

Strong vertical gradient of foliar moisture content within tall conifers

Jeffrey M. Kane

jkane@humboldt.edu

California State Polytechnic University

Lucy P. Kerhoulas

California State Polytechnic University

Olivia L. Moskowitz

California State Polytechnic University

Short Report

Keywords: Douglas-fir, fire behavior, live fuel moisture, redwood, Sitka spruce, tall trees

Posted Date: March 25th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-8960176/v1>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Additional Declarations: No competing interests reported.

Version of Record: A version of this preprint was published at Fire Ecology on July 24th, 2026. See the published version at <https://doi.org/10.1186/s42408-026-00555-8>.

Abstract

Background

Foliar moisture content (FMC) is a central determinant of plant flammability and strongly influences fire behavior and effects. Characterization of FMC in most fire models is often quite simplistic with limited consideration for within stand and tree variation. Theory and trait-based evidence suggest that FMC may vary vertically within the crowns of tall conifers due to hydraulic limitations and associated foliar morphology changes but has received limited direct examination. In this study, we examined whether FMC varied with vertical crown position in three of the tallest conifer species of northwestern California: coast redwood (*Sequoia sempervirens*), Douglas-fir (*Pseudotsuga menziesii*), and Sitka spruce (*Picea sitchensis*). Specifically, we tested whether: (1) FMC decreases with increasing crown position height, (2) the vertical FMC gradient persists across both new and old foliage, (3) the strength of the vertical FMC gradient varies by species, and (4) the vertical FMC gradient is associated with changes in leaf and shoot morphology.

Results

We found that FMC declined significantly with increasing relative crown position height for both new and old foliage in all three tree species. FMC near mid-crown positions approximately 20% higher than at treetops. New foliage had approximately 14% higher FMC than old foliage but had consistent relationships with crown position height. The differences in FMC among species were weak and smaller than expected, with mean values differing by less than 10% among species. FMC was associated with both leaf and shoot morphology but shoot mass area (SMA) was more strongly related to FMC than leaf mass area (LMA).

Conclusions

Our results provide evidence of strong vertical gradients in FMC within tall conifer crowns, likely driven by height-related hydraulic constraints and associated morphological changes. These findings suggest that FMC estimates derived from measurements of the upper-canopy, including many remote sensing approaches, may underestimate whole-crown moisture, and thus contribute to overestimation of crown fire initiation and spread. Incorporating vertical FMC gradients into fire behavior models could improve predictions of crown fire initiation and spread, particularly in tall forest systems.

Background

Foliar moisture content (FMC) in live woody plants is a central determinant of plant flammability with strong implications for fire behavior and effects (Xanthopoulos and Wakimoto 1993; Dimitrakopoulos and Papaioannou 2001; Weise et al. 2005; Pellizzaro et al. 2007; Varner et al. 2021). The high specific

heat of water, combined with the energetic requirements for evaporation prior to combustion, dampens fire ignition and spread (Simms and Law 1967). Most forest fire behavior models include FMC (Van Wagner 1977; Bradshaw et al. 1983; Scott and Reinhardt 2001), with many studies clearly identifying critical thresholds that are used to predict wildland fire dynamics (Dennison et al. 2008; Nolan et al. 2016; Pimont et al. 2019). Typically, these models rely on singular values to represent horizontal variation across a given landscape, and do not account for vertical variation.

Recent advances in process-based fire modeling hold promise to better represent within-crown variation in FMC but will require a deeper ecophysiological understanding of FMC and its implications to wildland fire (e.g., pyro-ecophysiology; Jolly and Johnson 2018; Dickman et al. 2023; Jolly et al. 2025). Given the rapid increases in global temperatures and increased incidence of wildfires throughout many forested ecosystems (e.g., Abatzoglou et al. 2021; Collins et al. 2022; Parisien et al. 2023), there is substantial need to improve our ability to estimate and represent FMC to better inform appropriate strategies to coexist with fire.

Woody plant species are well known to vary widely in FMC (e.g., Keyes 2006; Pivovarov et al. 2019). This variation largely reflects differences in plant morphology, physiology, and phenology in combination with climate and other environmental factors that influence annual and seasonal variation in FMC, such as soil moisture availability, vapor pressure deficit, and others (Schwilk and Ackerly 2001; Nolan et al. 2020; Ruffault et al. 2022). Increasing evidence suggests that leaf mass area (LMA) is a strongly influential morphological trait that can capture seasonal variation in water and carbon content of leaves among species (Nolan et al. 2018, 2022; Jolly et al. 2025), with implications toward leaf flammability (Krix and Murray 2018). In a recent study, LMA was negatively related to FMC and explained over 90% of the variation in FMC within and among 11 conifer species of the Intermountain Western US (Jolly et al. 2025). Together with repeated observations of vertical gradients in LMA across multiple species (Chin and Sillett 2019; Kerhoulas et al. 2020), these results suggest that gradients of foliar moisture may occur within trees across species, but to our knowledge this line of inquiry has not yet been directly investigated.

Despite advances in understanding, the physiological basis for within-tree vertical gradients in FMC remains less well understood. Theory suggests that leaves located higher in the canopy may exhibit lower FMC due to increased evaporative demand and reduced leaf water potential associated with gravitational and frictional constraints on water transport, i.e. hydraulic limitation (Ryan and Yoder 1997; Koch et al. 2004). The well-documented trend of increasing LMA with height in tall trees, coupled with the finding that FMC is negatively related to LMA (Nolan et al. 2018, 2022; Jolly et al. 2025) further supports the prediction that FMC decreases with height in tall crowns. Conversely, some evidence suggests that upper-canopy leaves may maintain comparable or even higher FMC than in lower crown positions through compensatory traits that can potentially mitigate height-related water stress. Some of these traits include increased cuticle thickness (Chin and Sillett 2019), greater exposure to atmospheric water deposits such as rain and fog, greater foliar uptake capacity (Kerhoulas et al. 2020), and greater stomatal regulation (Ambrose et al. 2010). There is also the possibility that within-tree FMC vertical

gradients are weak due to uptake of atmospheric water deposits throughout tree crowns via foliage (Limm et al. 2009), twigs (Chin et al. 2025), bark (Earles et al. 2016), and/or branch adventitious roots growing into canopy soils (i.e., arboreal histosols) (Sillett and Bailey 2003; Enloe et al. 2006; Sillett and Van Pelt 2007).

