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# Seasonal water availability drives trait variation in isolated Basin and Range *Pinus ponderosa*

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#### ABSTRACT

Tree species resistant to drought stress are likely to be more successful under the moisture-limited conditions predicted with climate change, and variation in drought-resistant traits can influence a species' sensitivity to change. Trait variation is often tied to the timing, amount, and type of precipitation a given forest stand is exposed to, and local topographic heterogeneity may exacerbate or mitigate soil moisture stress. Although drought resistance is well-studied in widespread tree species, knowledge is limited on trait variation in drought-resistant conifers with more narrow distributions or isolated populations.

*Pinus ponderosa* is amongst the most widespread conifers in semi-arid forests of western North America, and var. *scopulorum* occurs in some of the most arid portions of the species' range. In the Northern Basin and Range physiographic province of western North America, *scopulorum* is isolated to montane sky islands, making it a model system for testing the effects of climate and topography on trait variation in drought-resistant conifers. To investigate the relationship between interacting climatic and topographic conditions and drought-resistant traits, we sampled 55 stands across six ranges in Nevada and Utah to quantify trait variation in cone volume, wood density, latewood to earlywood ratio (LER), specific leaf area (SLA), and needle lifespan and asked how these traits vary across the regional climate gradient. We then used linear mixed models to explore whether seasonal climatic moisture deficit (CMD), monsoonality, aspect, elevation, or tree-level attributes are associated with trait variation.

Traits varied widely both within and among ranges, with trait responses strongly linked to seasonal water availability. Cone volumes and SLA increased with increasing summer (July-Aug) CMD, while cone volume decreased with increasing winter (Nov-Jan) CMD. Winter moisture stress was also tied to wood formation, as wood densities increased under greater cold season (Oct-Feb) CMD. Needle lifespan and LER were not shaped by seasonal CMD but rather by the degree of monsoonality, indicating that drought-resistant conifers may be able to take advantage of late-summer precipitation. Contrary to our expectations, local topographic variation had no influence on trait variation in the stands sampled here, while elevation and tree diameters were significant for wood traits alone. These findings suggest that both seasonal moisture stress and the timing of precipitation influence drought-resistant conifer trait variation in semi-arid environments and highlight the potential for these conifers to withstand extreme fluctuations in seasonal water availability, which is predicted to become more common as the climate continues to change.

#### 1. Introduction

As forests are increasingly threatened by hotter and more frequent droughts under rapid climate change (Brodribb et al., 2020), tree functional trait diversity will strongly influence forest persistence potential under increasing soil moisture stress (Aubin et al., 2016). Major ecosystem type conversion is expected from increased drought-related tree mortality (e.g. from forest to shrubland; Anderegg et al., 2013), leading to decreased forest cover (Allen et al., 2015) and declines in ecosystem productivity (Williams et al., 2013). It is therefore essential that we quantify the impact of drought stress on forest ecosystems to inform predictions of species responses to anticipated future climatic stress and support conservation and management efforts in these rapidly transforming landscapes (Hobbs et al., 2014).

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Ecosystem vulnerability to climate change will be determined by species' responses to novel climate and disturbance conditions (Lavorel and Garnier, 2002; Suding et al., 2008), which will filter species and individuals to only those plastic or tolerant enough to establish under these more extreme environments (Jump and Peñuelas, 2005). Species possessing drought-resistant leaf, wood, and seed morphological traits are likely to have an advantage under increasing climatic water stress (De Micco and Aronne, 2012), particularly in arid and semi-arid environments that are predicted to be heavily impacted by climate change (Lioubimtseva, 2004). Plants with greater longevity, such as conifers, lack the ability to adapt to rapid rates of climatic or environmental change (Christmas et al., 2016), and traits conferring success under extreme conditions will thus be critical for maintaining ecosystem type and function (Jump and Peñuelas, 2005) through increasing drought (Klein et al., 2013; Britez et al., 2014) and associated soil water limitations (O'Brien et al., 2017).

Species or stands occurring in more arid environments often possess drought-resistant phenotypes following repeated exposure to constrained seasonal water availability (Berner and Law, 2015) or variation in the timing of precipitation (Ziaco et al., 2018). Several morphological traits may be advantageous under such conditions, and both climatic water deficit (Berner and Law, 2015) as well as the frequency and duration of drought can drive conifer trait variation (Greenwood et al., 2017). For instance, needle lifespan may be reduced (Ozolinčius et al., 2009) or needles may be smaller (Cregg, 1994) and denser (Fernández et al., 1999), as decreased leaf area reduces water loss under increasing transpiration (Valladares & Sánchez-Gómez, 2006). Wood formation is responsive to drought stress as well, and increasing wood density is correlated with a reduced vulnerability to water-stress induced embolism (Hacke et al., 2001). Further, an increase in the ratio of latewood to earlywood could suggest a higher resistance to cavitation under severe drought (Domec and and Gartner, 2002), and latewood to earlywood ratios determine wood densities (Hannrup et al., 2001). Conifers may also produce larger cones under drier conditions (He et al., 2018), and cone sizes are generally positively correlated with seed number (Dickmann and Kozlowski, 1971; Caron and Powell, 1989) and seed size (Gleiser et al., 2019). Evidence of such trait response is often tied to the timing of water availability in a given year rather than to annual climatic conditions. Greater variability in intra-annual timing and frequency of precipitation decreases wood density (George et al., 2015), while increased summer precipitation can lead to a larger production of cones (Bisi et al., 2016; Wion et al., 2019). Wider trait variation or phenotypic plasticity to climatic moisture stress may increase the persistence potential of conifer species (Bisbing et al., 2020), and drought-resistant traits are likely to confer greater success under future, predicted climatic conditions (Aubin et al., 2016).

