RESEARCH ARTICLE

Identifying the Climate Conditions Associated With Extreme Growth States in Trees Across the Western United States

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ABSTRACT

Climate extremes—e.g., drought, atmospheric rivers, heat waves—are increasing in severity and frequency across the western United States of America (USA). Tree-ring widths reflect the concurrent and legacy effects of such climate extremes, yet our ability to predict extreme tree growth is often poor. Could tree-ring data themselves identify the most important climate variables driving extreme low- and high-growth states? How does the importance of these climate drivers differ across species and time? To address these questions, we explored the spatial synchrony of extreme low- and high-growth years, the symmetry of climate effects on the probability of low- and high-growth years, and how climate drivers of extreme growth vary across tree species. We compiled ring widths for seven species (four gymnosperms and three angiosperms) from 604 sites in the western USA and classified each annual ring as representing extreme low, extreme high, or nominal growth. We used classification random forest (RF) models to evaluate the importance of 30 seasonal climate variables for predicting extreme growth, including precipitation, temperature, and vapor pressure deficit (VPD) during and up to four years prior to ring formation. For four species (three gymnosperms, one angiosperm) for which climate was predictive of growth, the RF models correctly classified 89%–98% and 80%–95% of low- and high-growth years, respectively. For these species, asymmetric climate responses dominated. Current-year winter hydroclimate (precipitation and VPD) was most important for predicting low growth, but prediction of high growth required multiple years of favorable moisture conditions, and the occurrence of low-growth years was more synchronous across space than high-growth years. Summer climate and temperature (regardless of season) were only weakly predictive of growth extremes. Our results motivate ecologically relevant definitions of drought such that current winter moisture stress exerts a dominant role in governing growth reductions in multiple tree species broadly distributed across the western USA.

1 | Introduction

Increasing frequency and severity of extreme climate events are challenging forest productivity and resilience across the western United States of America (USA). In particular, droughts have been increasing in frequency, severity, and duration over the past two decades (Williams et al. 2022; Williams et al. 2020). Recent precipitation surpluses have

been similarly extreme in their amount and persistence. For example, the 2022–2023 winter in California was characterized by a rapid sequence of nine landfalling atmospheric rivers (DeFlorio et al. 2024) that impacted the western USA (Steinschneider et al. 2018), followed shortly by Hurricane Hilary. Both more frequent droughts and precipitation extremes are attributable to climate warming (Tseng et al. 2022; Williams et al. 2022), suggesting these impacts are likely to increase under a future climate. Critically, these extreme dry and wet conditions have led to similarly extreme impacts on western forests, such as amplified wildfires (Abatzoglou et al. 2019), widespread drought-induced tree mortality (Allen et al. 2010, 2015; Hammond et al. 2022), flooding-related tree mortality (Wang et al. 2019), and bark beetle outbreaks (Fettig et al. 2022), among others (Davis 2020). Such impacts have major consequences for the functioning of forest ecosystems in the western USA (Ghimire et al. 2015).

Tree-ring widths are often used to reconstruct the extent and severity of extreme climate events, but they are also useful to evaluate growth responses to climate. Large tree-ring datasets have been collected over decades to study past climate conditions (Cook et al. 2004; Meko et al. 2007) and a diversity of other phenomena (e.g., Graumlich 1991; Speer 2011; Swetnam and Betancourt 1990; Szejner et al. 2016). More recently, syntheses have leveraged community-assembled tree-ring datasets (Zhao et al. 2019) to produce macroscale inference about tree growth responses to climate (Gantois 2022; Girardin et al. 2024). Such studies often model tree growth as a function of moisture indices (e.g., precipitation, soil moisture, snow), temperature, and, sometimes, their interactions (e.g., vapor pressure deficit, computed drought indices). While dry, warm conditions tend to reduce growth, and elevated moisture inputs tend to enhance growth, results are not particularly coherent across studies (Chen et al. 2010; Klesse et al. 2020). This could be due to the implementation of a variety of different statistical approaches applied to tree growth data (Klesse et al. 2022; Tingley et al. 2012), many of which leverage some form of mixed-effects models (Peltier and Ogle 2023). Tree growth (e.g., ring width) responses to climate also show substantial spatial variation, possibly linked to genetics (Chen et al. 2004; Trotter et al. 2002), edaphic factors (Weigel et al. 2023), temporal variation attributed to climate warming (Peltier and Ogle 2020), or other factors (Wilmking et al. 2020).