If strong vertical gradients in FMC exist within trees, estimates may differ substantially among methodological approaches. For instance, estimates of FMC are commonly derived from either gravimetric sampling based on ground-based measurements or from spectral reflectance differences from aerial measurements using remote sensing techniques (Zahn and Henson 2011; Yebra et al. 2013). If a strong vertical gradient in FMC is present within trees, measurements and estimates may vary substantially between these approaches, with important implications for crown fire behavior (Van Wagner 1977; Bradshaw et al. 1983; Scott and Reinhardt 2001) and associated fire effects.

Tall conifer species of the temperate rainforests of northwestern California provide an ideal natural system for examining potential vertical gradients in foliar moisture content. Species such as coast redwood (*Sequoia sempervirens*), Douglas-fir (*Pseudotsuga menziesii*), and Sitka spruce (*Picea sitchensis*) attain exceptional heights and experience large within-crown gradients in microclimate, hydraulic tension, structural leaf traits (Oldham et al. 2010; Chin and Sillett 2019), and physiology (Mullin et al. 2009; Ambrose et al. 2010). Additionally, these forests also have a documented history of frequent low to moderate severity fire regime (Lorimer et al. 2009). Collectively, these tall temperate rainforests offer a unique opportunity to test hypotheses about height-related changes in FMC across one of the widest vertical forest gradients available.

We sampled live FMC across a large vertical gradient in three tall conifer species of northwestern California. The goal of this research was to determine if FMC varied vertically within tree crowns of large redwood, Douglas-fir, and Sitka spruce. The specific objective of this study was to examine the relationship between FMC and crown collection height in new and old foliage among the three conifer species. We hypothesized that: (1) FMC of both new and old foliage decreases with sample collection height due to gravity-driven hydraulic limitations (Koch et al. 2004), (2) FMC is higher in new foliage compared to old foliage, but relationships with crown position height are consistent, and (3) the strength of the vertical FMC gradient varies by species, with less variation with height observed in Sitka spruce compared to redwood or Douglas-fir due to its demonstrated higher foliar water uptake capacity and relatively lower rate of change in leaf mass area with crown collection height (Limm et al. 2009; Chin and Sillett 2017; Kerhoulas et al. 2020). Finally, we hypothesized that (4) decreases in FMC with height are associated with increases in LMA across all species (Jolly et al. 2025). Results of this research will advance our understanding of within-tree variation in FMC with implications toward enhancing methodological approaches to quantify FMC and improving modeled estimates of fire behavior and effects.

Methods

Study site and experimental design

The study was located in a remnant old-growth forest within the Yurok Redwood Experimental Forest near Klamath, California, USA (41.58202, -124.06361). The dominant conifer species included coast redwood, Douglas-fir, and Sitka spruce. The site has a temperate, cool-summer Mediterranean climate with a regular occurrence of summertime fog. Average daily temperatures are relatively stable, typically ranging from 15.0°C in the summer to 8.5°C in January. Rainfall occurs primarily in the winter months between October and March, with a 30-year average annual rainfall of 2110 mm between 1981 and 2010 (PRISM Climate Group 2025). During the study (November 2024–February 2025), average daily temperatures ranged from 2.9 to 13.5°C and had 1590 mm of accumulated rainfall (PRISM Climate Group 2025).

Soils at the study site are deep, well-developed profiles formed from easily weathered rocks of the Franciscan Formation. Melbourne series soils dominate the area, with small patches of Hugo and Atwell series and alluvial soils along the main drainage, High Prairie Creek (Adams et al. 2003). Topography is highly variable, with slopes ranging from 0–75%. Prior to Euro-American colonization, most redwood forests experienced predominantly low severity fire every 6–26 years (Lorimer et al. 2009). However, fire has been absent from the study location since at least 1900 (CALFIRE 2025).

Our experimental design involved sampling foliage from nine tall trees (three trees per species) with a minimum height of 60 m and a minimum diameter at breast height (dbh; 1.37 m) of 1.8 m (Appendix A). Trees were selected based on accessibility and suitability for safe climbing into the canopy and were accessed using established nondestructive climbing techniques (Jepson 2000; Kramer et al. 2018). Foliage sampling occurred during the wet season between November 2024 and February 2025, a period when access was permitted and did not coincide with activities of threatened or endangered wildlife species, such as Marbled Murrelet (*Brachyramphus marmoratus*) nesting. Within each tree, foliage was sampled at three vertical crown positions: crown base (bottom of the live crown), mid-crown (middle of the crown), and treetop (as near the treetop as was safe to climb). At each crown position, new (< 1 year) and old (> 1 year) foliage was sampled.

Data collection

Measurement of tree characteristics included dbh, total tree height, crown base height, and crown sampling height. All heights were measured as vertical distances from the ground to the respective height of interest using a 100-m tape hung from the treetop. For each foliar sample collection, we also recorded the diameter of the primary branch at its base adjacent to the bole.

Foliar moisture samples were collected at mid-day (11:00–15:00) on non-rainy days when the foliage was dry to minimize undesired influence of precipitation and dew (Zahn and Henson 2011). At each crown position, > 10 g of foliage were collected per sample (average = 53.8 g). New and old foliage were sampled separately and immediately placed into pre-weighed, labeled, 2 mm thick sealable plastic bags.

Samples were collected from the outer branches whenever possible, and from the mid-branch when necessary, but did not include branch wood or dead or damaged needles. Samples were kept in insulated coolers with ice packs to reduce moisture loss during transportation. Samples were refrigerated overnight when immediate lab processing was not possible. Foliage samples were weighed, removed from the plastic bag, placed into separate paper bags, and oven-dried for at least three days at 70°C. Each sample was removed from the paper bag and weighed after drying. We calculated percent foliar moisture content for each sample by subtracting the wet weight from the dry weight, dividing by the dry weight, and multiplying by 100.