Persistence potential may also be possible via local refugia if topographic heterogeneity buffers plant exposure to extreme climate conditions and preserves suitable habitat for establishment and growth (Vanwalleghem and Meentemeyer, 2009). Shaded hillslope aspects, for example, can increase soil moisture, likely attenuating regional climate effects on conifer growth (Hoylman et al., 2018). Conversely, topographic effects may intensify extreme climate stressors. For instance, south-facing aspects, where greater insolation generally causes higher temperatures and greater evapotranspiration, can amplify stress under increasingly harsh climatic conditions (Elliott and Kipfmueller, 2011; Elsen and Tingley, 2015). This interaction between topography and climate drives conifer growth (Tague et al., 2009) and distribution (Mckenzie et al., 2003) and is likely to influence morphological droughtresistant traits.

Moisture-limited forests of Nevada and Utah, USA, defined here as the northern region of the Basin and Range physiographic province of western North America (Fig. 1A; hereafter the "Northern Basin"), provide a unique context to study intraspecific conifer trait variation. *Pinus ponderosa* Douglas ex. Lawson is one of the most widespread conifers in semi-arid forests of western North America (Little 1971; Fig. 1A), occupying the lower elevational bounds of coniferous forests across much of its range (Conkle and Critchfield 1988; Steele 1992). Despite contiguous distribution in less xeric landscapes, occurrence in the Northern Basin is limited to 12 high-elevation, geographically-isolated sky islands (Charlet 1996; Willyard et al., 2017) that provide some relief from the extreme soil moisture limitations of the greater landscape (Grayson 2011; Soulard and Sleeter 2012; Fig. 1A). In the Northern Basin, low elevation *P. ponderosa* var. *scopulorum* (Engelm.) forests exist in some of the most arid portions of the species' range (Barrett et al., 1980). Variation in the timing and amount of precipitation is a hallmark of the monsoonality gradient in the Northern Basin (Adams and Comrie 1997; Romme et al., 2009; Dilts et al., 2015), and timing of moisture influences growth of *P. ponderosa* var. *scopulorum* and other dryland conifers (Redmond et al., 2017; Truettner et al., 2018).

Here, we used Northern Basin P. ponderosa var. scopulorum, henceforth scopulorum, to investigate the relationships between interacting climatic and topographic conditions on conifer morphological trait diversity across one of the most arid landscapes in western North America. We sampled 55 stands across six ranges in Nevada and Utah to quantify trait variation in cone volume, wood density, latewood to earlywood ratio (LER), specific leaf area (SLA), and needle lifespan to ask: how do morphological traits vary within and among ranges in isolated, moisture-limited forests as a function of climate and topography? As timing of moisture is important for conifers growing in semi-arid environments (Huxman et al., 2004; Assal et al., 2016; Zeng et al., 2019), we predicted that seasonal water stress would be highly influential in driving morphological variation. We further hypothesized that topographic factors, specifically aspect, would influence conifer trait morphology by mitigating or exacerbating extreme climatic conditions within these stands (Redmond and Kelsey, 2018). Our findings will be particularly relevant to assessing the persistence potential of conifer species growing in arid and semi-arid environments that are projected to be exposed to the increasing frequency and severity of drought.

#### 2. Methods

#### 2.1. Study species and area

*Scopulorum* is primarily distributed across lower montane forests of the Rocky Mountains and Intermountain West, USA, but is also a common forest type as far east as the Dakotas and Nebraska (Fig. 1A). The southwestern extent of the species' range is characterized by isolated stands in Nevada and Utah (Little, 1971). The climate is more arid in the southern portion of *scopulorum*'s distribution, where mean annual precipitation is 25 cm and annual temperatures average 10 °C (Barrett et al., 1980). At *scopulorum*'s northern extent, mean annual precipitation is as high as 64 cm while annual temperatures average 5 °C (Barrett et al., 1980).

The Northern Basin is generally characterized as a water-limited matrix of salt desert and sagebrush ecosystems, and widespread, yet isolated, high-elevation mountain ranges (~700 – 4300 m) provide cooler and moister conditions to support *scopulorum* and other conifers (Grayson, 2011; Soulard and Sleeter, 2012; Moreo et al., 2014). Within these ranges, *scopulorum* is generally flanked at lower elevations by shrub or woodland communities and at higher elevations by five-needle pine and fir forest (Grayson, 2011; Ziaco and Biondi, 2018; Ziaco et al., 2018). The Northern Basin captures a portion of the North American Monsoon (Higgins et al., 1997) in which a large proportion of total annual precipitation falls in late summer, but its influence decreases in significance across the southeast to northwest monsoonal gradient (Castro et al., 2007).

# 2.2. Plot selection

To identify *scopulorum* stands in the Northern Basin, we used both available vegetation layers classifying *scopulorum* forests as well as



**Fig. 1. A)** Distribution of *Pinus ponderosa* (in green) and *Pinus ponderosa* var. *scopulorum* (in blue; Flora of North America (Eds. 1993) distribution) with inset map of mountain ranges sampled for *P. ponderosa* var. *scopulorum* trait variation (n = 6) in the Northern Basin & Range physiographic province of North America (shaded). **B)** Maps of sampled plots overlaid on classified *scopulorum* distribution from the Southern Rocky Mountain lower montane forest vegetation layer extracted from the National Gap Vegetation Data (U.S. Geological Survey Gap Analysis Program 2016) for the Grant and Quinn Canyon Ranges, the Snake Range, the Wah Wah Mountains, the Spring Mountains, the Sheep Range, and the Clover Mountains. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

published records of occurrence from biogeographical surveys. First, we extracted the Southern Rocky Mountain lower montane forest vegetation category from the National Gap Vegetation Data (U.S. Geological Survey Gap Analysis Program, 2016) in ArcGIS 10.4.1. Next, we augmented this distribution layer using the *Atlas of Nevada Conifers* (Charlet, 1996), which provides additional distributional information and locations of cryptic stands.