Not surprisingly, one conclusion of such syntheses is that tree growth responses to climate are complex, varying across species, sites, and time (Pederson et al. 2020; Peltier, Anderegg, et al. 2022). For example, tree growth varies across spatial gradients associated with climate (Szejner et al. 2016; Yocom et al. 2022), but other factors such as soils, elevation, management, and changing drought frequency may also be important (Bose et al. 2020; Lebourgeois et al. 2005; Marqués et al. 2022; Scharnweber et al. 2011). Growth responses to climate may reflect changes with ontogeny or tree size (Anderson-Teixeira et al. 2022; Au et al. 2022). Differing tree traits across species, particularly those linked to hydraulic strategies, carbon reserve storage, rooting depth, and phenology, may also drive variation in growth responses (Belmecheri et al. 2018; Peltier, Guo, et al. 2022). In contrast, variation within species may reflect evolutionary histories of migration and gene flow among populations (McCullough et al. 2017; Sork et al. 2010).

Tree growth also reflects lagged impacts of past climate across a variety of timescales (Peltier et al. 2018). For example, drought may leave lasting impacts (i.e., legacies) on tree growth (Anderegg et al. 2015; Kannenberg et al. 2020), in turn, leaving legacies on ecosystem functions (Müller and Bahn 2022) such as carbon cycling (Liu et al. 2019; Schwalm et al. 2017). At the same time, moisture pulses from extreme wet periods may produce lasting positive enhancements to growth (Jiang et al. 2019). There is also evidence that both growth–climate responses and the magnitude of such climate legacies may not be consistent across space (sites) or time (Wilmking et al. 2020) and are changing under increased drought frequency (Anderegg et al. 2020; Peltier and Ogle 2019b). However, there is evidence that tree growth may become more synchronous with increasing aridity (Black et al. 2018). Overall, tree growth responses are likely non-linear (Dannenberg et al. 2019), reflecting complex saturating (Gantois 2022) or interacting responses to climate (Klesse et al. 2022; Marqués et al. 2022; Peltier et al. 2018; Peltier, Guo, et al. 2022) as conditions become more extreme. Such asymmetry has been characterized for responses to hydroclimate (Maxwell et al. 2024) but has rarely been assessed for the effects of temperature or other climate drivers.

Perhaps less appreciated is that statistical models applied to tree-ring data often perform worst during time periods we are most interested in: periods defined by extreme conditions. Models often explain nominal growth data relatively well but tend to overpredict low growth and/or underpredict high growth (e.g., Gelman and Pardoe 2007; Klesse et al. 2020; Knowe et al. 1997; Peltier et al. 2018). One factor contributing to this bias is the use of linear models that assume climate effects are symmetric across both wet and dry years. This can be appropriate, but low/high growth periods are often of most interest because they likely occur in response to extreme climate (e.g., drought/moisture pulses). Synthesis studies often explore how climate drives tree growth, but there is evidence that our predictive models do best at very large scales. For example, drought legacies emerge at large scales, but studies of the legacies of drought in individual sites or trees find extensive variation and weak signals for many sites (Gazol et al. 2020; Ovenden et al. 2021). Thus, a motivating question is: can we use the tree-ring data themselves to inform which climate variables are of the greatest importance for understanding extreme low- and high-growth conditions? Flexible, machine-learning approaches may represent an underutilized tool to investigate how extreme tree growth may be related to extreme climate (Bodesheim et al. 2022; Bond-Lamberty et al. 2014; Tei et al. 2021), as well as capture more complex, non-linear responses that can be computationally or conceptually difficult to evaluate with mixed-effects models (Breiman 2001; Hastie et al. 2009).

