

Modeling foliage density and leaf mass area dynamics in Intermountain Western USA conifers

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ABSTRACT

Leaf mass area (LMA) is a dominant trait quantifying tradeoffs between structure and physiology. LMA variations are driven by a combination of leaf density and morphology. LMA is widely used in ecosystem process models and in fire research to model live fuel moisture content (LFMC), a dominant predictor of wildland fire behavior. Despite its importance, LMA is often assumed as invariant both seasonally and between species. Here, we measured density, LMA, and foliar chemistry across 10 Intermountain USA conifer species and used these data to develop mechanistic models of foliar density and LMA. We first modeled density as the combination of three components: neutral detergent fiber (structural carbohydrates), non-structural carbohydrates, and crude fat. These foliar density estimates were then combined with all-sided surface-area-to-volume ratio (SAV) to predict LMA. These models adequately predicted interspecies foliar density and LMA across all 10 conifer species ($R = 0.77$ and $R = 0.81$, respectively) and intraspecies variations for intensively sampled Douglas fir ($R = 0.75$ and $R = 0.77$, respectively). Predicted density and LMA were applied to a mechanistic model to predict LFMC. Predicted LFMC were strongly correlated with measured LFMC across conifers ($R = 0.82$ and $R = 0.73$, respectively) and for Douglas fir ($R = 0.77$ and $R = 0.69$, respectively). This framework can improve seasonal LMA representation in ecosystem process models, advance our understanding of live vegetation-driven wildland fire behavior and can help explain the leaf trade-offs that regulate terrestrial productivity and global carbon and water cycles.

1. Background

Global terrestrial productivity is regulated by plant carbon uptake and limited by plant water loss. These processes are heavily influenced by the form and function of plant canopies. Plant canopy foliage is commonly characterized by a suite of traits that describe their morphology, life history strategies and trade-offs that maximize carbon gain based on the prevailing growing conditions (Reich et al., 1998; Onoda et al., 2017). These foliar traits collectively form the leaf economic spectrum (LES) which interacts to regulate productivity across biomes (Wright et al., 2004; Reich et al., 1997). Specific leaf area (SLA), or its reciprocal leaf mass area (LMA), is a primary LES component and it is strongly correlated to other leaf characteristics such as leaf longevity, net photosynthetic rates, and leaf chemical composition (Reich et al., 1997). LMA contrasts a plant's investment into either leaf structure or light-harvesting capabilities and varies several hundred fold across species and over ten-fold within species (Poorter et al., 2009). Understanding the inter- and intra-species drivers of LMA variations is critical to improve our understanding of the global carbon cycle.

Although LMA is a composite of both density and volume, density is the primary driver of variation within specific functional groups (Poorter et al., 2009). Among evergreen trees, differences in density account for approximately 80% of inter-specific LMA variation (Poorter et al., 2009; Poorter and Villar, 1997). Furthermore, when plants adjust LMA in response to environmental factors such as moisture, temperature, or nutrient availability, they typically do so by altering density rather than volume (Poorter et al., 2009; Poorter and Villar, 1997). These density fluctuations are rooted in the leaf's chemical composition, which varies significantly across growing seasons and between foliage age classes (Jolly et al., 2016). Increases in density and LMA are most strongly associated with higher concentrations of structural carbohydrates (cellulose and lignin) in cell walls, as well as the accumulation of non-structural carbohydrates (starch and soluble sugars) and lipids (crude fat) (Poorter et al., 2009; Onoda et al., 2017). Leaf chemistry variations and their drivers vary with plant phenological stage and responses to environmental cues (Jolly and Johnson, 2018;

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Griebel et al., 2023; Dickman et al., 2023). A more mechanistic understanding is needed to explain how chemical concentrations control leaf density variations and how this information can be used to model LMA variations seasonally and across foliage age classes and species.

Because LMA integrates leaf structure and photosynthetic capacity tradeoffs, it is an ideal input parameter for ecosystem process models (Bond-Lamberty et al., 2005; Moorcroft et al., 2001; Wan et al., 2025; White et al., 2000). LMA constrains relationships between leaf nitrogen content, longevity, and photosynthetic rates (Reich et al., 1998; Wright et al., 2004; Niinemets, 1999) and these relationships are often leveraged in process-based models (Wright et al., 2004). Further, process-based models like Biome-BGC and TECO use LMA along with modeled leaf carbon mass to derive dynamic estimates of Leaf Area Index (LAI) (White et al., 2000; Wan et al., 2025) which influences modeled carbon and water cycles. These LMA model inputs are commonly assumed to be static over time and within a given species or plant functional type and therefore do not account for any variations in either leaf area or biomass between foliage age categories or within and between growing seasons (Pierce et al., 1994; Friend et al., 1997; White et al., 2000).

In addition to its influence on ecosystem process models, LMA is leveraged to explore plant functional traits in other related disciplines such as wildland fire research. Dry weight-based 'fuel moisture contents' of living vegetation foliage, or live fuel moisture content (LFMC), is commonly used to predict wildland fire behavior (Rothermel, 1972; Pimont et al., 2019). The emerging field of pyro-ecophysiology (Jolly and Johnson, 2018; Dickman et al., 2023; De Dios, 2020), seeks to leverage LES components and other ecophysiology-based traits to explain seasonal and inter-species live fuel dynamics. The importance of LMA as a proxy for dry mass in predicting LFMC variability has been shown across various plant functional types and models (Brown et al., 2022; Griebel et al., 2023; Nolan et al., 2022). Recent mechanistic models of LFMC show that leaf density and/or LMA are the most important predictors of LFMC variations across a range of tree and shrub species (Jolly et al., 2025; Brown et al., 2025). Additionally, those models underscore the need to separately model previous year and current year foliage dry mass dynamics (Jolly et al., 2025). Therefore, a complete understanding of LMA variations seasonally and across foliage age classes and species can improve our ability to interpret LFMC measurements and model wildland fire behavior across space and time.

Despite the importance of LMA as a global scaling parameter and model input and its relevance to other disciplines such as wildland fire science, there are very few studies that explore the inter- and intra-species drivers of LMA variations. In mechanistic fire and ecosystem models, LMA is mathematically defined by the interaction between a tissue's volumetric density and the ratio of all-sided surface area to fresh volume (surface area to volume ratio, SAV). Thus, LMA can be scaled to density using SAV. Intuitively, seasonal photosynthesis and carbon allocation variations impact foliar density and area. Leaf phenological processes and development could impact density and area over time, leading to substantial variations in LMA within a growing season across foliage age classes. Indeed, several studies have reported strong intra-species, seasonal LMA variations (Yamaguchi et al., 2016; Araki et al., 2017); however, limited seasonal LMA modeling efforts have been undertaken. Although some novel approaches for modeling LMA variations over foliar development have been undertaken (Davi et al., 2008), these efforts do not account for the primary drivers of mass or area fluctuations, nor do they account for variations between foliage age classes where strong LMA differences have been noted (Jolly et al., 2025). Ultimately, a better understanding of the factors that drive seasonal density and LMA variations both within and between species and across foliage age classes is needed. This new knowledge could improve the ability to model foliar density and LMA variations for a variety of ecological applications.

LMA is related to foliar density ($\rho_{foliage}$) and foliar surface-area-to-volume ratio (SAV or sometimes SVR) measurements as follows (Poorter et al., 2009):

$$\rho_{foliage} \left(\frac{\text{kg}}{\text{m}^3} \right) = \text{LMA} \left(\frac{\text{kg}}{\text{m}^2} \right) \times \text{SAV} \left(\frac{\text{m}^2}{\text{m}^3} \right) \quad (1)$$

Thus, LMA could be estimated from modeled estimates of leaf density when scaled by an appropriate measurement of SAV. Previous work has shown that leaf dry weight or leaf density can be estimated effectively using measured seasonal leaf chemistry variation (Jolly et al., 2014, 2016) but these relationships have only been explored for a few conifer species. If a generalized model for leaf density and subsequent LMA were demonstrated, such an approach could provide a framework for modeling density, LMA and leaf chemistry relationships across all plants.

Here we introduce novel, mechanistic models that predict foliar density and subsequent LMA variations across 10 Intermountain Western United States conifer trees species by decomposing density variations based on seasonal and developmental changes in leaf chemistry. We apply these models to investigate the generality of relationships between foliar chemistry, density and LMA across multiple growing seasons for current year (new) and previous year (old) conifer foliage. We demonstrate the utility of these models by applying modeled estimates of density and LMA to a mechanistic live fuel moisture content model (LFMC) and we predict LFMC variations seasonally and across species for both foliage age classes. This new approach could be the first step towards a mechanistic model that could predict foliage density and LMA variations across all plants.