Of the 12 mountain ranges containing *scopulorum* in the Northern Basin, nine were identified as potential sampling locations, with three ranges immediately excluded due to documented low stand sizes (<10 individuals, Nelson, 1976; Charlet, 1996). Of the remaining nine, inaccessibility led to exclusion of three additional ranges. We ultimately sampled in six ranges – the Snake Range, Wah Wah Mountains, Grant and Quinn Canyon Ranges, Clover Mountains, Sheep Range, and Spring Mountains in the Northern Basin (Fig. 1A). The Grant and Quinn Canyon are adjacent ranges that lack separation by desert valleys and thus were considered one range, hereafter referred to as the Grant Range.

For these selected ranges, we then stratified the comprehensive scopulorum occurrence layer by aspect using a USGS DEM with 10 m resolution. Potential sampling locations were randomly selected from this stratified layer using the Sampling Design Tool in ArcGIS (Buja and Menza, 2013) to be a minimum of 400 m apart and equally distributed among aspect classes (N (315-45°), E (45-135°), S (135-225°), W (225-315°)). Within each range, we prioritized sampling across an even distribution of aspect classes wherever possible, but distribution data were not always accurate, and scopulorum frequently occurred on aspects different than previously classified. Potential sampling locations not falling within or adjacent to scopulorum were excluded, and those lacking a minimum density of scopulorum (defined as three mature trees > 30 cm diameter at breast height, DBH) were moved 50-100 m to capture the local stand. If scopulorum was not present within a 100 m radius, additional sampling locations were scouted and sampled on comparable aspects to increase the distribution of aspect classes. Stands with signs of recent disturbance (i.e. burned within the last 30 years) were excluded (Monitoring Trends and Burn Severity; Finco et al., 2012). Ultimately, a total of 55 stands were selected across the six mountain ranges and distributed as follows: 11 in Snake, 6 in Wah Wah, 5 in Grant, 4 in Clover, 12 in Sheep, and 17 in Spring (see Table S1 for stand-level characteristics).

# 2.3. Field sampling and sample processing

In one 0.04 ha (11.35 m radius) circular plot at each stand, we measured diameter, height, crown length, and average crown width of all mature scopulorum, defined as trees with a DBH > 30 cm (Poth and Fenn, 1998), with sample sizes ranging from a minimum sample requirement of three trees up to nine trees (maximum present in any 0.04 ha plot, Table S1). Basal area of both scopulorum and co-occurring species was measured with a prism (basal area factor 2.296  $m^2/ha$ ) to capture potential competition for resources. Then, to quantify trait variation, we measured cone volume and needle lifespan in the field and collected wood cores and needles for processing in the lab. Needle trait sampling was standardized by collecting samples on south-facing branches at heights between seven and 10 m from all trees present within the plot, as variation in crown position influences needle morphology (Ishii et al., 2002). Using the "counting cohorts" method from Pérez-Harguindeguy et al. (2013), needle lifespan was estimated for the entire branch by counting the number of annual needle cohorts that contained > 50 percent of the original foliage (e.g. a lifespan of five years if five annual cohorts with > 50% of needles were counted). One branchlet was then collected from this same branch for quantifying SLA in the lab. To quantify wood density from these same individuals, tree cores were collected at ground level and perpendicular to the hillslope, and core lengths and diameters were documented for fresh cores. Finally, cones were sampled by counting all fresh ground cones within the plot from the most recent year's cone crop, which were identified as

cones with reflexed and rigid scales and no sign of weathering (Gabrielson et al., 2012). This sampling strategy was necessary due to poor cone production during the period of sampling (summer, 2019). Instead, 25 open and intact ground cones of the most recent year's cone crop (as defined above) were opportunistically sampled and measured for weight, length, largest width, and smallest width. Cone volume was later calculated based on methods from Leslie et al. (2014) using cone length and the two widths.

In the lab, needle and core samples were dried at 70  $^\circ C$  for 72 h. For needle analyses, a random selection of 20 fascicles from a subset of three to four trees per plot - excluding current year's growth - were scanned with WinSEEDLE (Regent Instruments) to measure needle area. Specific leaf area (mm<sup>2</sup>/mg) was calculated as one-sided area of each needle divided by its oven-dry mass (Pérez-Harguindeguy et al., 2013). Wood density (g/cm<sup>3</sup>) was calculated as the oven-dry core mass divided by fresh core green volume (Chave et al., 2009), which was quantified by multiplying field-measured core length by core cross-sectional area (see Fajardo and Piper, 2011 for detailed methodologies). Cores were then mounted onto wooden bases and sanded with successively finer sandpaper, up to 600 grit. Lower quality cores (i.e. twisted) were excluded from processing. We captured high-resolution images (1200 dpi) of each core for ring-width analysis, using an Epson Expression 11000XL scanner (Seiko Epson Corporation, Suwa, Japan). Over the entire core, annual ring width, latewood width, and earlywood width were measured from the digital images using the computer program WinD-ENDRO (Regent Instruments), and the width of latewood was divided by width of earlywood for each ring and averaged by core to calculate mean LER. For samples reaching the pith or very near the pith, we also recorded the boundary between sapwood and heartwood and calculated the ratio of heartwood to sapwood (HW:SW) based on the length of each segment in the core.