The primary objective of this study is to evaluate which climate variables are most predictive of extreme low- and high-growth years, with the accompanying goal of informing regionally and physiologically relevant definitions of climate extremes. Extreme climate events are at the heart of major collaborative efforts to improve the predictions of the carbon cycle in the western USA (e.g., Reed et al. 2025). We ask four questions associated with understanding extreme growth in trees: (Q1) Synchrony of extreme growth events: How does the spatiotemporal pattern of extreme

growth differ between low- and high-growth years and across species? (Q2) Asymmetric versus symmetric climate responses: Are low- and high-growth states symmetric such that they are simply predicted by opposite extremes (e.g., low versus high) of the same climate variables? (Q3) Species-specific responses to climate: How do the important predictors of extreme low- and high-growth differ among tree species that are widespread across the western USA, and what are the potential reasons for differences among species? (Q4) Extreme climate conditions from a tree's perspective: How do climate conditions and climate correlations differ during low- and high-growth years relative to nominal-growth years? To address these questions, we compiled tree-ring widths for seven species (four gymnosperms and three angiosperms) occurring across the western USA. We classified annual ring widths into low-, high-, or nominal-growth categories. We leveraged the flexibility and predictive ability of classification random forest (RF) (Breiman 2001) to model the growth classes as a function of 30 seasonal climate variables, with a focus on precipitation, temperature, and vapor pressure deficit

(VPD) during and up to four years prior to ring formation. These RF analyses allowed us to identify the most important climate variables for predicting low- and high-growth states across multiple species broadly distributed across the western USA. Our results lend new insight into (1) the differential impacts of current and lagged climate on extreme growth states and (2) ecologically relevant definitions of climate extremes.

2 | Methods

2.1 | Tree-Ring Data

We focused on seven tree species occurring in the western USA for which sufficient tree-ring data are available (Figure 1), including four gymnosperms (*Picea engelmannii*, *Pinus edulis*, *Pinus ponderosa*, and *Pseudotsuga menziesii*) and three angiosperms (*Abies lasiocarpa*, *Populus tremuloides*, and *Quercus douglasii*). We downloaded raw tree-ring
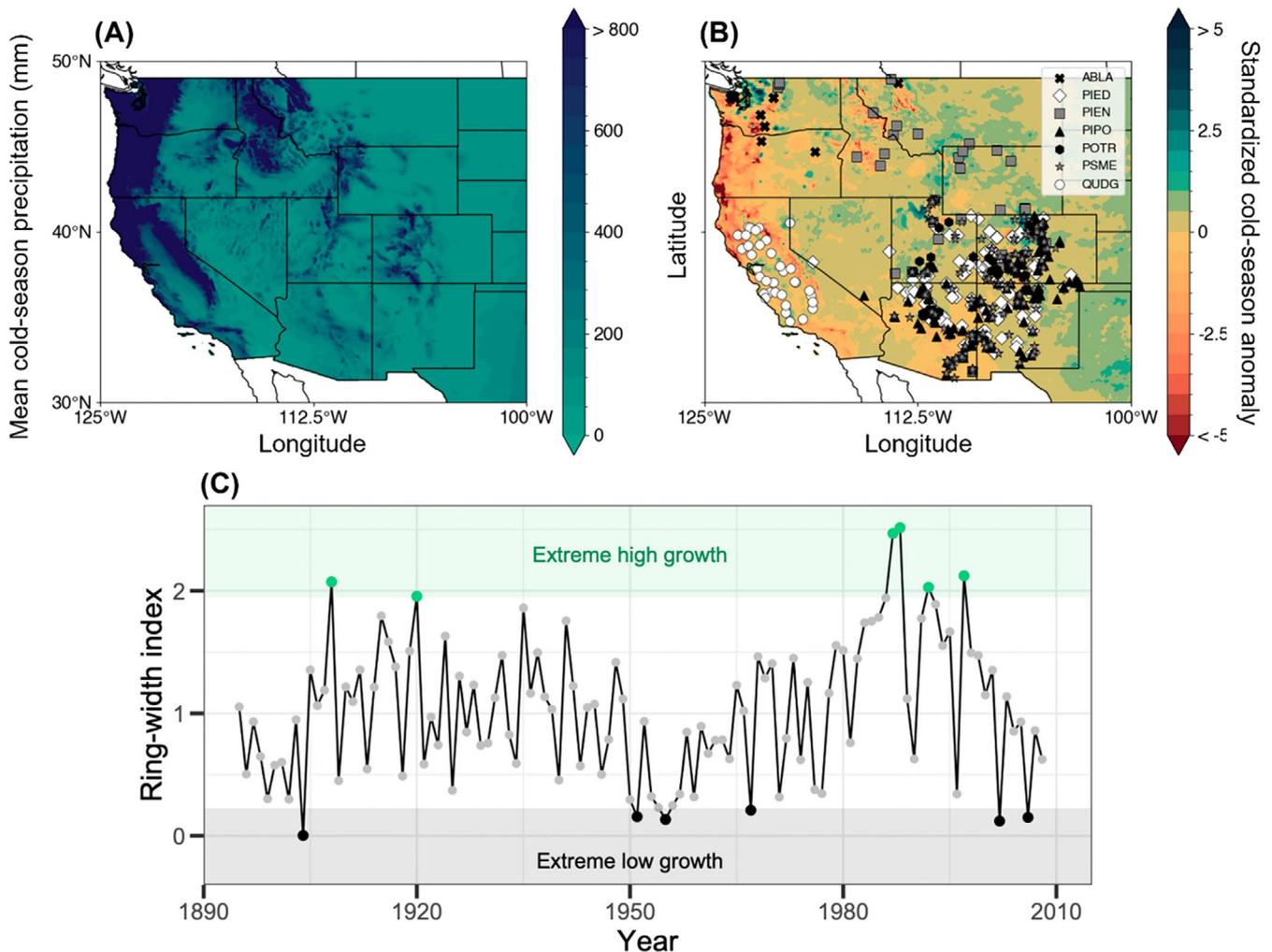
FIGURE 1 | (A) Mean historic cold-season ("winter", October–March) precipitation for the period 1960–1999 in the western USA, and (B) mean winter precipitation anomaly for the period 2000–2023 relative to the historic mean, with locations of tree-ring sites overlaid for each study species. Species codes are defined in Table 1. (C) An example ring-width index (RWI) chronology for a PSME (*Pseudotsuga menziesii*) site in New Mexico, USA. Years defined by extreme low growth (black symbols) are associated with RWI values that fall below the 5th percentile, while years defined by extreme high growth (green symbols) are associated with RWI values that fall above the 95th percentile. All other intervening years are defined as nominal-growth years (gray symbols). The low- and high-growth definitions are based on RWI percentiles determined across all years and all sites for each species (here, PSME). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