2. Methods

2.1. Sampling

We collected the current year ("new" foliage) and previous year's growth ("old" foliage) from live Douglas fir trees (*Pseudotsuga menziesii*, *PSEMEN*) from the beginning of March to the end of October in 2021, 2022, and 2024 at the Blue Mountain National Recreation Area on the Lolo National Forest, approximately 5 miles southwest of Missoula, MT, USA (Table 1) (Samples were not collected in 2023). Samples were collected at least weekly from green-up to needle hardening, late April to late June, and biweekly for the rest of the season. One intact terminal shoot was collected from sunlit portions of eight randomly selected mature trees within the stand, then stored in sealed bags in a cooler to prevent loss of moisture during transport to the laboratory. Trees were randomly selected between sampling dates to best represent stand-level conditions and not the conditions of an individual tree or trees within the stand. All samples were initially processed within four hours of collection.

In 2022, we expanded our sampling to include the following species: grand fir (*Abies grandis*, *ABIGRA*), subalpine fir (*Abies lasiocarpa*, *ABILAS*), western larch (*Larix occidentalis*, *LAROCC*), Engelmann spruce (*Picea engelmannii*, *PICENG*), whitebark pine (*Pinus albicaulis*, *PINALB*), lodgepole pine (*Pinus contorta*, *PINCON*), western white pine (*Pinus monticola*, *PINMON*), ponderosa pine (*Pinus ponderosa*, *PINPON*), and western hemlock (*Tsuga heterophylla*, *TSUHET*) (Table 1). New and old foliage were collected four times during the growing season from nine additional species across five additional sites in Western Montana and Idaho (Table 1) using the same protocol that was used for Douglas fir discussed above.

2.2. Foliage physical and physiological characteristics

In the laboratory, 12 old needles and 12 new needles (after new foliage emergence) were randomly selected from the shoots and weighed. Volume was determined using a balance density kit (Ohaus density kit). Weighed needles were then taped flat to a white piece of paper that included a surface area measurement reference and photographed.

Table 1

Description of sampling sites across Montana and Idaho, USA, used in the study. Temperature and precipitation summaries are 30-year annual means from the PRISM dataset (PRISM Climate Group 2025).

Site name	Species	Latitude (dec deg)	Longitude (dec deg)	Elevation m (ft)	Mean Ann Precip mm (in)	Mean Ann Temp °C (F)
Spring Gulch	PINCON, PICENG	46.7359	−114.5362	1162 (3812)	682.0 (26.9)	4.7 (40.5)
Blue Mountain	PINPON, PSEMEN	46.8298	−114.11812	1346 (4416)	445.5 (17.5)	6.8 (44.3)
Jerry Johnson	ABIGRA	46.4739	−114.88439	939 (3081)	939.8 (37)	6.4 (43.5)
St Mary's Peak	PINALB	46.5003	−114.20339	2091 (6859)	989.1 (38.9)	4.0 (39.2)
White Pine Creek	PINMON, TSUHET	47.7389	−115.67531	1024 (3360)	1106.9 (43.6)	5.5 (41.9)
TV Mountain #2	LAROCC, ABILAS	47.0026	−114.00282	1564 (5131)	688.8 (27.1)	6.0 (42.8)

Photographs were processed using ImageJ software (Schneider et al., 2012) to measure projected surface area in mm². Needles were gently unpeeled from the paper, placed into vials of de-ionized water, and left to rehydrate for 24 h at 4 °C in dark conditions. Rehydrated needles were weighed again to determine saturated mass, then dried in a 70 °C oven for at least 72 h and reweighed to determine dry mass (Conrad et al., 2024). These measurements yield the fresh mass, dry mass, and turgid (saturated) mass values that were used to calculate relative water content (RWC) and live fuel moisture content (LFMC) (Jolly et al., 2014). All weight measurement were made to the nearest 0.01 mg and all units were converted to standard units listed in Table 2.

2.3. Chemical components

The chemical components of foliar dry matter can be grouped into eight main classes of compounds: minerals, organic acids, non-structural carbohydrates (NSC), structural carbohydrates, soluble phenolics, protein, lignin, and lipids (Poorter et al., 2009). While the content per unit leaf area of all these components tends to increase with increasing leaf mass area (LMA), their concentrations change differently (Poorter et al., 2009). In this study, we measure foliage NSC, crude fat (CF), and neutral-detergent fiber (NDF) concentrations because they represent major components of leaf density and their relative abundance strongly contributes to variation in LMA (Poorter et al., 2009).

The remainder of the old and new needles for each sample period were separated and dried in a 60 °C oven for 48–72 h before grinding. Samples were first coarsely ground with a Wiley mill (Thomas Scientific, Swedesboro, NJ, USA). We then further homogenized and ground samples to a powder with a mixer mill (Retsch, Hann, Germany). These samples were used to measure new and old foliage total non-structural carbohydrates (NSC), crude fat (CF), and neutral-detergent fiber (NDF). Prior to weighing samples for NSC analyses, samples were again dried overnight at 60 °C. We followed protocol by Landhäusser et al. (2018) for NSC quantification. Briefly, soluble sugars were extracted from ground samples via ethanol at 90 °C. Total free sugars (glucose, fructose, sucrose) were then determined by NAD-linked enzymatic assays where invertase breaks down glucose and fructose for sucrose quantification, and fructose is converted to glucose by isomerase. After conversion of glucose to gluconate using hexokinase (glucose assay reagent, Sigma Aldrich), total sugars were determined photometrically at 340 nm. From the remaining pellet, starch was converted to glucose via α -amylase, followed by amyloglucosidase. Glucose hydrolyzate was then measured photometrically at 340 nm to determine starch content. We used serial dilutions of a glucose standard stock solution (1 mg mL⁻¹) for glucose quantification, and fructose and sucrose standards to ensure the efficacy of enzyme activities (Landhäusser et al., 2018). All chemicals were from Sigma Aldrich. We also used a synthetic standard

described by Landhäusser et al. (2018) as well as a laboratory standard from Ponderosa pine needles to ensure reproducibility.

Crude fat (CF), which expresses the quantity of isoprenoids, waxes, and oils present in the foliage, was determined using an ANKOM XT15 Extraction System (ANKOM, 2025b). Neutral-detergent fiber (NDF), which quantifies structural carbohydrates including cellulose, hemicellulose, and lignin, was determined using an ANKOM200 fiber analyzer following standard (ANKOM, 2025a).

Non-structural carbohydrates (NSC), are composed of starch and simple sugars, represent the plant's stored carbon that is not immediately used for structural biomass (Hartmann and Trumbore, 2016; Dickman et al., 2023). CF quantifies the isoprenoids, waxes, and oils present in the foliage, and are important storage compounds that plants can use as substrates for respiration, defense and communication (Hartmann and Trumbore, 2016). NDF quantifies structural carbohydrates including cellulose, hemicellulose, and lignin, which are major constituents of plant cell walls (Onoda et al., 2017; Hartmann and Trumbore, 2016). NSC and CF account for the dynamic, reservable components of leaf dry mass that reflect the plant's carbon allocation and metabolic status. NDF captures static, structural investments in the leaf that contribute to its physical properties and persistence. NSC, CF, and NDF are measured as a percentage of total dry mass. Collectively, these measurement yielded a suite of physical and chemical properties which can be used to explore the drivers of density/LMA variations both within and between species.

2.4. Modeling foliar density

Foliar density (ρ , equivalent to dry mass per unit volume or volumetric dry mass) is defined as the mass of dry material per unit volume. We resolve the variation in dry mass density (ρ) based on major chemical constituents: non-structural carbohydrates (NSC), structural carbohydrates (NDF), and crude fats (CF). Because foliage chemical composition differs significantly between current-year (new) and previous-year (old) foliage (Jolly et al., 2016), we developed separate linear models for new and old foliage and also evaluated a combined model that incorporates foliage age as a binary predictor.

Because the goal was to estimate the relative contribution of each biochemical constituent to density, the models were fit without an intercept term. This is justifiable because we expect that there is no theoretical intercept other than zero when NSC, NDF and CF are zero. In particular, NDF quantifies foliage structure, so the absence of any NDF would indicate that foliar density should approach zero. Here we test two general linear model forms. First, we construct separate models for new and old foliage using the following form:

$$\widehat{\text{Density}} = \beta_{\text{NSC}} \text{NSC} + \beta_{\text{CF}} \text{CF} + \beta_{\text{NDF}} \text{NDF} \quad (2)$$

Table 2

Mechanistic leaf mass area variable definition. Variables used as means in the model are shown with bar above abbreviations.

Variable	Abbreviation	Description	Units
Leaf mass area	LMA	Leaf mass per unit surface area	$\frac{\text{kg}}{\text{m}^2}$
Density	ρ	Volumetric dry mass	$\frac{\text{kg}}{\text{m}^3}$
Surface area to volume ratio	SAV	All-sided surface area to volume ratio	m^{-1}
Non-structural carbohydrates	NSC	Starch and soluble sugars	% dry mass
Crude fat	CF	Isoprenoids, waxes, and oils	% dry mass
Neutral detergent fiber	NDF	Cellulose, hemicellulose, and lignin	% dry mass

Table 3

Mechanistic live fuel moisture content variable and units definitions.