# 2.4. Analysis

To test for the effect of climate on scopulorum trait variation, we selected potential predictor variables that capture moisture availability and stress. Climatic moisture deficit (CMD, or sum of the monthly difference between a reference evaporation and precipitation; Hargreaves, 1975) is a well-documented climatic stressor for conifers growing in semi-arid regions (Flake and Weisberg, 2019; Urza et al., 2020), while monsoonality (defined as July-September precipitation divided by total annual precipitation) provides a measure of moisture relief during the growing season (Ziaco et al., 2018; Wion et al., 2019); these variables were thus selected as potential climate predictors to capture drought and seasonal moisture stress. Monthly climate data were extracted from ClimateWNA (Wang et al., 2006, 2012) for the length of the climate record (1901-2018), and monsoonality was calculated from July to September precipitation values. We then separated the climate data into two climate normal periods that correspond to temporal variation in trait development. We selected a five-year climate normal (2014 - 2018) for needle and cone trait analyses, given the average P. ponderosa needle lifespan of five years (Reich et al., 1996) and the two- to five-year period for cone crop development (Krannitz and Duralia, 2004; Lesser and Jackson, 2013). For models of wood density and LER, we selected a much longer timeframe, using all available climate data from 1901 to 2018 (118 years). This selection is supported by previous studies of Northern Basin scopulorum in which breast height diameters of 32-72 cm had maximum ages over 250 years (Ziaco and Biondi, 2018; Ziaco et al., 2018). We did not age our cores, but these diameter ranges were consistent with our core samples.

Next, due to the importance of timing of moisture in influencing conifer morphology, we explored seasonal rather than annual CMD and followed methods outlined in Redmond et al., (2017) to identify the consecutive months most strongly correlated with each trait sampled. Consecutive months with a p-value < 0.05 and Pearson's correlation coefficient (r) > 0.15 were chosen and combined into seasonal climate

predictor variables (Fig. S1). Cone volume was correlated with winter (November-January) and summer CMD (July-August, Fig. S1a). Wood density was also highly correlated with cold season CMD (October-February, Fig. S1b), while only August CMD met the thresholds as a monthly predictor for LER (Fig. S1c). SLA was correlated with summer CMD (July-August, Fig. S1d), and needle lifespan was most highly correlated with spring to early summer CMD (April-July, Fig. S1e). Monsoonality is defined by its seasonality, so this variable was not subject to this selection process and considered as-is in further analyses. We additionally used one-way Analysis of Variance (ANOVA) tests and post-hoc pairwise comparisons using Tukey's test to quantify variation in climate variables among ranges (Tables S2 & S3) in order to better characterize the local climates and identify significant differences among ranges.

Following climate variable selection, we quantified and assessed other factors predicted to influence trait response, including topographic, tree, and stand attributes. Aspect was the primary topographic gradient across our sampling sites and was included to test the effect of topographic position on trait morphology. To allow for more intuitive interpretation, we calculated folded aspect, which is the transformation of aspect around the north-south line so that east equals west and increasing values (1-180) are hotter and drier (McCune and Keon, 2002). Elevation was also included as a predictor to account for the elevational range of sampling locations. We additionally considered the following tree and stand attributes potentially important in driving trait variation: tree diameter (coring location and DBH), tree height, scopulorum basal area, basal area of all tree species, scopulorum tree crown volume, and scopulorum tree crown length. Both tree size and forest structure are documented to influence cone, needle, and wood trait variation (Krannitz and Duralia, 2004; Kašpar et al., 2019; Liu et al., 2020), while crown size can drive variation in needle morphology (Vanninen and Mäkelä, 2000). Crown volume was calculated using individual crown length and average width by employing methods outlined in Rautiainen et al. (2008). Total basal area of all species was included as a potential predictor to account for competition and shading.

To pare down variables from the full set, we ran a correlation analysis and evaluated potential predictor correlations against each trait. We ultimately selected the uncorrelated variables (r < 0.65) with the strongest evidence of influence on a given trait. Tree height, for instance, was highly correlated with DBH, crown volume, and crown length so was excluded as a potential predictor in order to retain these potential tree-level predictors. Elevation was only retained for the wood density model, as it was highly correlated with the seasonal CMD predictors selected for all other traits. We then fit separate linear mixed models for each trait with the "lmer" function from the "lme4" package (Bates et al., 2015) in R version 3.5.1 (R Core Team, 2018). All data had approximately normal distributions and were thus modeled using the default "Gaussian" family. Each individual trait was tested using a unique set of predictors (as defined above), but aspect was included in each model as an interacting term with seasonal CMD to account for the mitigating or exacerbating effects of topographic heterogeneity. Cone volume (n = 1299) was modeled at the cone level with summer CMD, winter CMD, monsoonality, aspect, summer CMD\*aspect, winter CMD\*aspect, scopulorum basal area, and mean scopulorum DBH as potential predictors. Wood density (n = 295) was modeled at the tree-level with cold season CMD, aspect, cold season CMD\*aspect, monsoonality, elevation and diameter at core height. The mean LER model (n = 225) included August CMD, aspect, August CMD\*aspect, monsoonality, and diameter at core height. Mean specific leaf area (n = 238) per tree was modeled using summer CMD, aspect, summer CMD\*aspect, crown volume, crown length, sample tree DBH, monsoonality, and total plot basal area of all species in the full model. Mean needle lifespan (n = 174) was modeled at the tree-level with early summer CMD, monsoonality, aspect, early summer CMD\*aspect, sample tree DBH, and total plot basal area of all species as potential predictors. All models included plot nested in

mountain range as a random effect.

Model selection was conducted by testing all combinations of predictors variables and selecting the model with the lowest Akaike Information Criterion (AIC) score if delta AIC with the full model was > 4, which provides statistical support for the reduced model (Burham and Anderson, 2002). If these criteria were not met, the full model was retained as the best model. Non-significant variables were retained if inclusion resulted in a lower AIC. Pseudo-R<sup>2</sup> values were produced through the "r.squaredGLMM" function from the package "MuMIn" (Barton, 2015), which produces marginal and conditional coefficients of the proportion of variance explained by fixed factors and both fixed and random factors, respectively.