Additional foliage and shoot samples were collected to quantify leaf and shoot morphological traits (LMA and SMA). At each crown position (crown base, mid-crown, and treetop) for each tree we collected three samples of both leaf ages (new and old). Samples were collected using the same methods described above. To quantify LMA on each shoot (approximately 8 cm in length), we first removed the leaves, scanned the leaves at 600 dpi (Epson America, Inc., Long Beach, CA, USA), and used ImageJ (National Institutes of Health, Bethesda, MD, USA) to digitally measure the projected leaf area (cm²). We then weighed the leaves after drying at 60°C for 48 h to determine leaf dry mass (g). Finally, we calculated LMA (g m⁻²) for each shoot by dividing total leaf dry mass by total leaf area and multiplying by 10,000.

In addition to LMA, we quantified shoot mass area (SMA), as redwood foliage grows in shoots (i.e., leaves are not shed individually); by using SMA, our FMC data would be potentially more comparable across the three conifer species. Further, because twig uptake of water can quickly increase woody water content by > 50% in conifers (Chin et al. 2025), the effects of fine stems' FMC are likely of comparable importance to fire behavior and effects as leaf FMC. To calculate SMA on each shoot, we followed the same steps as for LMA calculation but also included stems. Thus, SMA (g m⁻²) was calculated for each shoot by dividing the shoot dry mass by the shoot area and multiplying by 10,000. To account for within-crown morphological variability from each sample, LMA and SMA were calculated based on the average of three replicates per crown position height and foliage age.

Data analysis

To address our first three hypotheses, we applied a linear mixed effects modelling approach using the *lmer* function in the *lme4* package (Bates et al. 2015) in the R statistical environment (version 4.4.3, R Development Core Team 2025). This approach was used to determine if FMC significantly varied by foliage age (new and old foliage), species (redwood, Douglas-fir, and Sitka spruce), and crown collection height (m). For crown collection height, we considered both absolute crown collection height and relative crown collection height. Relative crown collection height was calculated as the ratio between absolute crown collection height and total tree height. All models included a random intercept term for individual trees to account for the lack of independence of sampling different crown position heights within the same tree. Candidate models included all individual, additive, and interaction combinations of the fixed effects including: foliage age, species, and crown collection height (absolute or relative). To address our

fourth hypothesis, we applied the same linear mixed effects modeling approach as above but replaced foliage age and crown collection height with morphology measurements (LMA and SMA) and employed the same random effects structure. We also compared which morphological variable, LMA or SMA, was more strongly associated with crown collection height.

All candidate models were evaluated for multicollinearity using the `vif` function in the `car` package (Fox and Weisberg 2019). Explanatory variables with variance inflation factors > 2 were excluded from consideration from the candidate 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). Statistical significance of each variable was evaluated at $\alpha = 0.05$ using a Type III analysis of variance. Model performance was evaluated using marginal (R^2_m ; variance explained by fixed effects only) and conditional (R^2_c ; variance explained by both fixed and random effects) coefficients of determination. We also assessed performance by calculating the root mean squared error (RMSE) of each model.

Results

We found support for our first two hypotheses, with FMC consistently decreasing with crown collection height in both new and old foliage across all species (Fig. 1). An additive model including relative collection height ($p < 0.001$), foliage age ($p < 0.0001$), and species ($p = 0.186$), performed well ($R^2_m = 0.52$, $R^2_c = 0.70$, RMSE = 7.7%). FMC values across all samples, foliage age classes, and species ranged between 98 and 175%. A portion of this variation was associated with foliage age, where new foliage (mean = 138%) had approximately 14% higher FMC than old foliage (mean = 124%), but the effect of foliage age on FMC across the vertical gradient was consistent. Relative collection height (i.e., collection height expressed as proportion of total tree height) was more informative than absolute collection height. Modeled FMC at a relative collection height of 0.5 (50% of total tree height) was about 20% higher than at a relative collection height of 1.0 (treetop).

Our third hypothesis was not supported, as species had a weak effect on FMC and observed differences were not in the expected direction (Fig. 1). Although the species term was retained in the most informative model, average FMC differed by only 2–8% among species. Contrary to our expectations, Douglas-fir ($134 \pm 4\%$) and redwood ($132 \pm 3\%$) had similar average FMC values and Sitka spruce ($126 \pm 3\%$) exhibited lower values. We also did not find a significant interaction effect of species and relative collection height that would indicate the strength of the relationship with FMC varied among species.

Our fourth hypothesis was supported, with FMC decreasing as LMA increased ($p = 0.015$; $R^2_m = 0.16$, $R^2_c = 0.51$, RMSE = 11.8%). However, FMC exhibited a stronger negative relationship with SMA (Fig. 2) than with LMA. An additive model including SMA ($p < 0.0001$) and species ($p = 0.333$) outperformed the corresponding model including LMA and species ($R^2_m = 0.24$, $R^2_c = 0.38$, RMSE = 11.4%). Modeled FMC at an SMA of 150 g m^{-2} was about 17% higher than at an SMA of 250 g m^{-2} . Variation in SMA was more

strongly associated with sampling height ($R^2_m = 0.41$, $R^2_c = 0.54$) than variation in LMA ($R^2_m = 0.07$, $R^2_c = 0.82$).

Discussion

To our knowledge, this study is the first to demonstrate clear evidence for a strong vertical gradient in FMC within both new and old foliage of tall trees. We demonstrate that FMC decreases with increasing canopy position height across three tree species and that new foliage (< 1 year) had higher FMC than old foliage (> 1 year). Differences in FMC among the three tree species were relatively small; however, morphological traits explained a substantial amount of variation. Interestingly, we found that SMA was better associated with foliar moisture content changes than LMA. The results of this study have implications for the development of foliar moisture content models with potential influence on canopy fire initiation and spread.