Variable	Abbreviation	Description	Units
Live fuel moisture content	LFMC	Percent of dry mass	$\frac{\text{kgH}_2\text{O}}{\text{kgDM}} \times 100$
Relative water content	RWC	Percent of saturated moisture	$\frac{\text{kgH}_2\text{O}}{\text{kgH}_2\text{OSat}} \times 100$
kappa	κ	Volumetric saturated water mass	$\frac{\text{kgH}_2\text{OSat}}{\text{m}^3}$
Volumetric water mass	VWM	Mass of water per unit volume	$\frac{\text{kgH}_2\text{O}}{\text{m}^3}$

Next, we test a combined model using base definition in Eq. (2) with the addition of a dummy variable for foliage age class as follows:

$$\widehat{\text{Density}} = \beta_{\text{NSC}} \text{NSC} + \beta_{\text{CF}} \text{CF} + \beta_{\text{NDF}} \text{NDF} + \beta_{\text{NewOld}} D_{\text{NewOld}} \quad (3)$$

Where D_{NewOld} is a dummy variable for foliage age class and is defined as: $D_{\text{NewOld}} = 1$ where foliage age class is “New” and $D_{\text{NewOld}} = 0$ where foliage age class is “Old”. The three chemical components used for the mechanistic density model provide an estimate rather than a complete accounting of all chemical variations that impact foliar density changes. Although the focus of our study is on NSC, CF, and NDF, which represent major investments in mobile carbon/energy (NSC, CF) and structural investment (NDF), we acknowledge that components critical for growth, defense, and nutrient cycling, such as proteins, lignin, minerals (ash), and organic acids, are necessary for complete calculation of total foliar density.

2.5. Statistical analysis

All analyses were conducted in Python (V. 3.12.4) using NumPy (V. 2.2.5), Pandas (V. 2.2.3), SciPy (V. 1.15.2), and StatsModel (V. 0.14.5). Before model development, we compared new and old foliage using t-tests for density, LMA, NSC, CF, and NDF. We then used a two-way ANOVA to test the effects of species and foliage age class on density. To model density, we fit three Ordinary Least Squares (OLS) regressions: separate models for new and old foliage using Eq. (2), and a combined model that included a foliage-age class dummy variable using Eq. (3). All models were fit using the statsmodels package (statsmodels.formula.api.ols). To characterize seasonal variations in foliar density, LMA, NSC, CF and NDF, we calculated percent variability as follows:

Percent variability = $((\text{max} - \text{min})/\text{min}) \times 100$ where max and min are seasonal extreme values for a given measured value.

We tested common OLS assumptions for all three model. Specifically, we tested for independence of errors with Durbin–Watson statistic, the Breusch–Pagan test for homoscedasticity, the Anderson–Darling test for residual normality and we assessed potential multi-collinearity using variance inflation factors (VIF), and the cross-correlations of independent variables. All model fits were assessed using five-fold cross-validation. We calculated mean absolute error (MAE) and the Pearson correlation between observed and predicted density for each fold and we report cross-validation results as mean $\pm$ standard deviation across folds. Full data analysis and the modeling pipeline from Jupyter Notebook are provided in the accompanying GitHub repository (<https://github.com/firelab/MechanisticFoliarDensityModel>).

2.6. Predicting leaf mass area

Leaf mass area (LMA) represents the mass of foliage per unit area (Poorter et al., 2009). It is used in parallel with its reciprocal, specific leaf area (SLA). Measured LMA was calculated from all-sided projected surface area and dry weight using the following equation:

$$LMA \left(\frac{\text{kg}}{\text{m}^2} \right) = \left(\frac{\text{Dry Weight (mg)}}{\alpha * \text{Surface Area (mm}^2\text{)}} \right) \quad (4)$$

where α is a species-specific constant to scale from one-sided projected foliage surface area to all-sided surface area. Scaling may be required, as LMA and SLA are typically calculated from one-sided projected surface area (Poorter et al., 2009). However, all-sided surface area is a more relevant metric for combustion science due to its role in heat transfer, and (all-sided) surface area to volume ratio (SAV, also commonly expressed as SVR).

We used modeled foliar density (ρ) to predict leaf mass area. LMA is defined as the ratio of dry mass to leaf surface area. It can be calculated from foliar density and all-sided SAV as follows:

$$LMA = \frac{\text{Density}(\rho)}{\text{SAV}} \quad (5)$$

2.7. Predicting live fuel moisture content

As an application of the Density/LMA model, we use predicted Density/LMA to drive a mechanistic LFMC model to explore seasonal and inter-species variations in dry weight-based moisture content (Jolly et al., 2025). The model uses either density or LMA and SAV to represent foliar dry mass (Brown et al., 2025; Jolly et al., 2025). We tested the application of mechanistic LMA as an input to the LFMC model (Variant 5), which uses time varying relative water content (RWC), LMA, and fixed values for surface area to volume ratio (SAV) and the scalar kappa (κ) (Jolly et al., 2025). This was the best general form of the mechanistic LFMC model (Brown et al., 2025; Jolly et al., 2025). LFMC can be calculated mechanistically as follows:

$$\text{LFMC} = \left(\frac{\frac{\text{RWC}}{100} * \bar{\kappa}}{\text{LMA} * \text{SAV}} \right) * 100 \quad (6)$$

κ describes the particle saturated water mass relative to its volume and can be calculated using measurements from the saturation step of RWC and normalized by the fresh particle volume as follows:

$$\kappa = \left(\frac{\text{Saturated Water Mass}}{\text{Volume}} \right) = \left(\frac{\text{Turgid Mass} - \text{Dry Mass}}{\text{Volume}} \right) \quad (7)$$

Turgid Mass is the mass of the fuel particle in kilograms after rehydration, Dry Mass is the oven dry sample mass in kilograms, and

Table 4

Mean LMA (kg/m^2), density (kg/m^3), SAV (m^{-1}), and chemical values (% of dry weight) by species and foliage age class for 10 Intermountain Western US conifers.

Species	Foliage	LMA (kg/m^2)	Density (kg/m^3)	SAV (m^{-1})	NSC%	CF%	NDF%
ABIGRA	New	0.06	276.07	4457.91	4.56	4.49	33.08
	Old	0.09	399.07	4259.48	5.62	5.42	37.60
ABILAS	New	0.08	328.31	4249.73	5.04	6.91	37.05
	Old	0.11	423.94	3967.03	7.45	7.89	35.12
LAROCC	New	0.05	268.32	5144.82	7.36	6.70	34.95
PICENG	New	0.09	314.72	3447.29	12.36	3.97	40.58
	Old	0.13	471.54	3760.69	17.57	3.00	41.15
PINALB	New	0.09	362.12	4290.45	4.29	6.60	39.62
	Old	0.11	439.70	4031.01	6.07	8.41	37.08
PINCON	New	0.08	356.94	4449.59	5.94	4.52	42.27
	Old	0.10	457.87	4672.73	8.94	3.57	42.87
PINMON	New	0.07	319.57	4421.96	4.22	3.99	41.65
	Old	0.08	408.14	5399.69	5.32	5.18	41.20
PINPON	New	0.09	370.82	4149.72	7.02	6.25	43.40
	Old	0.12	457.84	3932.63	5.32	7.28	39.87
PSEMEN	New	0.07	324.13	4890.92	9.01	2.40	33.08
	Old	0.10	453.55	4402.77	15.58	2.97	30.07
TSUHET	New	0.06	273.05	5371.61	4.05	6.43	33.02
	Old	0.08	396.83	4854.59	5.62	6.68	33.27

volume is the measured fresh sample volume (m^3). Mean values for SAV and κ by species and foliage age class are shown in Table 6.

LFMC can also be calculated using volumetric quantities by normalizing the numerator and denominator by the particle volume. Kappa can be used to scale the measured RWC to volumetric water mass (VWM) as follows:

$$\text{VWM} = \left(\frac{\text{RWC}}{100} * \kappa \right) \quad (8)$$

The VWM is the product of RWC (scaled to fraction from percent by dividing by 100) and κ . If we consider the LFMC as a simple ratio of the VWM and volumetric dry mass, which is equivalent to its density (ρ), the following equation describes the LFMC, allowing us to use modeled density to directly predict LFMC:

$$\text{LFMC} = \left(\frac{\text{VWM}}{\text{Density } (\rho)} \right) \times 100 \quad (9)$$

Therefore, we applied our modeled LMA values to Eq. (6) along with field measured RWC and mean species and foliage age class κ and SAV and our modeled foliar density values to Eq. (9) along with field measured VWM to estimate live fuel moisture content. We then compared these estimates to field-measured, seasonal LFMC values across all 10 conifer species for both new and old foliage.