Finally, to explore the influence of heartwood and sapwood composition on wood density, we used one-way ANOVA and Tukey's test to determine whether or not HW:SW varied among ranges. These data were not significantly different and therefore not considered further (but see supplementary Table S4 for results). All analyses were conducted in R version 3.5.1 (R Core Team, 2018).

# 3. Results

#### 3.1. Northern Basin scopulorum stand descriptions and climate

The *scopulorum* stands we sampled occurred at varying elevations and aspects and differed markedly in co-occurring forest species composition (Table S1) among ranges. In the southern portion of our study area, the Spring, Sheep, and Clover generally had more continuous *scopulorum* distributions in which the species dominated on cooler and wetter aspects with co-occurrence of other tree species at ecotones. At the northern extent of sampling, the Snake, Grant, and Wah Wah *scopulorum* stands were often smaller stands occurring in drainages or valley bottoms. These disjunct stands were generally surrounded by woodland or shrub communities, with the exception of several highelevation stands (>2600 m) in the Snake that co-occurred with *Pseudotsuga menziesii* var. *glauca (Mirb.)* (Douglas-fir) and *Pinus flexilis* James (limber pine). *Scopulorum* average basal area ranged from 12.52 to 22.96 m<sup>2</sup>/ha among ranges (Table S1; Fig. S2). Across the 55 plots sampled, few trees exhibited signs of insects, disease, or stress.

Climate also varied widely among mountain ranges in the Northern Basin. Over the full record of climate observations (1901–2018), climate varied among ranges and across years (Fig. 2). Annual cumulative CMD was generally higher in ranges in the southern portion while lower in most northern ranges, with interannual variation within each range (Fig. 2a). Interannual variation in monsoonality was also evident within ranges, and monsoonal precipitation inputs were highly variable among ranges (Fig. 2b). There was a general trend over the entire climate record of an increase in annual cumulative CMD but little change in monsoonality (Fig. 2a and 2b).

All climate variables differed significantly among ranges (ANOVA, Table S2, p < 0.001). While seasonality of CMD varied among ranges across the Northern Basin, there was a trend of increasingly wet winters with latitude in most ranges in the northern portion of our study area, while southern ranges lacked clear geographical patterns in CMD (Table S5). Monsoonality was significantly different among many ranges (Table S3) and trended towards higher values (i.e., greater monsoon influence) in the southern extent of our study area, although there was a monsoonal influence on ranges in the northern portion as well (Table S5). The proportion of monsoonal precipitation changed in more recent years, with monsoonality increasing in all ranges from 2014 to 2018 (Table S5).

# 3.2. Variation in scopulorum cone, wood, and needle traits

### 3.2.1. Cone volume

Mean cone volume was highly variable, ranging from  $117 \pm 3.0 \text{ cm}^3$  in the Snake to  $69 \pm 1.8 \text{ cm}^3$  in the Spring (Fig. 3a; Table S6). Cone



Fig. 2. Annual climate data values extracted at sampled plots for the entire climate record (1901–2018; Wang et al. 2006, 2012) for a) annual cumulative climatic water deficit (CWD; mm) and b) monsoonality, or percentage of annual precipitation falling in July-September. The solid color lines show the mean for each range, and shaded areas represent a 95% confidence interval. The trends over time are represented by the black lines.



**Fig. 3.** Probability density functions of *Pinus ponderosa* var. *scopulorum* **a**) cone volume (cm<sup>3</sup>), **b**) wood density (g/cm<sup>3</sup>), **c**) latewood to earlywood ratio (LER), **d**) specific leaf area (SLA;  $mm^2/mg$ ), and **e**) needle lifespan (years) by range. Dashed lines represent range-wide trait means.

volume was influenced by summer and winter CMD (p < 0.05; Table 1). Cone volume increased with greater summer CMD (Fig. 4a) and decreased with greater winter CMD (Fig. 4b). Topographic and treelevel predictors were not retained in the best model of cone volume, and monsoonality was retained but was not significant. Marginal R<sup>2</sup> was 14 percent, and conditional R<sup>2</sup> was 38 percent (Table 1).

### 3.2.2. Wood traits

The Sheep had the highest wood density with a mean of  $0.57 \pm 0.01$  g/cm<sup>3</sup>, while trees with the lowest density wood grew in the Grant (0.51  $\pm 0.01$  g/cm<sup>3</sup>, Fig. 3b; Table S6). Wood density was best explained by cold season CMD, elevation, and diameter at coring height (p < 0.05, Table 1). Densities increased with greater cold season CMD (i.e. on drier sites; Fig. 4c) and at higher elevations (Fig. 4d). Additionally, wood density decreased with increasing tree diameter (Fig. 4e). Marginal R<sup>2</sup> was nine percent, and conditional R<sup>2</sup> was 12 percent (Table 1).

Trees in the Spring had the highest amount of latewood proportionate to earlywood, with mean LER of 0.62  $\pm$ 0.01, compared to the lowest LER in the Clover at a mean of 0.48  $\pm$ 0.01 (Fig. 3c; Table S8). Climatic effects on wood formation were also evident in *scopulorum* LER, which increased with a heavy monsoon influence (Fig. 4f). Consistent with wood density, LER also decreased with increasing tree diameter (Fig. 4g). Marginal R<sup>2</sup> was five percent, and conditional R<sup>2</sup> was 18 percent (Table 1).