The detection of a strong vertical gradient in FMC within tall trees corroborates and connects previous research examining tree water and morphological relationships. Our observations of decreased FMC are consistent with documented decreases in leaf water potential along vertical gradients within trees (e.g., Chin and Sillett 2019; Kerhoulas et al. 2020). Leaves at higher crown positions experience greater hydraulic limitation, resulting in lower leaf water potential and reduced FMC. Our data collection occurred outside of the typical fire season in the region. We anticipate that FMC values during the summer and late fall would be much lower, especially during an extended drought, and that the strength of the vertical gradient may be more pronounced during drier periods. Future studies that examine seasonal variation in this vertical gradient are needed. Because our study intentionally focused on very tall trees, additional research that examines the vertical patterns within smaller trees more representative of most fire-prone forests is warranted.

The vertical gradient of FMC was more strongly associated with relative crown collection height than absolute crown collection height. We had expected that absolute height would be more influential because of the collective effect of gravitation and frictional forces on water potential that are increasingly exerted with height above the ground (Ryan and Yoder 1997; Koch et al. 2004). The stronger relationship of relative height suggests that sun exposure or associated microclimate differences within the vertical crown gradient may also influence FMC. More simply, increased sun exposure at treetops may further reduce FMC in addition to height-related influences. Prior research has demonstrated that microclimatic factors, such as vapor pressure deficit, are associated with live fuel moisture (Griebel et al. 2023).

Despite our comparisons of FMC across three different species of tall trees, we did not find a strong influence of species. Our top models included species as an informative variable, but species tended to explain little variation in FMC. This finding suggests that FMC variation in tall trees may be driven more strongly by hydrostatic constraints and microclimate than by species-specific traits (leaf morphology, physiology, and rooting strategies). We did not find support for our hypothesis that Sitka spruce would

have the highest FMC and smallest change across the vertical gradient compared to redwood or Douglas-fir. In fact, Sitka spruce FMC values were slightly lower on average than the other two species. Preliminary results from a companion study indicate that foliar water uptake capacity increases with height in these three species but is negatively related to FMC (Hewitt and Kerhoulas, unpublished data). One possibility is that increased uptake capacity in Sitka spruce reflects greater cuticular or epidermal damage (Kerhoulas et al. 2020). While this condition can facilitate water uptake, it is also likely to contribute to greater leaf moisture loss during warmer and drier periods. Nonetheless, the small sample size of our study likely limited our ability to detect species-level differences, especially given our observations of high variation in FMC among individual trees. Future studies that examine differences in FMC along vertical gradients among species would benefit from examining a wider number of individuals across each species.

Our results suggest that the influence of the vertical hydraulic gradient on FMC outweighs potential compensatory strategies such as increasing cuticle thickness or atmospheric water uptake. Both LMA and SMA increased with foliage height within the tree crown across all three species and were associated with lower FMC in both new and old leaves. This pattern suggests vertical variation in leaf and shoot morphology reinforces the observed decline of FMC with increasing water stress. Our observations of clear relationships between leaf morphology and FMC are consistent with other studies that have demonstrated these across species, foliage ages, and seasons (Nolan et al. 2018, 2022; Jolly et al. 2025). Notably, SMA was more informative and more strongly related to FMC than LMA. We speculate that SMA may better characterize FMC than LMA because trees can uptake and store moisture within their shoots as well as their leaves (Limm et al. 2009; Chin et al. 2025).

While our study focused on determining relationships of FMC with vertical height and leaf morphology, the resulting models indicated substantial unexplained variation in FMC among individual trees. This outcome suggests there are other factors that influence FMC among trees that were not accounted for in our study. This unexplained variation may reflect differences among individual trees in rooting depth and access to soil moisture and groundwater. Prior research has demonstrated clear differences in FMC associated with soil moisture availability and rooting depth among plant functional types (Brown et al. 2022), however, we are unaware of any studies that have examined variation within trees of a given species. Individual trees also likely varied in their competitive environments, such as the size, density, and composition of neighboring trees. Existing research on this topic is limited, but some have demonstrated effects of stand density and age on FMC (Krix and Murray 2018, McNamara et al. 2019, Kane et al. 2023). In addition to the potential influence of neighboring trees on soil moisture availability, it is possible that neighboring trees can also influence the light and microclimate within a crown that may contribute variation in FMC. Future studies that integrate these influences would advance our understanding and improve predictive FMC models.

Conclusions

Our findings of strong vertical gradients in FMC across three tall tree species provide insights that can help advance our understanding of the factors that contribute to the spatial variation in FMC. These results have direct implications for methodological considerations, enhanced estimations of FMC, and better predictions of fire behavior and effects. Since most methods used to estimate FMC rely on remote sensing technologies (e.g., satellites, airborne sensors) that sample the upper portion of tree crowns, our results suggest that such approaches may underestimate FMC that could contribute to overestimation of crown fire initiation and spread. Because FMC varies widely within trees, predictions of fire behavior and effects will likely benefit from models that explicitly represent vertical crown gradients in FMC. Considering the advancement of computational fluid dynamic models of wildland fire, development of 3-D representations of FMC would be complementary to these efforts and likely improve our ability to predict fire behavior and effects. Given rapid increases in global fire activity, improving our ability to predict wildfires is essential. Efforts that promote greater understanding toward the important factors that contribute to wildland fire behavior, such as FMC, can help advance this effort.

Abbreviations

AIC	Akaike information criterion
DBH	diameter at breast height
FMC	foliar moisture content
LMA	leaf mass area
RMSE	root mean squared error
SMA	shoot mass area

Declarations

Acknowledgements

We thank Nicholas Kerhoulas, Rebecca Hewitt, and Cory Nielson for help with fieldwork; Jim and Naomi Campbell-Spickler for private access to our study site; the Pacific Southwest Research Station for granting a research permit (#046636) to work in the Yurok Redwood Experimental Forest within Six Rivers National Forest.

Authors' contributions

JMK and LPK designed the study. LPK and OLM collected data. JMK conducted statistical analysis and developed the initial manuscript draft. JMK, LPK, and OLM reviewed and edited drafts of the manuscript.

LPK secured research funding.

Funding

The research was supported by funding from Save the Redwoods League (Grant #178).

Data availability

All data developed and used in this study will be made available upon reasonable request to the corresponding authors.

Competing interests

The authors declare that they have no competing interests.