3. Results

3.1. Density and LMA model parameters across 10 conifer species

Mean LMA, density, SAV, NSC, CF, and NDF for 10 conifer species tested are presented in Table 4. Mean LMA, density, and chemical variables were consistently higher in old foliage than new foliage across all species. SAV showed the opposite pattern, with new foliage generally showing higher values than old foliage, reflecting the finer needle structure of younger tissues. The lowest mean density and LMA values were measured for western larch (LAROCC) new foliage ($268.3 \text{ kg}/\text{m}^3$ and $0.05 \text{ kg}/\text{m}^2$, respectively) and the highest values were recorded for Engelmann spruce (PICENG) old foliage ($471.54 \text{ kg}/\text{m}^3$ and $0.13 \text{ kg}/\text{m}^2$, respectively). The highest SAV values were observed in Western hemlock (TSUHET) new foliage (5371.61 m^{-1}) and the lowest values were observed in Engelmann spruce (PICENG) new

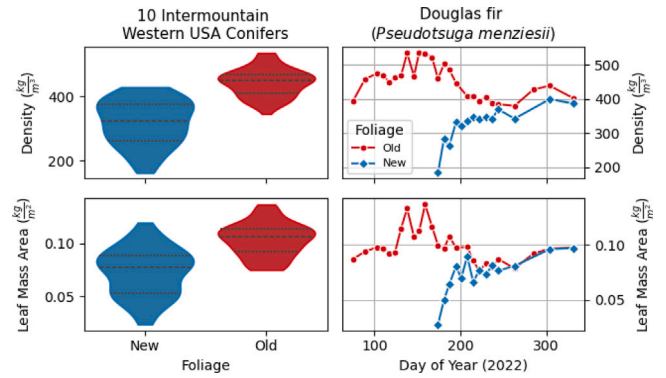


Fig. 1. Distributions for 10 Intermountain Western USA conifers for density ($n = 110$) and LMA ($n = 110$) for new and old foliage (left column). Example time series plots of density ($n = 40$) and LMA ($n = 40$) for new and old Douglas fir foliage sampled at Blue Mountain in 2022 (right column). Variable descriptions and units are given in Table 2.

foliage (3447.29 m^{-1}). The lowest NSC concentrations were observed in western hemlock (TSUHET) new foliage (4.05%) and the highest mean NSC values were seen in Engelmann spruce (PICENG) old foliage (17.57%). The lowest average CF contents were seen in Douglas fir (PSEMEN) new foliage (2.40%) and the highest were recorded in Whitebark pine (PINALB) old foliage (8.41%). The lowest average NDF concentrations were observed in Douglas fir (PSEMEN) old foliage (30.07%) and the highest values were seen in ponderosa pine (PINPON) new foliage (43.40%).

Ranges and percent variability for all model parameters for Douglas fir are presented in Table 5. These ranges reflect the full growing season, from the beginning of March to the end of October, from 3 years of data. The remaining 9 species were sampled only in 2022 from mid June to the end of September. Thus, ranges for species other than Douglas fir are narrower and do not reflect full seasonal variability, and are not presented here. New foliage exhibited high variability in density, LMA, CF, and NDF, with percent variability values of 118%, 251%, 670%, and 117%, respectively. This reflects the development of current-year foliage, during which expansion, membrane and cuticle formation, and progressive cell-wall thickening result in large structural changes. Old foliage showed comparatively constrained variability for these traits, consistent with the physiological stabilization that occurs once needles reach full maturity. NSC content was the only trait for which old foliage displayed greater variability than new foliage, with a percent variability of 709% in old foliage versus 337% in new foliage. This reflects mature needles serving as a flexible reservoir for carbohydrate storage and remobilization during new needle development or varying environmental conditions.

Fig. 1 illustrates both the distribution of foliage characteristics across 10 Intermountain Western USA conifer species and the seasonal dynamics of Douglas fir foliage in 2022. The top panel presents foliage density, while the bottom panel shows LMA, each separated by foliage age. Across all 10 species, old foliage density and LMA were significantly different than new foliage ($t = -11.52$, $p < 0.01$ (density) and $t = -8.44$, $p < 0.01$ (LMA)), with a median density of $449.1 \text{ kg}/\text{m}^3$ versus $325.4 \text{ kg}/\text{m}^3$ respectively. Standard deviations for old and new foliage density were $43.1 \text{ kg}/\text{m}^3$ and $69.8 \text{ kg}/\text{m}^3$, respectively. In Douglas fir, old foliage density peaked just before new needle emergence, followed by a decline. New foliage density rose sharply in June during needle development and continued to increase modestly through July. LMA patterns mirrored those of density. Old foliage had a higher median LMA ($0.106 \text{ kg}/\text{m}^2$) than new foliage ($0.077 \text{ kg}/\text{m}^2$), though with slightly lower variability (standard deviations of $0.016 \text{ kg}/\text{m}^2$ and $0.022 \text{ kg}/\text{m}^2$, respectively), and this difference was also

Table 5

Ranges and percent variability for density (kg/m^3), LMA (kg/m^2), NSC, CF, and NDF (% dry mass) for Douglas fir. Percent variability was calculated as $((\text{max}-\text{min})/\text{min}) \times 100$.

Foliage	Density Min–Max (%Var)	LMA Min–Max (%Var)	NSC Min–Max (%Var)	CF Min–Max (%Var)	NDF Min–Max (%Var)
New	183.19–399.65 (118)	0.03–0.10 (251)	3.6–15.7 (337)	0.4–3.3 (670)	18.7–40.5 (117)
Old	379.72–535.38 (41)	0.08–0.14 (79)	3.1–25.4 (709)	1.7–4.4 (160)	21–39.5 (88)
All	183.19–535.38 (192)	0.03–0.14 (395)	3.6–25.4 (709)	0.4–4.4 (925)	18.7–39.5 (117)

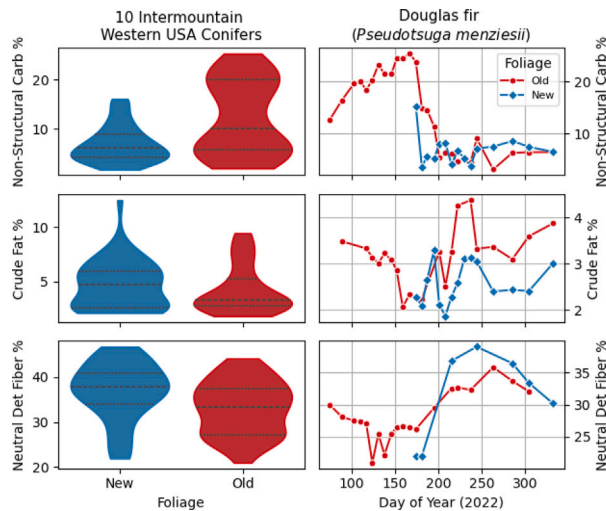


Fig. 2. Distributions for 10 Intermountain Western USA conifers for NSC ($n=110$), CF ($n=110$), and NDF ($n=110$) for new and old foliage (left column). Example time series plots of non-structural carbohydrate ($n=42$), crude fat ($n=35$), and neutral-detergent fiber ($n=27$) for new and old Douglas fir foliage sampled at Blue Mountain in 2022 (right column). Variable descriptions and units are given in Table 2.

significant. Seasonally, old foliage LMA increased sharply prior to new needle emergence, then declined. New foliage LMA rose in June and, by July, converged with old foliage values, with both showing a gradual increase through the remainder of the growing season.

Fig. 2 presents the distribution and seasonal dynamics of NSC, CF, and NDF across 10 conifer species (left column) and in 2022 Douglas fir foliage (right column). NSC differed strongly between foliage ages ($t = -4.61$, $p < 0.001$), with old foliage showing a higher median (10.1%) and substantially greater variability (standard deviation 7.5%) than new foliage (median 6.2%; standard deviation 3.7%). CF values were broadly similar between age classes and were not significantly different between foliage age classes ($t = 0.92$, $p > 0.05$), though new foliage had a slightly higher median (4.7%) than old foliage (3.3%). CF variability was nearly identical (standard deviation 2.2% for both), although new foliage extended to higher maximum values. NDF was significantly different between foliage age classes ($t = 3.08$, $p < 0.01$). New foliage had a higher median (37.8%) and greater variability (standard deviation 6.5%) than old foliage (median 33.3%; standard deviation 5.9%). In Douglas fir, old foliage NSC showed a pronounced peak just before new needle emergence, followed by a rapid decline, while new foliage NSC remained low throughout the growing season. CF showed a clear separation between age classes, with old foliage consistently higher than new foliage, though both followed similar seasonal trajectories with a peak in September. New foliage NDF increased steadily with needle development across the growing season.