# 3.2.3. Needle traits

Specific leaf area was higher in the Clover where mean SLA values were 2.80  $\pm$ 0.07 mm<sup>2</sup>/mg, while the lowest values were in the Spring at 2.45  $\pm$ 0.05 mm<sup>2</sup>/mg (Fig. 3d; Table S6). Summer CMD was the only tested predictor with a significant effect on SLA (p < 0.05, Table 1), with SLA increasing with summer CMD (Fig. 4h). However, the best AIC model included the interaction between summer CMD and aspect. This interaction was not significant (p = 0.057) but suggests a trend of summer CMD having a positive relationship with SLA on more northern aspects but a neutral-to-negative relationship on more southern aspects (p = 0.057, Table 1, Fig. S3). Basal area of all species, as well as crown volume, crown length and tree DBH were not retained in the best model of SLA. Marginal R<sup>2</sup> was 12 percent, and conditional R<sup>2</sup> was 38 percent (Table 1).

Needles with the longest lifespan were found in the Grant (3.5 year mean; 3-year median), while the shortest lifespan was in the Clover (1.8 years; 2-year median; Fig. 3e; Table S6). Needle lifespan was driven by monsoonality (p < 0.05; Table 1), with lifespan decreasing with greater monsoonality (Fig. 4i). This model predicted needle lifespan to be one year longer in sites with the most winter-dominated precipitation regimes than in sites with greater monsoonal influence. No topographic, tree, or stand-level predictors were retained in the best model. Marginal  $R^2$  was 15 percent, and conditional  $R^2$  was 49 percent (Table 1).

### 4. Discussion

Forest persistence under the extreme and prolonged drought conditions predicted with climate change will depend on tree species' capacity to cope with extreme moisture stress. Conifers possessing drought-resistant traits will likely be at an advantage under increasing climatic water limitations, and this advantage will be particularly important for conifers already growing in arid or semi-arid environments. In Northern Basin *scopulorum*, regional gradients of seasonal climatic moisture deficit and monsoonality were particularly influential in shaping trait variation, suggesting that the morphology of *scopulorum* in stands at the edge of its range varies as a function of the seasonality of water availability and limitations. However, contrary to our expectations, local topographic variation had no influence on trait variation for the stands tested here. The lack of significance of aspect on *scopulorum* may be best explained by its local distribution on favorable landscape positions in the semi-arid Northern Basin (e.g. valley bottoms; Charlet,

#### Table 1

Estimated regression coefficients (B) and P-values from linear mixed effect models (LMM) predicting P. ponderosa var. scopulorum traits of cone volume, wood density, latewood to earlywood ratio (LER), specific leaf area (SLA), and needle lifespan. Scaled climate predictor variables include summer (July-Aug) climatic moisture deficit (CMD) for SLA, early summer (Apr-July) CMD for needle lifespan, and cold season (Oct-Feb) CMD for wood density. Cone volume was modeled with summer (July-Aug) CMD and winter (Nov-Jan) CMD. Monsoonality (MSN) was included in all trait models, while elevation was only included in the wood density model. Scaled folded aspect was included as the topographic predictor, along with the interaction term between aspect and CMD. Tree-level variables to predict traits include diameter for wood density, LER, SLA, and needle lifespan. Plot level P. ponderosa var. scopulorum basal area (BA) and mean diameter were tree predictors for cone volume, while crown volume and length were included for SLA. Needle models contained total plot basal area to reflect competition and shading. Random effects were plot nested within mountain range. Marginal (fixed effects) and conditional (fixed and random effects)  $R^2$  values are given for each model. Bolded p-values are significant (p < 0.05), while p-values of non-significant predictors retained in the models are not bolded. Dashes denote non-significant predictors tested and removed from the model based on AIC values.

Response	Predictors	β	Р	Marginal R <sup>2</sup>	Conditional R <sup>2</sup>
Cone	Intercept	87.68	< 0.0001	0.14	0.38
Volume	Summer CMD	11.99	0.0002		
	Winter CMD	-7.55	0.0397		
	Aspect	_	_		
	Aspect X	_	_		
	Summer CMD				
	Aspect X	_	_		
	Winter CMD				
	Monsoonality	_4 94	0 1865		
	Mean Diameter	-	0.1005		
	Basal Area				
Wood	Intercept	0.54	<0.0001	0.00	0.12
Density	Cold Season	0.04	<0.0001	0.09	0.12
Density	CMD	0.02	<0.0001		
	Aspect	0.01	0 4787		
	Aspect V	-0.01	0.4707		
	Cold Season	-	_		
	CMD				
	CIVID Moncoonality				
	Flouration	-			
	Diameter	0.013	0.0090		
IED	Intercept	0.56	<0.001	0.05	0.18
LEIV	Aug CMD	0.50	<0.0001	0.05	0.10
	Acrost	-	-		
	Aspect V	-	-		
	Aspect A	-	-		
	Monsoonality	0.02	0.0224		
	Diameter	_0.02	0.0356		
SI A	Intercent	2.60	<0.0000	0.12	0.38
5L/1	Summer CMD	0.08	0.0122	0.12	0.50
	Aspect	0.00	0.3270		
	Aspect V	-0.03	0.3279		
	Summer CMD	-0.00	0.0374		
	Monsoonality				
	Crown Volume				
	Crown Length	_	_		
	Total Basal	-	_		
	Area	-	_		
	Diameter				
Needle	Intercept	2 71	-0.0001	0.15	0.40
Lifesnan	Farly Summer	2.71	<0.0001	0.15	0.49
Lifespair	CMD				
	Aspect	_	_		
	Aspect X	_	_		
	Early Summer				
	CMD				
	Monsoonality	-0.28	0.0001		
	Total Basal	-	-		
	Area				
	Diameter	-	-		



**Fig. 4.** Partial residual plots from the linear mixed effects model predicting *P. ponderosa* var. *scopulorum* traits of cone volume (cm<sup>3</sup>) as a function of **a**) the influence of summer climatic moisture deficit (July and August CMD; mm) and **b**) winter (November-January) CMD (mm); wood density (g/cm<sup>3</sup>) as a function of **c**) cold season (October-February) CMD (mm), **d**) elevation (m), and **e**) diameter at coring location (cm); latewood to earlywood (LER) as a function of **f**) monsoonality (July, August, September precipitation divided by total annual precipitation) and **g**) diameter at coring location (cm); specific leaf area (SLA; mm<sup>2</sup>/mg) as a function of **h**) summer (July and August) CMD (mm); and **i**) needle lifespan (years) as a function of monsoonality. All models included a nested random intercept of plot within mountain range (p < 0.05). The shaded areas represent a 95% confidence interval.