widths from the International Tree Ring Databank (ITRDB) for these species. While the ITRDB is biased towards "sensitive" trees, it remains the most comprehensive collection of publicly available tree-ring data in the USA, and evidence suggests the ITRDB correctly captures the direction of climate responses in more representative trees (Klesse et al. 2018). We obtained additional data for *P. tremuloides* from two published datasets (Ireland et al. 2014). After filtering for quality, availability, and formatting, data were available for 609 sites, with the number of sites varying across species from 45 (*P. tremuloides*) to 180 (*P. menziesii*; Table 1 and Figure 1C). For *P. edulis*, *P. ponderosa*, *P. menziesii*, and *P. tremuloides*, we focused on sites in the southwestern USA ("Southwest," including Arizona, New Mexico, Colorado, and Utah); *A. lasiocarpa* and *Q. douglasii* served as interesting comparisons as their study sites were disjunct from the Southwest species, occurring in the Pacific Northwest and the Sierra Nevada in California, respectively. Sites used for *P. engelmannii* spanned between the *A. lasiocarpa* sites and the northern edge of the Southwest study region.

We detrended raw ring widths for age-related effects by fitting modified negative exponential curves to core-level, ring-width series using the R package dplR (Bunn 2008), thus producing ring-width indices with a mean of one for each core. We computed site-level chronologies by averaging the annual core-level ring-width indices across cores for each year within a site (all unique ITRDB sites only supported one species). Thus, each site-level ring-width index (hereafter, RWI) chronology provides a single timeseries representing average, site-level growth responses each year. RWI values greater than one represent above-average growth, and values between zero and one represent below-average growth, regardless of site or species. To align

the RWI data with the climate data (below), we used RWI data from 1895 onwards.

We used a quantile ranking system to categorize each annual RWI as indicative of "low" (RWI < 5th percentile), "high" (RWI > 95th percentile), or "nominal" (all other RWIs) growth relative to all annual RWI values (ca. 1895-present) for each species (see Figure 1C). The 5th and 95th percentiles were determined across all sites for each species, such that the same low and high RWI cut-offs were applied across all sites. We also explored defining these percentiles within each site (Text S1), which had little impact on our initial results. The across-site rankings identify growth extremes regardless of site and allow for different sites to have differing frequencies of low- or high-growth years.