References

1. Abatzoglou, J.T., D.S. Battisti, A.P. Williams, W.D. Hansen, B.J. Harvey, and C.A. Kolden. 2021. Projected increases in western US forest fire despite growing fuel constraints. *Communications Earth & Environment* 2 (1): 227. <https://doi.org/10.1038/s43247-021-00299-0>.
2. Adams, M.B., L.H. Loughry, L.L. Plaugher. 2004. Experimental forests and ranges of the USDA Forest Service. NE-GTR-321. U.S. Department of Agriculture, Forest Service, Northeastern Research Station.
3. Ambrose, A.R., S.C. Sillett, G.W. Koch, R. Van Pelt, M.E. Antoine, and T.E. Dawson. 2010. Effects of height on treetop transpiration and stomatal conductance in coast redwood (*Sequoia sempervirens*). *Tree Physiology* 30 (10): 1260–72. <https://doi.org/10.1093/treephys/tpq064>.
4. Anderson, H.E. 1990. Moisture diffusivity and response time in fine forest fuels. *Canadian Journal of Forest Research* 20 (3): 315–325.
5. Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67 (1). <https://doi.org/10.18637/jss.v067.i01>.
6. Bradshaw, L.S., J.E. Deeming, R.E. Burgan, and J.D. Cohen. 1983. *The 1978 National Fire-Danger Rating System: Technical Documentation*. General Technical Report. INT-GTR-169. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. <https://doi.org/10.2737/INT-GTR-169>.
7. Brown, T.P., Z.H. Hoylman, E. Conrad, Z. Holden, K. Jencso, and W.M. Jolly. 2022. Decoupling between soil moisture and biomass drives seasonal variations in live fuel moisture across co-occurring plant functional types. *Fire Ecology* 18 (1): 14. <https://doi.org/10.1186/s42408-022-00136-5>.
8. Burnham K.P., and D.R. Anderson. 1998. *Model Selection and Inference: A Practical Information-theoretic Approach*. Springer. New York, New York, USA.
9. CALFIRE. 2020. *CalFire FRAP-Fire Perimeters*. <https://frap.fire.ca.gov/frap-projects/fire-perimeters/>. Assessed September 21, 2025.

10. Chin, A.R.O., A. Gessler, P. Guzmán-Delgado, R.D. Manzanedo, M. Saurer, and J. Hille Ris Lambers. 2025. Rainwater uptake in conifer twigs: Five experiments tell a story of absorption, storage, and transport. *Journal of Experimental Botany* 76 (12): 3515–26. <https://doi.org/10.1093/jxb/eraf087>.
11. Chin, A.R.O., and S.C. Sillett. 2019. Within-crown plasticity in leaf traits among the tallest conifers. *American Journal of Botany* 106 (2): 174–86. <https://doi.org/10.1002/ajb2.1230>.
12. Collins, L., H. Clarke, M.F. Clarke, S.C. McColl Gausden, R.H. Nolan, T. Penman, and R. Bradstock. 2022. Warmer and drier conditions have increased the potential for large and severe fire seasons across south-eastern Australia. *Global Ecology and Biogeography* 31 (10): 1933–48. <https://doi.org/10.1111/geb.13514>.
13. Dennison, P.E., M.A. Moritz, and R.S. Taylor. 2008. Evaluating predictive models of critical live fuel moisture in the Santa Monica Mountains, California. *International Journal of Wildland Fire* 17 (1): 18–27. <https://doi.org/10.1071/WF07017>.
14. Dickman, L.T., A.K. Jonko, R.R. Linn, I. Altintas, A.L. Atchley, A. Bär, A.D. Collins, J. Dupuy, M.R. Gallagher, J.K. Hiers, C.M. Hoffman, S.M. Hood, M.D. Hurteau, W.M. Jolly, A. Josephson, E.L. Loudermilk, W. Ma, S.T. Michaletz, R.H. Nolan, J.J. O'Brien, R.A. Parsons, R. Partelli-Feltrin, F. Pimont, V. Resco de Dios, J. Restaino, Z.J. Robbins, K.A. Sartor, E. Schultz-Fellenz, S.P. Serbin, S. Sevanto, J.K. Shuman, C.H. Sieg, N.S. Skowronski, D.R. Weise, M. Wright, C. Xu, M. Yebra, and N. Younes, 2023. Integrating plant physiology into simulation of fire behavior and effects. *New Phytologist* *nph.18770*. <https://doi.org/10.1111/nph.18770>
15. Dimitrakopoulos, A.P., and K.K. Papaioannou. 2001. Flammability assessment of Mediterranean forest fuels. *Fire Technology* 37 (April): 143–52.
16. Earles, J.M., O. Sperling, C. L.C.R. Silva, A.J. McElrone., C.R. Brodersen, M.P. North, and M.A. Zwieniecki. 2016. Bark Water Uptake Promotes Localized Hydraulic Recovery in Coastal Redwood Crown. *Plant, Cell & Environment* 39 (2): 320–28. <https://doi.org/10.1111/pce.12612>.
17. Enloe, H.A., R.C. Graham, and S.C. Sillett. 2006. Arboreal histosols in old-growth redwood forest canopies, northern California, *Soil Science Society of America Journal* 70 (2): 408-418.
18. Fox J., and S. Weisberg S. 2019. *An R companion to Applied Regression*. Sage. Thousand Oaks, California.
19. Griebel, A., M.M. Boer, C. Blackman, B. Choat, D.S. Ellsworth, P. Madden, B. Medlyn, V. Reco de Dios, A. Wujeska-Klaue, M. Yebra, N. Younes Cardenas, and R.H. Nolan. 2023. Specific leaf area and vapour pressure deficit control live fuel moisture content. *Functional Ecology* 37 (3): 719–731. <https://doi.org/10.1111/1365-2435.14271>.
20. Hair, J.F., W.C. Black, B.J. Babin, and R. Anderson. 2018. *Multivariate Data Analysis*. Cengage, United Kingdom.
21. Jepson, J., 2000. *The Tree Climber's Companion*. Beaver Tree Publishing, Longville, MN.
22. Jolly, W.M., E.T. Conrad, T.P. Brown, and S.C. Hillman. 2025. Combining ecophysiology and combustion traits to predict conifer live fuel moisture content: A pyro-ecophysiological approach. *Fire Ecology* 21 (1): 19. <https://doi.org/10.1186/s42408-025-00361-8>.