3.2. Model testing

Two-way ANOVA revealed significant effects of species ($p = 0.002$) and foliage age class ($p < 0.001$) on density, with old foliage consistently denser than new foliage across all species. The species $\times$ foliage interaction was not significant ($p > 0.05$), indicating that although species differed in overall density, the magnitude of the age-class difference was similar between species. These results justified evaluating separate OLS models for new and old foliage to allow age classes to differ in their relationships with NSC, NDF, and CF, as well as a combined model including foliage age as a dummy variable. We therefore compared three model structures: separate new-foliage and old-foliage OLS models, and a single model with foliage age included as an interaction term. These equations were fit across 10 Intermountain US conifer species, then applied to Douglas fir to demonstrate the model's ability to capture intra-specific seasonal dynamics.

Plots of model residuals against all independent variables showed no signs of non-linearity. Durbin–Watson statistics were 1.385 (NS), 1.441 ($p < 0.01$) and 1.335 ($p < 0.01$) for the New Foliage, Old Foliage, and the Combined Model, respectively, suggesting that some serial autocorrelation is present for old foliage and the combined models and results should be interpreted with caution. Anderson–Darling normality tests and examination of QQ-plots suggest that residuals are normally distributed (0.179 (NS), 0.410 (NS) and 0.745 (NS) for new foliage, old foliage, and for the combined model, respectively). Breusch–Pagan tests indicated that the New Foliage Model was homoscedastic (NS), while both the Old Foliage Model ($p < 0.05$) and the Combined Model ($p < 0.01$) exhibited heteroscedasticity. We addressed this by using the HC3 option in OLS fitting to ensure that standard errors are robust to heteroscedasticity. Multicollinearity diagnostics showed low pairwise correlations among predictors (ranges of -0.35 to 0.09 for new foliage, -0.63 to 0.36 for old foliage, and -0.48 to 0.25 for the combined model). Variance Inflation Factors for NSC, NDF, and CF were moderate, (4.45, 10.80, and 5.51 for the new-foliage model; 2.95, 9.84, and 6.13 for the old-foliage model; and 2.63, 8.49, and 5.65 for the combined model) suggesting some degree of multicollinearity between independent variables. For the final, combined model, multicollinearity is most pronounced minimal for NSCs and most pronounced for NDF but all VIFs were below 10 suggesting that minimal to moderate multicollinearity is present for all variables. Because these values are ratios that represent the fractional biomass of individual chemical components, this is to be expected.

We evaluated the predictive performance of each model using 5-fold cross-validation. The combined model showed the strongest overall performance, with an average MAE of 44.12 ± 2.77 and a mean correlation of 0.78 ± 0.065 between predicted and observed density. The new-foliage model performed substantially worse, exhibiting both higher error ($MAE = 51.03 \pm 11.19$) and highly variable predictive strength ($R = 0.48 \pm 0.3$) across folds. The old-foliage model achieved the lowest absolute error ($MAE = 35.61 \pm 4.32$) and a moderate correlation ($R = 0.63 \pm 0.14$). The combined model was therefore selected as the final model because it provides strong, consistent predictive skill for both new and old foliage. The final fitted equation is:

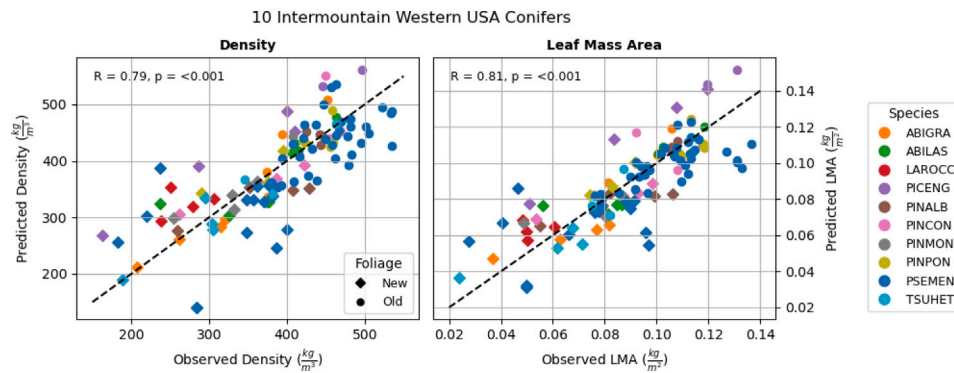


Fig. 3. Performance of density model using NSC, CF, and NDF as mechanistic inputs for 10 Intermountain Western USA Conifers (left column) and as an input for the mechanistic LMA model (right column). This density model is highly correlated with measured density ($R = 0.79$) ($n = 110$). Predicted LMA is also highly correlated with measured LMA ($R = 0.81$) ($n = 110$). R and p values represent Pearson correlations between predicted and observed values.

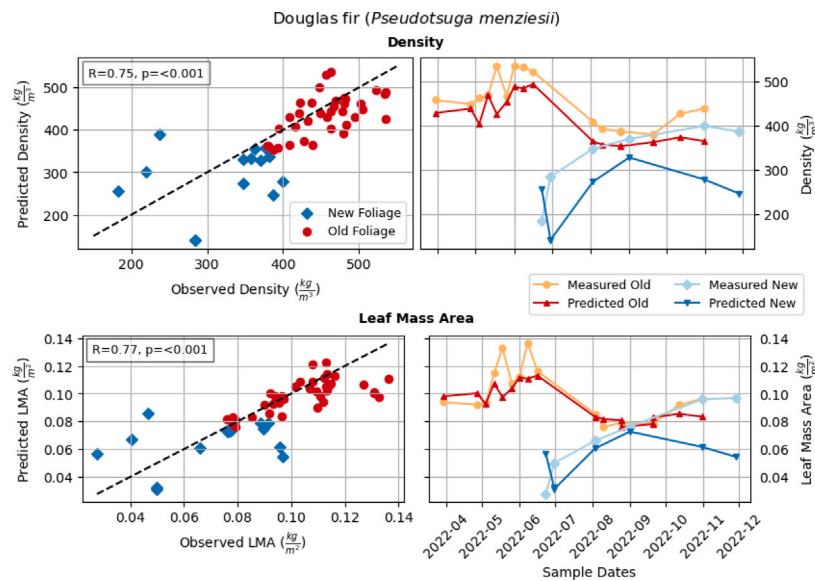


Fig. 4. Top panel shows the performance of density model using NSC, CF, and NDF as mechanistic inputs for Douglas fir ($n = 110$). This density model is moderately strongly correlated with measured density ($R = 0.75$). Bottom panel shows the performance of leaf mass area predictions using the density model as mechanistic LMA model inputs for Douglas fir. This model adequately characterizes 2022 seasonal Douglas fir dynamics in new foliage ($n = 14$) and old foliage ($n = 37$) (left column) and is moderately strongly correlated with measured LMA across four growing seasons ($R = 0.77$) (right column). R and p values represent Pearson correlations between predicted and observed values.

$$\widehat{\text{Density}} = (987.81) \text{NSC} + (802.66) \text{CF} + (849.37) \text{NDF} + (-98.88) \text{NewOld } D_{\text{NewOld}}$$

$$F = 2030, \quad p < 0.01$$

All three predictor variables were significant in the final model ($p < 0.01$). The foliage-age dummy variable was also significant ($p < 0.01$), indicating that new foliage was 98.88 kg/m^3 less dense than old foliage after accounting for chemical composition.

3.3. Modeling density and LMA

The left panel of Fig. 3 shows the measured and predicted density values calculated across all 10 species. Modeled density adequately characterizes between species differences and is highly correlated with observed density ($R = 0.79$). Because the regression models were fit without an intercept, we report Pearson correlation coefficients for all predictions. The top panel of Fig. 4 shows a time series and regression of predicted and observed Douglas fir density. Modeled density adequately characterizes seasonal dynamics and is strongly correlated with observed density ($R = 0.75$).

The right panel of Fig. 3 shows the observed and predicted LMA values calculated across all 10 Intermountain US conifer species. Predicted LMA, calculated using modeled density and mean SAV by species for new and old foliage Table 6, is highly correlated with observed LMA ($R = 0.81$). The bottom panel of Fig. 4 shows predicted and observed Douglas fir LMA. LMA predictions characterize seasonal dynamics and are highly correlated with observed LMA ($R = 0.77$).

3.4. LFM prediction parameters across 10 conifer species

To demonstrate the utility of the model, we evaluated the ability of the LMA model to predict live moisture content using Eqs. (6) and (9). Mean LFM, RWC, VWM, and kappa for 10 conifer species are presented in Table 6. Across all species, new foliage consistently exhibited substantially higher LFM than old foliage. RWC showed relatively small differences between age classes, with most species maintaining values between 79%–90% saturation regardless of foliage age. VWM followed a similar pattern to LFM, with new foliage showing higher values than old foliage across nearly all species. Kappa also tended to be higher in new foliage, reflecting greater fuel loading in younger

Table 6

Mean LPMC, RWC, VWM and kappa (κ) by species and foliage age class for 10 Intermountain Western US conifers.