2.2 | Climate Data

We obtained monthly values of precipitation (mm), mean air temperature (°C), and maximum vapor pressure deficit (VPD, mbar) from the PRISM data product (PRISM Climate Group 2024). Climate timeseries (4 km) were extracted for each site for the period 1895–2022 and trimmed to the length of the site-level RWI records. We calculated seasonal climate variables according to a cold season (October–March, "winter") or warm season (April–September, "summer") for the year of ring formation and for four years prior to ring formation (a total of five periods, current and lagged). We characterized general site-level climate by calculating mean annual precipitation (MAP) and mean annual temperature (MAT). See Table S1 for a summary of climate variables.

2.3 | Random Forest Models

To determine the importance of different seasonal and lagged climate variables for predicting extreme growth, we used classification random forests (RF) (Breiman 2001). RF methods are well-known for their "automated feature engineering" whereby relationships of the response to potential covariates and their interactions are captured naturally by the procedure (Breiman 2001; Hastie et al. 2009). RF methods are particularly well-suited to modeling complex relationships between a response and many covariates, including all possible interactions among those covariates (Hastie et al. 2009). In addition, variable importance/selection procedures are well-developed for RF methods (Breiman 2001), providing a convenient way to assess the importance of covariates based on models that are more likely to best reflect complex relationships. RF methods have been used in a few past studies of tree growth to evaluate the relative importance of different climatic and disturbance variables (Bond-Lamberty et al. 2014; Tei et al. 2021). In this study, we applied classification RF models to (1) low growth versus all other growth classes (nominal and high growth combined), denoted as "low-growth models," or (2) high growth versus all other growth classes (nominal and low growth combined), denoted as "high-growth models." For each of these low- and high-growth classification models, we adjusted for the imbalance of cases among classes to improve the within-class errors (Chen et al. 2004) because the extreme

TABLE 1 | Study species, species code, and sample sizes (number [*N*] of sites, trees, and annual tree-ring records); most data were obtained from the International Tree-Ring Data Bank (ITRDB).

Species	Code	*N* sites	*N* trees	*N* rings
Abies lasiocarpa (subalpine fir)	ABLA	33	898	113,398
Picea engelmannii (Engelmann spruce)	PIEN	46	1392	345,889
Pinus edulis (pinyon pine)	PIED	130	489	1,383,563
Pinus ponderosa (ponderosa pine)	PIPO	170	6114	1,297,915
Populus tremuloides (aspen)	POTR	45	984	76,837
Pseudotsuga menziesii (Douglas fir)	PSME	180	8353	2,275,294
Quercus douglasii (blue oak)	QUDO	35	2709	448,816

classes only represent ~5% of the data. We also implemented regression RF models with RWI data to identify which climate variables are most important for predicting growth magnitude (RWI), allowing us to explore if those variables differ from the important predictors for classifying extreme growth (classification RF).

We initially used *P. edulis* as a test case to evaluate different specifications of the RF models (Text S1 and Table S2). Based on these exploratory models (Table S3), we implemented models for all seven species that used seasonal climate variables: total cold-season (winter) and warm-season (summer) precipitation, and mean winter and summer temperature and VPD, resulting in 30 climate variables (3 climate variables × 2 seasons × 5 years = 30; see Table S1). Given that site-level static characteristics and prior ring widths are often important predictors of ring width or RWI (e.g., Klesse et al. 2020, 2023), we implemented two main variants of the RF models: (1) "climate-only models" that included MAP, MAT, and the seasonal climate covariates and (2) "full models" that included lag-RWI, year, and a categorical site indicator, along with MAP, MAT, and the seasonal climate covariates (Table S2). The climate-only models allowed us to explicitly explore the relative importance of different climate variables for predicting low- and high-growth states. The full models are useful for identifying non-climate-related factors that may explain additional variability in the occurrence of extreme-growth states.

To investigate how the probability of extreme growth is related to important climate variables, we obtained variable importance values. Importance values were calculated for all covariates in both the climate-only and full models using the permutation approach of Breiman (2001), implemented in the R package randomForestSRC using the functions rfsrc, subsample, and extract.subsample (Ishwaran and Kogalur 2019). We also calculated confidence intervals for our final, focal models (see Table S3). Importance values are measured as the difference in out-of-bag (OOB) prediction or classification error when using a covariate as observed versus using a randomly permuted version of the covariate. Thus, large differences in error indicate the importance of a covariate for classification, while small differences indicate the covariate to be of little importance.