23. Jolly, W. M., and D.M. Johnson. 2018. Pyro-ecophysiology: Shifting the paradigm of live wildland fuel research." *Fire* 1 (1): 8. <https://doi.org/10.3390/fire1010008>.
24. Kane, J.M., L.P. Kerhoulas, and G.S. Goff. 2023. Conifer encroachment increases foliar moisture content in a northwestern California oak woodland. *International Journal of Wildland Fire* 32 (5): 728–37.
25. Kerhoulas, L.P., A.S. Weisgrau, E.C. Hoeft, and N.J. Kerhoulas. 2020. Vertical gradients in foliar physiology of tall *Picea sitchensis* trees. *Tree Physiology* 40 (3): 321–32. <https://doi.org/10.1093/treephys/tpz137>.
26. Keyes, C.R. 2006. Role of foliar moisture content in the silvicultural management of forest fuels. *Western Journal of Applied Forestry* 21 (4): 228–231. <https://doi.org/10.1093/wjaf/21.4.228>.
27. Koch, G.W., S.C. Sillett, G.M. Jennings, and S.D. Davis. 2004. The limits to tree height. *Nature* 428 (6985): 851–54. <https://doi.org/10.1038/nature02417>.
28. Kramer, R.D., S.C. Sillett, and R. Van Pelt. 2018. Quantifying aboveground components of *Picea sitchensis* for allometric comparisons among tall conifers in North American rainforests. *Forest Ecology and Management* 430 (December): 59–77. <https://doi.org/10.1016/j.foreco.2018.07.039>.
29. Krix, D.W., and B.R. Murray. 2018. Landscape variation in plant leaf flammability is driven by leaf traits responding to environmental gradients. *Ecosphere* 9 (2): e02093. <https://doi.org/10.1002/ecs2.2093>.
30. Limm, E.B., K.A. Simonin, A.G. Bothman, and T.E. Dawson. 2009. Foliar water uptake: A common water acquisition strategy for plants of the redwood forest. *Oecologia* 161 (3): 449–59. <https://doi.org/10.1007/s00442-009-1400-3>.
31. Lorimer, C.G., D.J. Porter, M.A. Madej, J.D. Stuart, S.D. Veirs Jr., S.P. Norman, K.L. O'Hara, and W.J. Libby. 2009. Presettlement and modern disturbance regimes in coast redwood forests: Implications for the conservation of old-growth stands. *Forest Ecology and Management* 258 (7): 1038–54. <https://doi.org/10.1016/j.foreco.2009.07.008>.
32. McNamara B.A., J.M. Kane, and D.F. Greene. 2019. Post-fire fuel succession in a rare California, USA, closed-cone conifer. *Fire Ecology* (15): 39. <https://doi.org/10.1186/s42408-019-0059-3>.
33. Mullin, L.P., S.C. Sillett, G.W. Koch, K.P. Tu, and M.E. Antoine. 2009. Physiological consequences of height-related morphological variation in *Sequoia sempervirens* foliage. *Tree Physiology* 29 (8): 999–1010. <https://doi.org/10.1093/treephys/tpp037>.
34. Nolan, R.H., M.M. Boer, V. Resco De Dios, G. Caccamo, and R.A. Bradstock. 2016. Large-scale, dynamic transformations in fuel moisture drive wildfire activity across southeastern Australia. *Geophysical Research Letters* 43 (9): 4229–38. <https://doi.org/10.1002/2016GL068614>.
35. Nolan, R.H., C.J. Blackman, V. Resco De Dios, B. Choat, B.E. Medlyn, X. Li, R.A. Bradstock, and M.M. Boer. 2020. Linking forest flammability and plant vulnerability to drought. *Forests* 11 (7): 779. <https://doi.org/10.3390/f11070779>.
36. Nolan, R.H., B. Foster, A. Griebel, B. Choat, B.E. Medlyn, M. Yebra, N. Younes, and M.M. Boer. 2022. Drought-related leaf functional traits control spatial and temporal dynamics of live fuel moisture

- content. *Agricultural and Forest Meteorology* 319 (May): 108941. <https://doi.org/10.1016/j.agrformet.2022.108941>.
37. Nolan, R.H., J. Hedo, C. Arteaga, T. Sugai, and V. Resco de Dios. 2018. Physiological drought responses improve predictions of live fuel moisture dynamics in a Mediterranean forest. *Agricultural and Forest Meteorology* 263 (December): 417–27. <https://doi.org/10.1016/j.agrformet.2018.09.011>.
 38. Oldham, A.R., S.C. Sillett, A.M.F. Tomescu, and G.W. Koch. 2010. The hydrostatic gradient, not light availability, drives height-related variation in *Sequoia Sempervirens* (Cupressaceae) leaf anatomy. *American Journal of Botany* 97 (7): 1087–97. <https://doi.org/10.3732/ajb.0900214>.
 39. Parisien, M.-A., Q.E. Barber, M.L. Bourbonnais, L.D. Daniels, M.D. Flannigan, R.W. Gray, K.M. Hoffman, P. Jain, S.L. Stephens, S.W. Taylor, and E. Whitman. 2023. Abrupt, climate-induced increase in wildfires in British Columbia since the mid-2000s. *Communications Earth & Environment* 4 (1): 309. <https://doi.org/10.1038/s43247-023-00977-1>.
 40. Pellizzaro, G., P. Duce, A. Ventura, and P. Zara. 2007. Seasonal variations of live moisture content and ignitability in shrubs of the Mediterranean Basin. *International Journal of Wildland Fire* (16): 633–641. <https://doi.org/10.1071/WF05088>.
 41. Pimont, F., J. Ruffault, N. K. Martin-StPaul, and J.-L. Dupuy. 2019. Why is the effect of live fuel moisture content on fire rate of spread underestimated in field experiments in shrublands? *International Journal of Wildland Fire* 28 (2): 127–37. <https://doi.org/10.1071/WF18091>.
 42. Pivovarov, A.L., N. Emery, M. Rasoul Sharifi, M. Witter, J.E. Keeley, and P.W. Rundel. 2019. The effect of ecophysiological traits on live fuel moisture content. *Fire* 2 (2): 28. <https://doi.org/10.3390/fire2020028>.
 43. PRISM (2025) PRISM Climate Group, Oregon State University, www.prism.oregonstate.edu/Data created June 25, 2020, Accessed January 24, 2026.
 44. R Development Core Team. 2025. *R: A Language and Environment for Statistical Computing*. V. 4.5.0. R Foundation for Statistical Computing, released.
 45. Ruffault, J., J.-M. Limousin, F. Pimont, J.-L. Dupuy, H. Cochard, and N. Martin-StPaul. 2022. SurEau-Ecos-FMC: Mechanistic modelling of fuel moisture content (FMC) at leaf and canopy scale under extreme drought. *Geoscientific Model Development* 15: 5593–5626. https://doi.org/10.14195/978-989-26-2298-9_199.
 46. Ryan, M.G., and B.J. Yoder. 1997. Hydraulic limits to tree height and tree growth. *BioScience* 47 (4): 235–42. <https://doi.org/10.2307/1313077>.
 47. Schwilk, D.W., and D.D. Ackerly. 2001. Flammability and serotiny as strategies: Correlated evolution in pines. *Oikos* 94 (2): 326–36. <https://doi.org/10.1034/j.1600-0706.2001.940213.x>.
 48. Scott, J.H., and E.D. Reinhardt. 2001. *Assessing crown fire potential by linking models of surface and crown fire behavior*. Research Paper RMRS-RP-29. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. <https://doi.org/10.2737/RMRS-RP-29>.
 49. Sillett, S.C., and M.G. Bailey. 2003. Effects of tree crown structure on biomass of the epiphytic fern *Polypodium scolieri* (Polypodiaceae) in redwood forests. *American Journal of Botany* 90 (2): 255–