Species	Foliage	LFMC (%)	RWC (% sat)	VWM (kg m^{-3})	kappa (kg m^{-3})
ABIGRA	New	218.10	90.23	565.77	630.62
	Old	122.33	89.79	482.31	538.13
ABILAS	New	171.85	88.59	530.22	599.37
	Old	110.81	86.45	461.66	534.29
LAROC	New	220.88	84.77	574.63	679.34
PICENG	New	240.78	88.41	622.52	708.14
	Old	110.77	88.39	514.65	583.76
PINALB	New	175.49	85.86	587.44	687.50
	Old	119.37	84.45	518.22	516.69
PINCON	New	203.01	83.68	650.86	776.03
	Old	111.12	79.28	505.62	639.13
PINMON	New	200.36	85.56	608.69	712.60
	Old	125.00	78.60	510.18	649.08
PINPON	New	184.15	82.05	638.26	779.25
	Old	120.28	80.95	544.67	675.60
PSEMEN	New	198.68	87.91	568.71	652.04
	Old	108.17	89.99	474.50	528.85
TSUHET	New	224.60	88.12	560.35	642.97
	Old	128.64	88.87	491.95	554.90

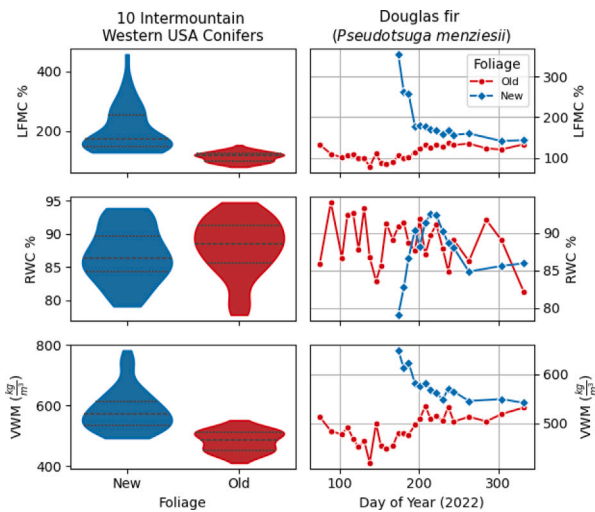


Fig. 5. Distributions for 10 Intermountain Western USA conifers for LFMC ($n = 110$), RWC ($n = 110$), and VWM ($n = 110$) for new and old foliage (left column). Example time series plots of LFMC ($n = 41$), RWC ($n = 41$), and VWM ($n = 41$) for new and old Douglas fir foliage sampled at Blue Mountain in 2022 (right column). Variable descriptions and units are given in Table 3.

needles. The lowest mean LFMC values were observed in Douglas fir (PSEMEN) old foliage (108.17%), while the highest occurred in Engelmann spruce (PICENG) new foliage (240.78%). RWC ranged narrowly, with the lowest values in Western white pine (PINMON) old foliage (78.60%) and the highest in grand fir (ABIGRA) new foliage (90.23%). The lowest VWM values were found in Subalpine fir (ABILAS) old foliage (461.66 kg m^{-3}), whereas the highest were recorded in Lodgepole (PINCON) new foliage (650.86 kg m^{-3}). Kappa showed lowest values in Douglas fir (PSEMEN) old foliage (528.85 kg m^{-3}) and the highest in Ponderosa pine (PINPON) new foliage (779.25 kg m^{-3}).

Violin plots of LFMC, RWC, and kappa across 10 conifer species are shown in the left column of Fig. 5. New foliage exhibited substantially higher LFMC, with a median of 172% compared to 116% in old foliage, and was far more variable (standard deviation 75% versus 16%). SAV values were broadly similar between age classes, though new foliage

had slightly higher median values and greater variability (standard deviation 833 m^{-1} compared to 460 m^{-1} in old foliage). RWC showed minimal differences between age classes. New foliage RWC had a median of 86.4% and old foliage 88.5%, with nearly identical standard deviations of 4.15% and 4.25%. In contrast, kappa displayed a clear age-related shift, with new foliage having higher median values (672% versus 544%) and greater variability (standard deviation 97% versus 58%).

Seasonal patterns in 2022 Douglas fir are shown in the right column of Fig. 5. LFMC remained consistently higher in new foliage, particularly during spring and early summer, reflecting active growth and greater water retention. New foliage RWC increased steadily with needle development, whereas old foliage showed a gradual decline during late summer and fall. VWC showed a clear separation between age classes, with new foliage consistently higher than old foliage. New foliage VWC decreased throughout the growing season, while old foliage increased.

3.5. Predicting live fuel moisture content

LFMC can be calculated using volumetric quantities by normalizing the numerator and denominator by the particle volume. If we consider LFMC as a simple ratio of the volumetric water mass (VWM) and volumetric density, we can use the mechanistic density model to directly estimate LFMC (Eq. (9)). The left column of Fig. 6 shows the LFMC calculated using our density model as an input across 10 conifer species. These LFMC predictions were strongly correlated with observed LFMC ($R = 0.82$). To demonstrate the model's ability to capture intra-specific seasonal dynamics, we also show the LFMC model for Douglas fir using the density model as an input in the bottom panel of Fig. 7. Predicted Douglas fir LFMC was highly correlated with observed LFMC ($R = 0.77$) and the model effectively captures seasonal dynamics in new and old foliage.

We can also use LMA predictions to estimate live fuel moisture content using a mechanistic LFMC model that provides a pyroecophysiology-based approach to fuel moisture modeling (Jolly et al., 2025). The LFMC model uses LMA as a key input representing the dry mass component of LFMC (Eq. (6)). The right column of Fig. 6 shows the mechanistic LFMC model (Variant 5) using our LMA predictions as an input across 10 conifer species. This version of the LFMC model captures the between species variation in LFMC and is strongly correlated with measured LFMC across foliage age class ($R = 0.73$). The LFMC model for Douglas fir using LMA predictions as an input is shown in the top panel of Fig. 7. Predicted Douglas fir LFMC using LMA was correlated with observed LFMC ($R = 0.69$) and the model effectively captures seasonal dynamics in new and old foliage. Mean inputs for the mechanistic LFMC model variant 5 are shown in Table 6.

4. Discussion

Here we have presented a mechanistic model for conifer foliar density and leaf mass area (LMA) that describes how foliar development and carbon allocation may influence their seasonal and inter-species variations. These models are a useful first step toward decomposing foliar density and LMA variations into metrics that can be easily quantified and compared across species and plant functional types. This approach provides a foundation for future explorations in additional conifer species and other plant functional types.

Foliar density and LMA are central plant traits that characterize trade-offs between photosynthetic activity, leaf structure, leaf longevity and nutrient allocation, and canopy fuel properties, yet they are consistently treated as a static, species-specific constant in ecosystem models. Observed intra-specific, developmental variation in Douglas fir density and LMA across the growing season show that this assumption is untenable. Across new and old Douglas fir foliage, density ranged from 183 to 535 kg m^{-3} with a percent variability of 192% and LMA

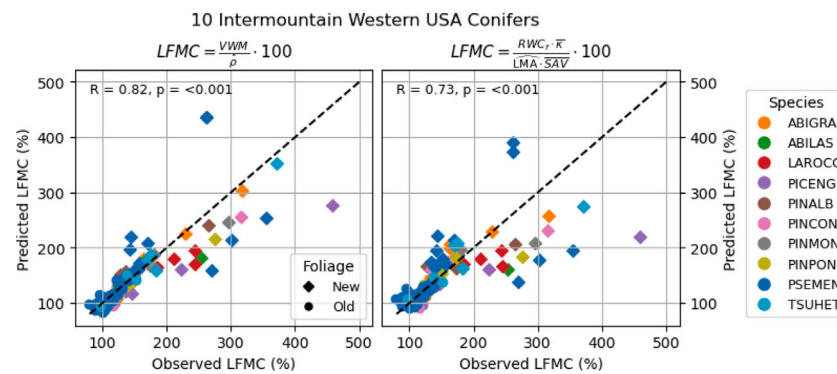


Fig. 6. Performance of density model and LMA predictions as inputs for LFMF across 10 Intermountain Western Conifer Species ($n = 110$). The left column shows modeled density as an input for LFMF model variant 5 from Jolly et al. (2025) which is strongly correlated with measured LFMF ($R = 0.82$). The right column shows predicted LMA as an input for LFMF, which is also well correlated with measured LFMF ($R = 0.73$). R and p values represent Pearson correlations between predicted and observed LFMF.