1996), where topographic mediation may not influence individual persistence and morphological variation. Our results highlight the strong influence of seasonal moisture stress and timing of precipitation on morphological variation in drought-resistant conifers growing in semi-arid environments. The wide range of trait variation that we observed also suggests that trait variability may help drought-resistant conifers withstand extreme fluctuations in seasonal water availability, which is predicted to become more variable and less predictable for arid and semi-arid ecosystems of western North America as the climate continues to change.

#### 4.1. Climatic influence

Trait diversity in many drought-adapted conifers is strongly linked to water availability (Sánchez-Gómez et al., 2011; Berner and Law, 2015), and temporal and spatial variation in local climate may further influence morphological response (Rigling et al., 2002; López et al., 2010). The amount and timing of moisture are particularly important for conifer growth (Hankin et al., 2019; Zeng et al., 2019), with both leaf area (Grier and Running, 1977) and wood formation (de Luis et al., 2007) associated with growing season water availability. In semi-arid forests of western North America specifically, winter precipitation and summer moisture availability are documented to constrain conifer growth (Redmond et al., 2017), including other *scopulorum* stands growing near our study area (Truettner et al., 2018; Ziaco et al., 2018). Great Basin

*P. ponderosa* can also plastically respond to warm, dry climate conditions by altering physiological functioning to increase hydraulic conductivity (Maherali and Delucia, 2000). Our assessments of Northern Basin *sco-pulorum* trait variation are consistent with these findings of seasonal water availability shaping conifer morphology in water-limited environments.

Moisture stress directly influences reproductive success as well, and conifer reproductive output can increase in response to hotter, drier conditions during cone initiation (Roland et al., 2014; Crain and Cregg, 2018). Despite reproductive traits generally being considered highly conserved (Vasudeva et al., 2004), environmental conditions drive substantial variability in cone morphology (Gil et al., 2002; Dangasuk and Panetsos, 2004). Growing season water availability is frequently identified as a driver of cone production, however the direction of the relationship between cone or seed traits and moisture deficits can vary depending on the duration of dry conditions (He et al., 2018). In P. ponderosa, seed and cone production can be highly variable among individual trees and growing environments (Krannitz and Duralia, 2004); warmer, drier conditions during cone initiation are positively correlated with cone production (Owens and Blake, 1985), whereas seed production is tied to summer precipitation during the first year of cone development (Keyes and Manso, 2015). Although we were unable to quantify Northern Basin scopulorum seed production due to a poor crop year, increasing cone size with increasing aridity may indicate greater investment in reproduction under stress (Khurana and Singh, 2004),

while decreasing cone size with moisture stress may suggest allocating resources toward growth and pest defense (Lauder et al., 2019), as seed production is typically correlated with cone size (Dickmann and Kozlowski, 1971; Caron and Powell, 1989). Our findings of increasing cone size under increasing summer moisture limitation are in line with other *P. ponderosa* findings and suggest that Northern Basin *scopulorum* reproductive output is influenced by moisture stress during the period of cone initiation and early development. While winter precipitation is not a well-documented driver of cone production, it is a significant driver of local *scopulorum* growth (Truettner, 2020), and our results are consistent with this response to winter moisture stress.

Drought-resistant conifers may also vary in wood formation and morphology as a response to water limitations (Pacheco et al., 2016; Larter et al., 2017). Wood density, for example, increases due to increasing tracheid cell wall thickness as cell growth is reduced under moisture-limited conditions (Hacke et al., 2001). Denser wood is driven by an increase in the LER via a shift from larger earlywood tracheids to smaller, denser latewood tracheids (Björklund et al., 2017). Individual trees or species with larger latewood widths could reflect a strategy for greater drought resistance, as latewood has a higher resistance to embolism under low water potential than earlywood (Domec and Gartner, 2002). This wood formation response is evident in other scopulorum stands, where tracheid number and size are directly linked to soil water content (Ziaco et al., 2018; Ziaco, 2020). The timing of water availability is also a strong driver of wood development. Winter precipitation drives soil water recharge in mountainous regions of western North America (Maurer and Bowling, 2014), directly influencing growing season water availability and subsequent tree growth (Allen et al., 2019). This cool season precipitation is not only a dominant form of moisture for P. ponderosa growth in semi-arid environments (Kerhoulas et al., 2017; Ziaco et al., 2018) but also positively associated with earlywood width (Carrillo et al., 2016). In the Northern Basin scopulorum stands sampled here, cool season moisture limitations led to increasing wood density yet no measurable impact on LER. This trait was instead influenced by monsoonality, as it is for P. ponderosa in other portions of the species' range (Griffin et al., 2013; Kerhoulas et al., 2017). Monsoonality likely influences the timing and duration of latewood formation, as the proportion of latewood to earlywood generally increases with water limitations (Martinez-Meier et al., 2008; Arzac et al., 2018). Work on local scopulorum has found variation in seasonal water dependence based on tree size (Truettner, 2020), which could explain our findings of lower wood density and decreased LER with greater diameters, as larger trees relying on winter moisture likely develop more earlywood due to extended available soil moisture. Moreover, our finding of increased wood density with elevation is likely the influence of increased LER from lower temperatures at higher elevation impeding earlywood formation (Dolezal et al., 2019) or driven by reduced tracheid diameters that are less susceptible to cavitation from freezing and thawing at higher elevations (Willson and Jackson, 2006). The wood morphological response of the Northern Basin scopulorum sampled here provides additional evidence for a seasonal climate effect on wood formation in P. ponderosa (Ziaco et al., 2018; Truettner, 2020) and other drought-resistant conifers (Camarero et al., 2010).