61. <https://doi.org/10.3732/ajb.90.2.255>.
50. Sillett, S.C., and R. Van Pelt. 2007. Trunk reiteration promotes epiphytes and water storage in an old-growth redwood forest canopy. *Ecological Monographs* 77 (3): 335–59. <https://doi.org/10.1890/06-0994.1>.
51. Simms, D.L., and M. Law. 1967. The ignition of wet and dry wood by radiation. *Combustion and Flame* 11(5): 377-388.
52. Van Wagner, C.E., 1977. Conditions for the start and spread of crown fire. *Canadian Journal of Forest Research* 7(1): 23-34.
53. Varner, J.M., S.M. Hood, D.P. Aubrey, K. Yedinak, et al. 2021. Tree crown injury from wildland fires: causes, measurement and ecological and physiological consequences. *New Phytologist* 231 (5): 1676–1685. <https://doi.org/10.1111/nph.17539>.
54. Weise, D.R., R.H. White, F.C. Beall, and M. Etlinger. 2005. Use of the cone calorimeter to detect seasonal differences in selected combustion characteristics of ornamental vegetation. *International Journal of Wildland Fire* 14 (3): 321. <https://doi.org/10.1071/WF04035>.
55. Xanthopoulos, G. and R.H. Wakimoto. 1993. A time to ignition–temperature–moisture relationship for branches of three western conifers. *Canadian Journal of Forest Research* 23 (2): 253-258. <https://doi.org/10.1139/x93-034>.
56. Yebra, M., P. E. Dennison, E. Chuvieco, et al. 2013. A global review of remote sensing of live fuel moisture content for fire danger assessment: Moving towards operational products. *Remote Sensing of Environment* 136 (September): 455–68. <https://doi.org/10.1016/j.rse.2013.05.029>.
57. Zahn, S., and C. Henson. 2011. *A Synthesis of Fuel Moisture Collection Methods and Equipment—a Desk Guide*. National Technology and Development Program Report No. 1151. USDA Forest Service, National Technology and Development Center.