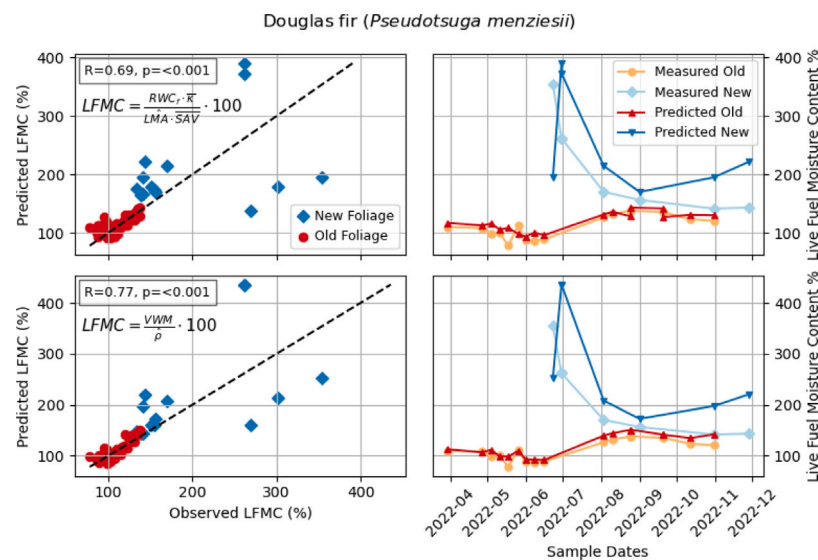


Fig. 7. Performance of density model and LMA predictions as inputs for LFMF for Douglas fir. The top row shows predicted LMA as an input for LFMF model variant 5 from Jolly et al. (2025) which is strongly correlated with measured LFMF ($R = 0.69$). The bottom row shows modeled density as an input for LFMF using time-varying VWM and predicted density, which is also highly correlated with measured LFMF ($R = 0.77$). Both LFMF predictions adequately characterize seasonal Douglas fir LFMF dynamics in new foliage ($n = 14$) and old foliage ($n = 37$) (left column). R and p values represent Pearson correlations between predicted and observed LFMF.

ranged from 0.03 to 0.14 kg m⁻², showing a 4.7-fold difference over the growing season and a percent variability of 395%. These patterns are associated with changes in chemical components including non-structural carbohydrates (NSC), crude fats (CF) and neutral detergent fiber (NDF), which also show large seasonal variations. Mechanistically linking density and LMA to these chemical components provides a useful way to explore how developmental, carbon, and environmental factors may contribute to variation in these traits. This offers more flexibility than assuming fixed LMA values and it provides a better foundation for integrating these variations into future ecosystem process models.

By breaking down density into individual chemical components, we quantify the allocation of carbon into different types of dry matter (e.g. structural vs. storage compounds), providing a more detailed picture of carbon investment in the leaf. These findings are consistent with other studies that show that changes in lipids (crude fats), structural (NDF) and non-structural carbohydrates (NSC) induced the largest changes in LMA in some tree species (Poorter et al., 2009). New foliage allocates carbon to the construction of structural biomass

(NDF), with changes in this component being a major driver of the increase in dry mass (LMA) as the needle matures. Correlations between chemical components and foliage density for new foliage showed that neutral detergent fiber was most strongly related to density variations ($R = 0.633$). While NSC and CF are present and their dynamics may contribute to LMA variation, the primary investment in the early stages appears to be in building the physical structure. Correlations between density and chemistry for old foliage showed that density variations were mostly driven by non-structural carbohydrates ($R = 0.78$). In contrast, old foliage appears to serve more significantly as a storage reservoir for carbon, primarily in the form of NSC and density variations are heavily influenced by seasonal NSC dynamics.

The mechanistic density/LMA model chemical inputs capture many critical plant functions into a few easily measured variables. We observed more than a three fold variation in the NSC concentrations of old Douglas fir foliage leading up to budbreak. This is consistent with other conifer species, such as Red pine and Jack pine, where large increases in foliar density that were associated with a translocation of starch were observed before budbreak (Jolly et al., 2016). This carbon serves as a

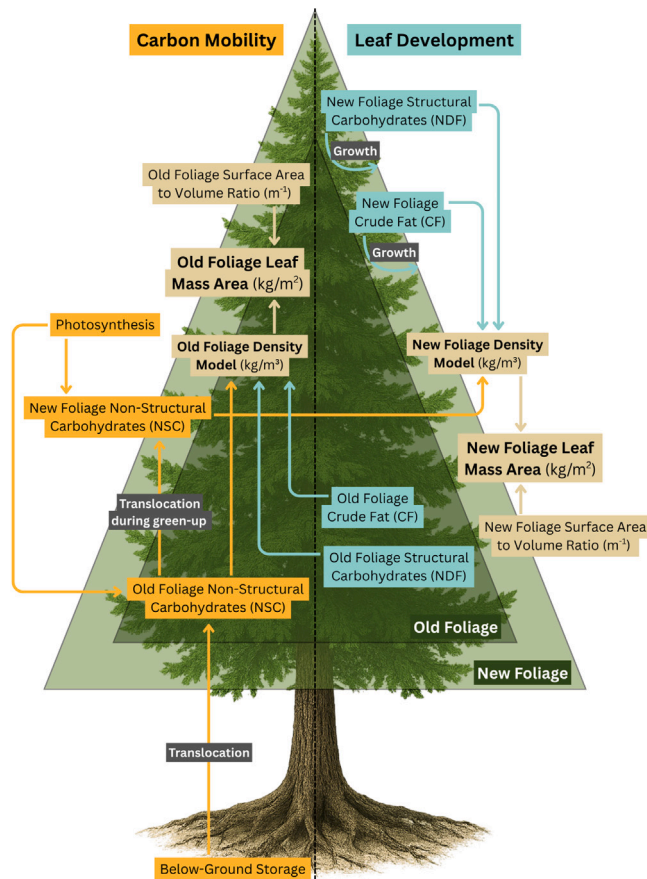


Fig. 8. Conceptual framework of ecophysiological processes that drive seasonal and inter-species variations in leaf mass area. Carbon dynamics are the main controls on old foliage dry mass, whereas leaf development drives seasonal increases in new foliage. Carbon mobility is shown on the left with orange arrows and text. Leaf development is shown on the right, with blue arrows and text. Beige arrows and text represent interactions between key variables in the mechanistic model.

'bank' to provide carbon to support the growth of adjacent new foliage during green-up. In contrast, seasonal variations in NSC of new foliage were small, owing to the fact that most of the carbon produced through photosynthesis or translocated from other parts of the plant is used immediately to support foliar structural growth. While NSC variations are strongly related to tree carbon allocation and demand, variations in both crude fat and neutral detergent fiber across foliage age classes are more strongly related to structural foliar development.

CF variations show clear increases during new foliage development. As new foliage develops, cuticles form and thicken along the leaf or needle surface to provide both mechanical strength and environmental protection. Despite being thin, foliar cuticles can account for a significant percentage of leaf biomass due to their high density (Onoda et al., 2012). The steady increase in CF during foliar maturation quantifies this developmental process along with the production of other lipids. As the growing season progresses, CF in new foliage approaches old foliage values. Other studies have confirmed these increases in CF across other conifer species (Jolly et al., 2014, 2016) and have also contrasted those variations with other plant functional types (Qi et al., 2016). CF is an important metric that can characterize seasonal foliage development and aid in better understanding subsequent LMA variations between new and old foliage. CF variations during foliage maturation also co-occur with increases in foliage structure.

NDF is a metric that captures the amount of dry mass allocated to foliage structural compounds such as cellulose, hemicellulose and lignin. As expected, we observed a nearly 2.5 fold increase in new foliage NDF concentrations during needle development, indicating the production of new primary and secondary cell walls during green-up. Ultimately, the combination of NDF and CF effectively capture the foliar chemical changes that occur during needle maturation and collectively are sufficient to describe the influences of these changes on subsequent leaf mass area. In contrast, NDF for old foliage were relatively stable throughout the growing season. However, because NDF represents the fundamental structural investment in foliage and constitute such a large portion of total dry mass, it is necessary to capture seasonal variation in developed foliage.

Our work focused primarily on describing density and subsequent LMA variations in Temperate evergreen trees with the exception of Western Larch. Because full seasonal sampling was only conducted for Douglas fir and sampling for other species was more limited, observed patterns should be interpreted cautiously and may not generalize across evergreen taxa. Evergreen trees typically invest carbon into leaf structure and protective cuticles during leaf flushing because these trees must be able to withstand harsh winter conditions. Indeed, we observed steady increases in the dry weight percentages of NDF and CF during leaf maturation and these two variables were the best time-varying predictors for dry weight variations in new foliage. In contrast, we observed strong seasonal NSC variations in old foliage as a function of the translocation of carbon stored in either stems or roots to old foliage after the trees broke dormancy but before new leaves emerged. Together, these seasonal variation explained most of the nearly 5-fold differences in LMA we observed in our frequently-sampled Douglas fir as well as across our 10 species surveyed at multiple points during the growing season. It is likely that evergreen shrubs behave similarly but it is less clear whether similar dynamics could be observed for other plant functional types. Other studies have shown that evergreens allocate more carbon to structure when compared to deciduous plants (Mediavilla et al., 2008) but the overall inclusion of structural and non-structural carbohydrates and crude fats may be sufficient to characterize LMA variations across plant functional types. More work is needed to understand how our results might scale across grasses, shrubs and trees with different leaf lifespans.