For the most important climate variables, we created partial dependence plots (Friedman 2001) for the climate-only classification RF models using the partial.rfsrc function in the randomForestSRC package in R. For 2D plots, we used the fitted RF models to predict the probability of extreme low- and high-growth years at specific (gridded) values of two seasonal climate variables, averaging (marginalizing) over the observed values of all other covariates; we treated one of these variables as the focal variable and the other as the conditioning variable to explore how the probability of extreme growth varied as a function of the focal variable, given specific values of the conditioning variable. We also generated reference plots, which are simply 1D partial dependence plots that describe how the probability of extreme growth varies in relation to the focal climate variable, thus marginalizing over all other covariates, including those we conditioned on to create the 2D plots.

2.4 | Climate Conditions Associated With Extreme Growth

To understand extreme climate conditions from a tree's perspective, we evaluated the range of conditions that distinguish extreme- from nominal-growth years. Specifically, we evaluated how the top five most important climate variables differed during low-, nominal-, and high-growth years. First, we used the kstest function in scipy.stats Python package to conduct Kolmogorov–Smirnov tests to determine if the distributions of important climate variables differed for low- versus high-, low- versus nominal-, and high- versus nominal-growth years. Second, we computed pairwise correlations between the climate variables for low-, nominal-, and high-growth years to determine if the important climate covariates are more strongly or weakly correlated during extreme- relative to nominal-growth years. A stronger correlation between two climate variables during extreme-growth years suggests that specific combinations of climate conditions are "required" to give rise to an extreme-growth state. Conversely, weaker correlations during extreme-growth years suggest that the two climate variables act more independently to affect the probability of extreme growth. We used the independent_corr function in the CorrelationStats Python package to test for differences in pairwise climate variable correlations, which computed *P*-values based on the magnitude of the correlations and the number of observations (N) used to compute each correlation.

3 | Results

3.1 | High-Growth Years Are Less Synchronous Than Low-Growth Years

We found evidence for greater synchrony in low- than in high-growth years. Extreme low- and high-growth frequencies varied over time (Figure 2) and were relatively independent of site-level MAP (Figure S1). To explore the synchrony of extreme growth (Q1), we focus on the four species whose distributions overlap in the Southwest (*P. edulis*, *P. ponderosa*, *P. tremuloides*, and *P. menziesii*). In this region, high growth was not spatially synchronous: at least one site had high growth in nearly every (95.9%) year, and most (87%) of these high-growth years were only shared by a few (< 10%) sites (Figure 2, green bars). Conversely, low-growth years tended to be more synchronous (Figure 2, black bars): at least one site had low growth in 84.6% of the years, 18.1% of which were shared by at least 10% of the sites. For example, over a quarter of the sites had low growth in multiple years (e.g., 1902, 1904, 1951, 1956, 2002; Figure 2, black bars); notably, these years correspond to known widespread regional droughts in the western USA.