Figures

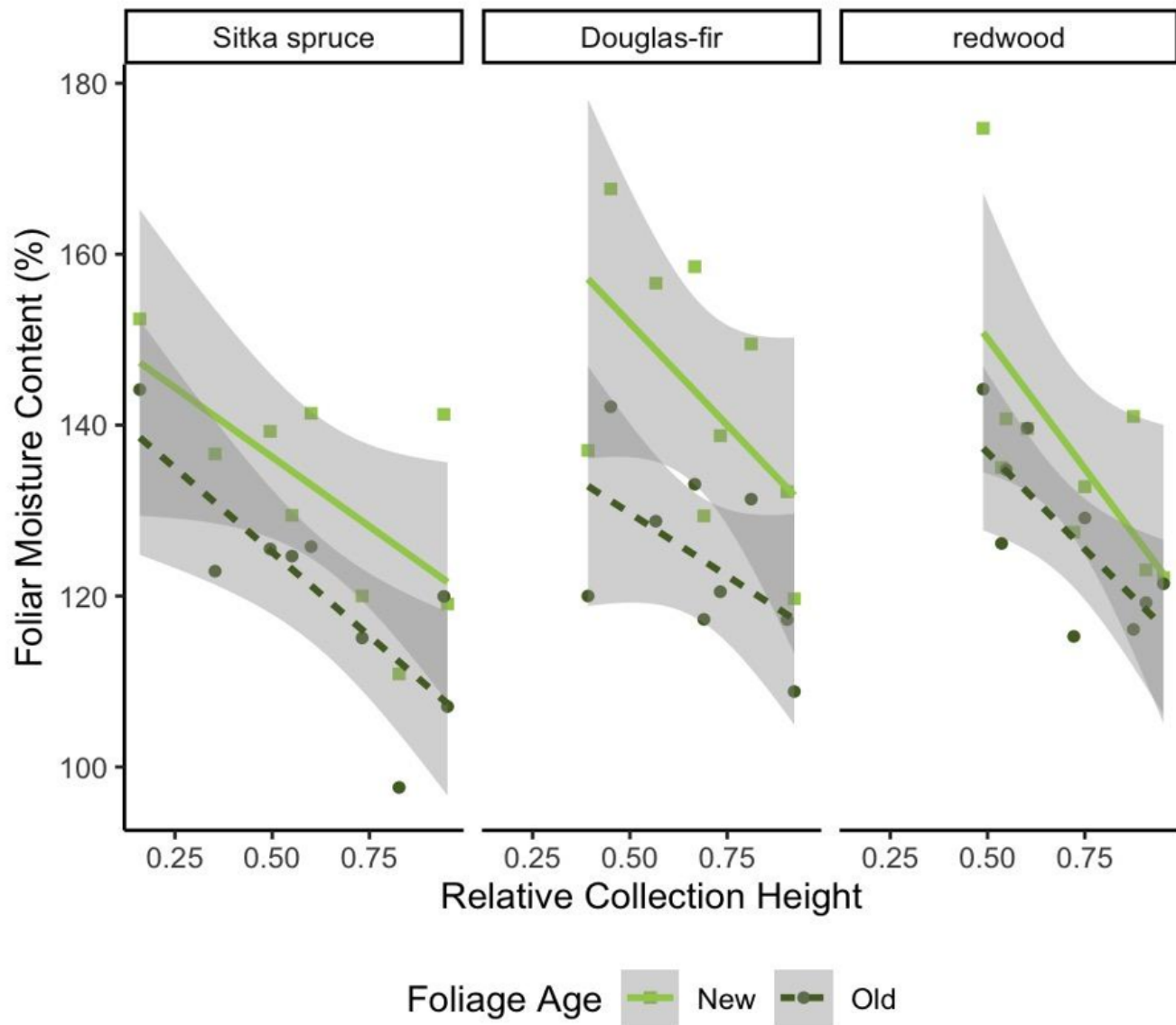


Figure 1

Foliar moisture content as a function of relative collection height and foliage age across three tall conifer species. Relative collection height was the vertical height of the sampled foliage relative to the total height of the sampled tree. Lines represent modeled relationships and the shading represents 95% confidence intervals.

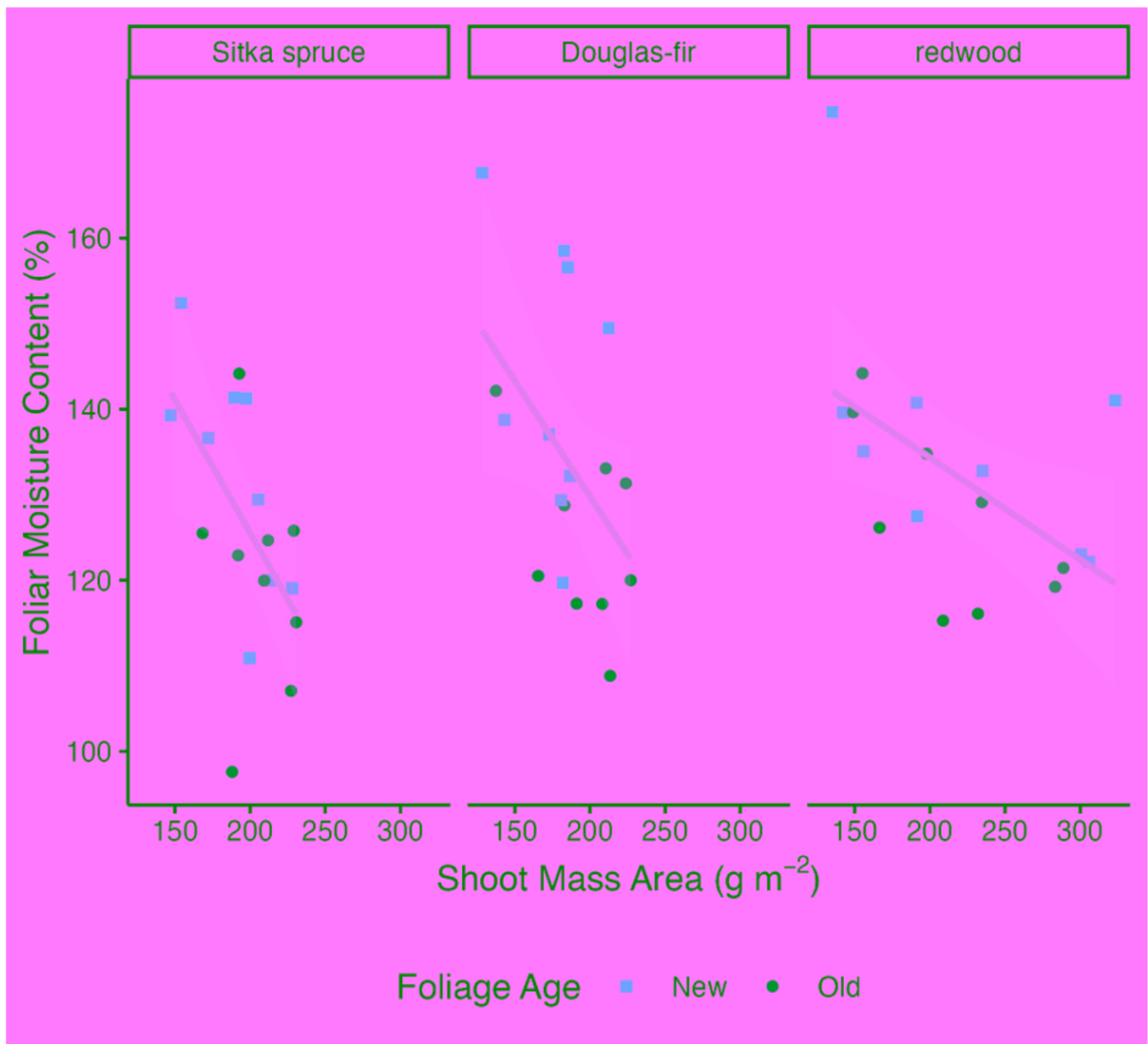


Figure 2

Foliar moisture content as a function of shoot mass area across three tall conifer species. Foliage age is depicted visually but was not considered as a variable in the candidate models selected. Lines represent modeled relationships and the shading represents 95% confidence intervals.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [AppendixA.docx](#)