Our sampling strategy assumes that cross-sectional data that are collected across the same site, species, and foliage age class, reflects the longitudinal trajectory of an individual leaf or needle. This ergodic assumption allows us to develop an implicitly time-dependent model without requiring time as an explicit variable. Although leaf development is generally deterministic, micro-climatic differences and individual variability introduce some noise. However, because comprehensive non-destructive sampling is impossible, we accept this baseline variability in our temporal sampling scheme.

4.1. Relevance for wildland fire behavior modeling

While it is critical to understand LMA itself, LMA is also used extensively in other types of physiology-based modeling. Plant traits such as their dry weight moisture contents, or Live Fuel Moisture Content (LFMC), are used commonly in fire behavior models to predict wildfire spread and intensity and those models are sensitive to change in live moisture contents inputs (Jolly, 2007). Here we demonstrate a use of the mechanistic density model by using it alongside volumetric water mass (VWM) to predict LFMC variations seasonally and across species. We also demonstrated a use of the mechanistic LMA model by coupling it with a novel mechanistic live fuel moisture content (LFMC) model (Jolly et al., 2025) to predict LFMC. LMA is a crucial metric of fuel availability, used to compute several critical physical fuel properties required by fire behavior models (Brown et al., 2025). As LMA increases, the amount of dry fuel per unit leaf area and crown volume also increases, making LMA a direct indicator of potential fuel

load (Brown et al., 2025) while also accounting for seasonal changes in foliage biomass (Jolly et al., 2025). Canopy foliar biomass, or fuel loading, is directly computed by multiplying LAI with LMA, provided LAI is corrected for foliar orientation or fractional cover (Fang et al., 2019; Bahrami et al., 2022). This provides a direct measure of the amount of combustible material available within a vegetated area. Thus, accurate LMA predictions are critical for calculating the amount of available crown fuel.

The mechanistic LFMC model aims to provide a framework for the decomposition of LFMC into variables that are physiologically-relevant and that can be modeled across species, space, and time (Jolly et al., 2025). The model addresses the independent variability of water weight and dry weight by expressing LFMC as an emergent property derived from four key physical and chemical plant particle traits: Leaf Mass per Area (LMA), Relative Water Content (RWC), Surface-Area-to-Volume ratio (SAV), and the volumetric saturated water holding capacity (κ). Thus, the success of decomposing LFMC hinges significantly on the consideration of each model variable in the context of their driving processes. A conceptual figure of these variations is shown in Fig. 8. The integration of mechanistic LMA predictions into the (Jolly et al., 2025) live fuel moisture model improves the LFMC framework by providing a dry mass input that is grounded in specific physiological and biochemical components, enhancing the mechanistic understanding of LFMC fluctuation. Different compositions of dry matter will burn differently; NSC and CF are generally highly combustible. Integrating the quantity of chemical components within dry mass into fire models will link the plant's leaf economic strategy to its flammability.

Ultimately, the goal is to couple the mechanistic LMA model with a leaf water balance model that explains RWC changes to facilitate more accurate predictions of vegetation response to climate and disturbance. This coupled model can then be used to other ecosystem process models that include wildfire as disturbance to better predict short and long term effects of wildfires on ecosystems such as FATES (Koven et al., 2020).

4.2. Applications in remote sensing

LMA is also critical in remote sensing applications because it represents the dry matter content component needed to accurately determine moisture content from spectral measurements. Remote sensing approaches used to map LFMC rely on estimating Equivalent Water Thickness (EWT) and Dry Matter Content (DMC), where DMC is equivalent to LMA (Yebara et al., 2013). Accurately estimating DMC is a significant challenge because water content masks the dry matter absorption features, which makes estimation difficult when vegetation is wet (Yebara et al., 2013). The LMA prediction offers a physiological measurement that can be used alongside DMC estimations to improve the ability to map live fuel variations using remote sensing. LMA is also a crucial input parameter in Radiative Transfer Models (RTMs) used for canopy optical modeling. RTMs like PROSPECT, which characterize leaf optical properties, are combined with canopy models to estimate both LMA and EWT. The successful inversion of these models to solve for LFMC depends on the accuracy of the DMC estimate, which can be improved by our mechanistic LMA predictions.

4.3. Applications in ecosystem process modeling

LMA is a key component of the Leaf Economic Spectrum (LES), reflecting universal trade-offs in resource investment and return. The LES runs from a strategy of low LMA and quick return on investments of nutrients and dry mass to high LMA and slow return (Wright et al., 2004). Ecosystem models like BIOME-BGC (White et al., 2000) and FATES (Koven et al., 2020) leverage these LMA-driven strategies to describe leaf form and related plant strategies. LMA is also broadly correlated with leaf nitrogen concentrations across biomes, so in models that calculate photosynthesis based on nitrogen content, like BIOME-BGC,

LMA acts as a critical scaling factor. These models generally assume LMA to be a fixed value inside a species or a functional group, despite LMA exhibiting significant variability within a species, across different environmental gradients, and even within a single plant or growing season, with most terrestrial species in the field exhibiting LMA values ranging between 30 and 330 (Poorter et al., 2009). Thus, it does not make sense to treat LMA as a fixed variable because it is a highly dynamic and physiologically regulated trait that responds to environmental conditions and phenological cycles. Our density-driven model provides dynamic LMA predictions that incorporate carbon allocation strategies and phenology, which can be used to improve ecosystem process models. By implementing mechanistic LMA predictions, process models can more realistically represent LMA-driven resource strategies and account for their responses to season and environment.

Additionally, LMA is a key input in canopy models like the Parsimonious Canopy Model (PCM) for simulating leaf biomass and LAI, which are vital for calculating Gross Primary Production (GPP) (Bahrami et al., 2022). LAI, which quantifies the amount of leaf area in an ecosystem, is directly calculated from leaf biomass (B_l) and Specific Leaf Area (SLA, the inverse of LMA). Incorporating the mechanistic LMA model can improve our understanding of how assimilated carbon is allocated to leaf biomass and how these physiological changes influence overall LAI and GPP dynamics. Specifically, the LMA model can help capture the early onset of leaf development during green-up and corresponding LAI increase, addressing a known limitation in current models (Bahrami et al., 2022).

Our study focused completely on predicting variations in sunlit LMA, but the impacts of within canopy variations when leaves are shaded can also have a large impact on LMA. LMA typically increases along a relative canopy height gradient (Legner et al., 2014). It may be possible to leverage our model to provide sunlit LMA estimates to more complex models that use within-canopy photosynthetically active radiation (PAR) to predict LMA at various canopy levels. Additionally, our LMA model could be linked to other dynamic, tree physiology models that account for seasonal variations in the allocation of NSCs to leaves, stems and roots and that account for seasonal carbon storage, such as the CASSIA model that has been developed for pine species (Schiestl-Aalto et al., 2015). Overall, linking tree-based carbon storage models with canopy LMA models could help better describe the spatial and temporal variations of LMA. These estimates could be linked to other ecosystem process-based models to assess processes of and interactions between the carbon, water and nutrient cycle of forests.

4.4. Broader implications for global ecosystems

Poorter et al. (2009) underscored the need to better describe LMA variations based on their chemical composition. Our work extends these efforts to provide a framework that can explain these seasonal and inter-species differences in LMA in relation to the carbon mobility and foliar development strategies of conifer trees. Our results demonstrate that leaf phenology and development are the primary drivers of LMA variations in both new and old foliage. Poorter et al. (2009) noted that a large portion of LMA variation remains unexplained, and our work may help clarify some of these patterns within conifers. Our findings suggest mechanisms that could be relevant more broadly and may provide a starting point for exploring density and LMA variations in other plant functional types.

5. Conclusion

Here we have presented a novel, ecophysiology-based model of density that integrates physiologically relevant components of foliar dry mass to predict leaf mass area variations across a wide cross section of Intermountain Western US conifers. While LMA has historically been treated as a static parameter within species or functional groups to simplify large-scale simulations, our results suggest that assuming

LMA invariance limits a model's ability to capture essential seasonal and age-dependent fluctuations. By capturing the dynamic carbon and phenological cycles that govern dry matter variations, this new model can improve the representation of seasonal LMA in process models, advance our understanding of vegetation-driven wildland fire behavior and, more broadly, explain the leaf trade-offs that regulate terrestrial productivity and global carbon and water cycles.

CRedit authorship contribution statement

Ella M. Keefer: Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **W. Matt Jolly:** Writing – original draft, Supervision, Methodology, Formal analysis, Conceptualization. **Elliott T. Conrad:** Methodology, Data curation. **Tegan P. Brown:** Methodology, Data curation. **Samuel C. Hillman:** Methodology, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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