3.2 | Random Forest Ability to Predict Tree Growth

Despite the flexibility of regression RF models (Text S2), they only accounted for 39.3%–65.9% (full models) and 10.0%–63.3% (climate-only models) of the variation in RWI across the study species (Table S3 and Figure S2). Moreover, the regression RF
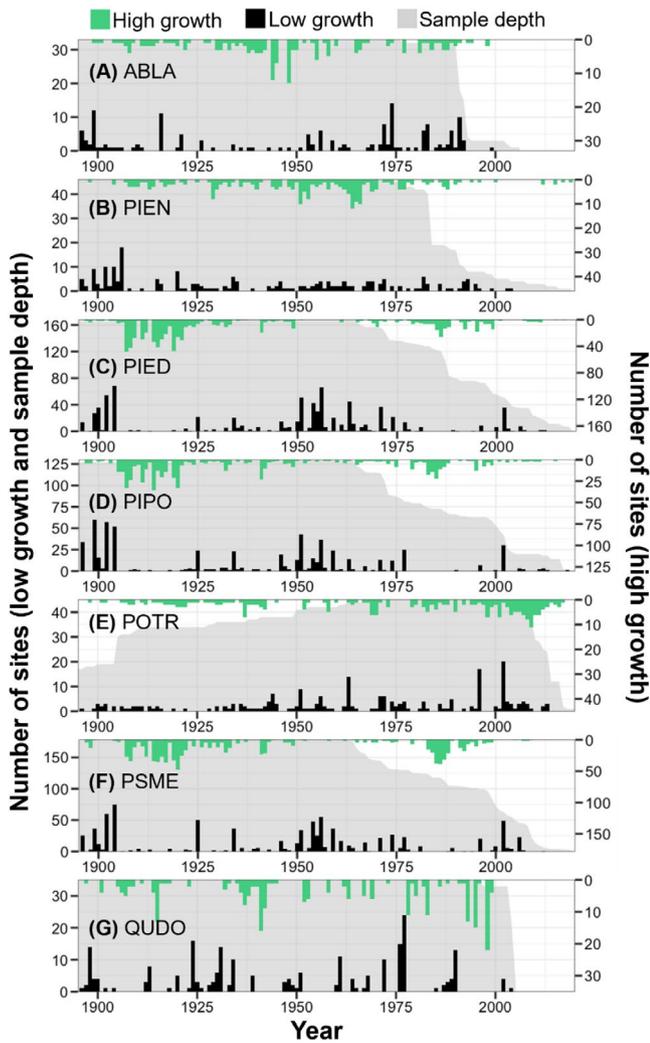
FIGURE 2 | Number of sites yielding high growth (green) and low growth (black) in each year for: (A) ABLA, (B) PIEN, (C) PIED, (D) PIPO, (E) POTR, (F) PSME, and (G) QUDO. See Table 1 for the definition of species codes and the total number of sites for each species ("*N* sites"). Sample depth (gray region) indicates the number of sites yielding ring-width index (RWI) data.

models consistently over-predicted low RWI (low growth) and under-predicted high RWI (high growth; Figure S2), similar to mixed-effects models in other studies. Importantly, our primary focus is on understanding the factors governing the occurrence of these extreme growth states, motivating the use of classification RF applied to the extreme low and high growth categorical data.

The classification RF full models generally performed better for classifying low-growth (2%–22% classification error) than high-growth (5%–34% error) years (Table 2). This pattern was also reflected in the climate-only models (reported below), whereby classification RF successfully predicted low-growth (classification error <11%) and high-growth (error <20%) years for four species (*Q. douglasii*, *P. menziesii*, *P. ponderosa*, and *P. edulis*) (Table 2). For both the regression and classification RF models (full and climate-only versions), model performance was comparatively low for the other three species (*A.*

TABLE 2 | Model performance statistics for the classification RF models applied separately to low- and high-growth states.