As individuals balance the need for carbon acquisition with water loss through transpiration, needle morphology (Adams et al., 2015) and lifespan (Ozolinčius et al., 2009) are also sensitive to water availability, yet responses can be counter to expectations (Niinemets, 2001; Poorter et al., 2009; John et al., 2017). Specific leaf area is a commonly sampled morphological trait for assessing needle photosynthetic capacity and drought-tolerance (e.g. Valladares and Sánchez-Gómez, 2006; Sánchez-Gómez et al., 2011; Delzon, 2015); SLA and mass are documented to vary widely and be most limited by light and temperature conditions (Poorter et al., 2009). Given the wide range of factors influencing leaf morphology, we expected seasonal water availability – the strongest limiting factor in semi-arid environments (Running et al., 2004) – to be most influential in shaping needle traits. The timing and availability of

water over the growing season (summer to fall) does appear to influence needle morphology and retention in Northern Basin scopulorum, for which we observed increasing SLA with increasing summer moisture stress and longer needle retention with winter-dominated precipitation. Our results are counter to generally-held expectations of decreasing leaf size under decreasing water available for carbon assimilation (e.g. Grier and Running, 1977; Waring et al., 1978; Luo et al., 2004). Some research supports greater leaf surface area during growing season water constraints (Meier and Leuschner, 2008), and P. ponderosa SLA is documented to increase with increasing water stress (Weiskittel et al., 2008). Declining lifespans under increasing monsoonality suggests that Northern Basin scopulorum may be able to take advantage of this late growing season precipitation and does not need to retain costly needles. The significance of seasonal precipitation is consistent with P. ponderosa growth response to the timing of precipitation in other portions of the Northern Basin (Ziaco et al., 2018) and provides additional evidence that timing of moisture influences morphological variation in semi-arid conifers (e.g. Berner and Law, 2015).

Our findings highlight the importance of seasonal water availability in driving scopulorum morphological variation across regional climate gradients, but we acknowledge that temporal variation in climate conditions is also playing a strong role in trait development (George et al., 2019). Across the Northern Basin region sampled, the long-term climate record shows notable interannual variation for both CMD and monsoonality (Fig. 3.), suggesting that scopulorum tolerates and grows under a wide range of conditions. High interannual climate variability may explain the moderate influence of the Northern Basin's monsoonal gradient on morphological variation across the region, and regional P. ponderosa stands are likely adapted to tolerate variation in monsoonality with limited consequences on trait expression. Unfortunately, our use of mean monsoonality over the selected climate periods in our analyses did not capture this variability, potentially impacting our ability to explore the full effect of climate on traits. Our results suggest that an examination of the effect of monsoonality occurring at a finer temporal resolution is warranted. Response to climate seasonality, and possibly variability, through variation in stress-resistant traits underlines the ability of *scopulorum* to morphologically respond to water limitations in this semi-arid environment.

# 4.1.1. Potential response to climate change

Although projections of the North American Monsoon vary, models consistently predict greater variability in amount and timing of late summer precipitation across the southwestern United States (Hoell et al., 2016; Pascale et al., 2017), and aridity is expected to increase in the Northern Basin (Seager et al., 2013). The predicted increases in drought frequency and severity for this region would lead to reduced water availability and the potential for constraints on tree growth and survival. Conifers occurring in semi-arid environments do, however, possess drought-resistant traits and are thus likely well-poised to accommodate shifts in the timing and availability of moisture. The recent 2012-2016 drought (Koch and Coulston, 2018) provides evidence to indicate that scopulorum has the capacity to take advantage of late-season monsoonal precipitation despite limited growth during the summer growing period (Strachan, 2016). Drought resistance will be critical to scopulorum persistence, particularly as moisture becomes less consistent and less available. Our evidence of morphological variation as a function of seasonal water availability, combined with high trait variability within stands, indicates that Northern Basin scopulorum have regional persistence potential.

# 5. Conclusions

The diversity of drought-resistant morphological traits within Northern Basin *scopulorum* as well as the species' ability to respond to water limitations increase its persistence potential under future, extreme climatic conditions. However, as seasonal moisture availability is a strong driver of scopulorum trait variation, novel conditions are likely to challenge even drought-resistant, highly-variable Northern Basin scopulorum. The response of scopulorum trait diversity is also a product of interacting genetic and environmental influences, and this study only directly assessed the environmental component. The lack of a topographic influence on the stands sampled here highlights the role of genetics in driving trait variation, as scopulorum is likely more strongly adapted to regional climate than conditions associated with topographic variation (but see De Kort et al., 2020). Manipulative experiments paired with genetic data will be needed to test this expectation and identify thresholds of scopulorum's capacity to respond to moisture limitations at varying scales. Testing trait plasticity in response to interannual environmental conditions and the role of genetic variation in the expression of these traits will provide further insight into the future of scopulorum. Despite this remaining knowledge gap, our findings contribute to a better understanding of the role that seasonal water availability plays in semi-arid forests, which will be particularly significant as these ecosystems are threatened with increasingly stressful and variable conditions.

#### CRediT authorship contribution statement

Tessa R. Putz: Methodology, Investigation, Formal analysis, Writing - original draft. Alexandra K. Urza: Conceptualization, Methodology, Writing - review & editing. Lacey E. Hankin: Formal analysis, Writing - original draft, Writing - review & editing. Sarah M. Bisbing: Conceptualization, Methodology, Writing - review & editing, Supervision, Project administration, Funding acquisition.

#### **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.

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# Appendix A. Supplementary material

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