour, and for fuel management planning. Given the increased incidence of fire activity and severity in fire-prone ecosystems over the past few decades (Westerling 2016; Parks and Abatzoglou 2020), there is a strong need to better predict crown fire behaviour and its contributing factors, such as foliar moisture content. This need is likely to increase over the coming decades due in part to the potential for climate change to extend the duration of low foliar moisture content below critical thresholds of crown fire ignition and spread (Ma *et al.* 2021).

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**Data availability.** Data are available at <https://doi.org/10.6084/m9.figshare.20485665> (Kane et al. 2022).

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