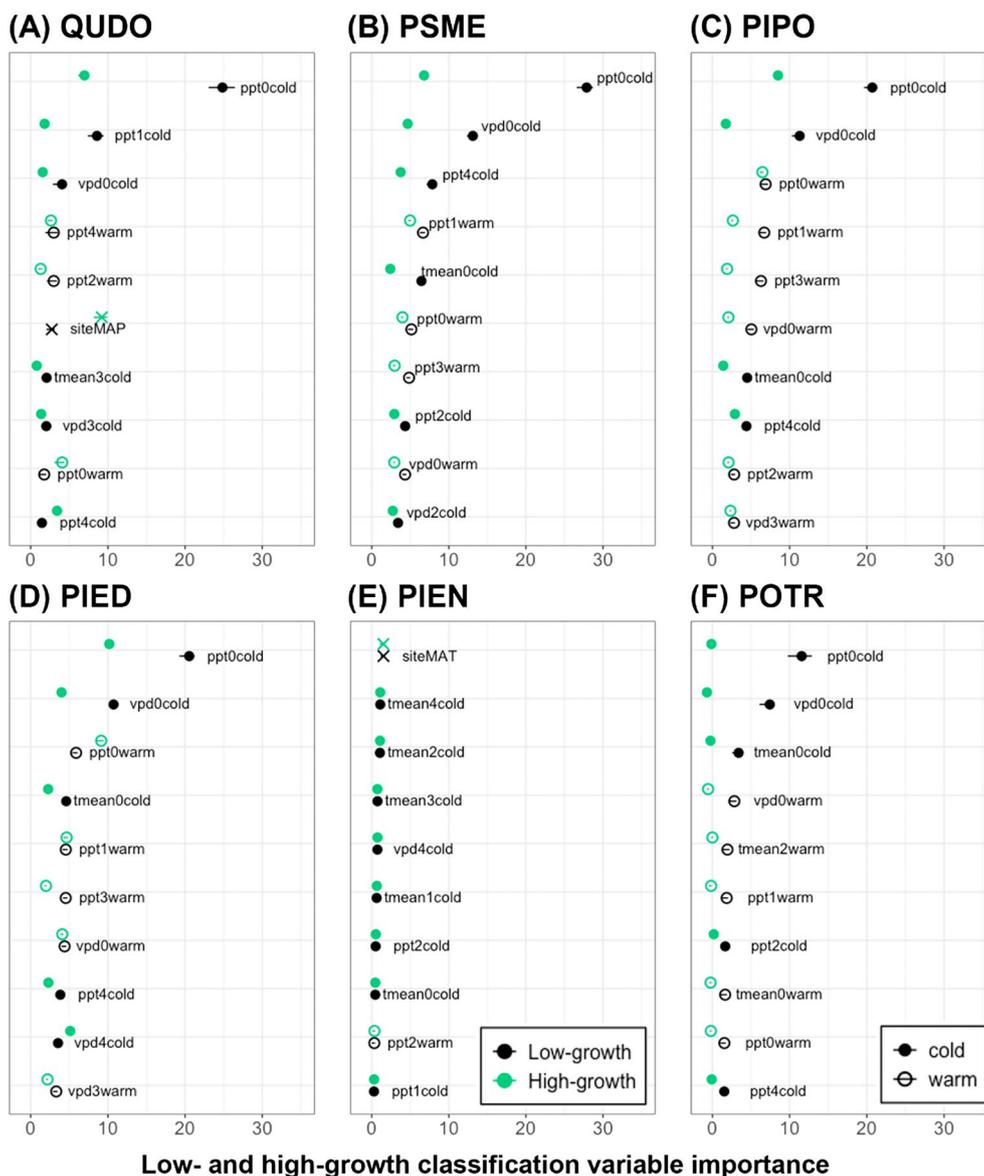| Species	Low-growth classification error		High-growth classification error	
	Full (%)	Climate-only (%)	Full (%)	Climate-only (%)
QUDO	2.0	2.0	5.4	4.9
PSME	6.7	8.6	8.5	15.0
PIPO	7.5	10.9	9.6	19.8
PIED	5.2	7.2	11.8	17.8
ABLA	19.1	39.7	18.0	34.8
PIEN	14.8	35.2	33.9	38.8
POTR	21.9	44.6	24.8	56.6

Note: Lower classification error (for the focal low or focal high growth class) indicates better model performance. Species are ordered from the overall lowest to the highest classification error. The full model includes all climate variables, in addition to the prior year's RWI, site ID, and year (see Table S2). Species codes are defined in Table 1.

lasiocarpa, *P. engelmannii*, and *P. tremuloides*) (Table 2 and Figure S2).

3.3 | Most Important Climate Variables for Predicting Extreme Growth

In the full models, lag-RWI ranked in the top five most important variables for all seven species for both the low- and high-growth classification RF models, with the exception of high growth for *P. engelmannii* (Figure S4 and Table S3). Winter precipitation immediately preceding ring formation ("current" cold season) ranked among the top five predictors for six species (the exception, again, was *P. engelmannii*). Only six other seasonal climate variables ever ranked in the top five, with each only ranking high for one or two species (Table S3). Other variables unrelated to seasonal climate commonly in the top five were year (five species) and site-level MAP (four species).

Focusing on the classification RF climate-only models, differences in the variable importances of different climate variables suggest asymmetric responses (Q2) and species-specific responses to some climate variables (Q3). For the aforementioned four species (*Q. douglasii*, *P. menziesii*, *P. ponderosa*, and *P. edulis*), current winter precipitation was the single most important predictor of low growth (notably high importance) and the first or second most important for high growth (Figure 3 and Table S4). Current winter VPD was the second most important predictor of low growth for the three conifers and the third most important for *Q. douglasii*. Current summer precipitation and VPD were comparatively less important than current winter precipitation and VPD. However, current summer precipitation ranked in the top six for low growth for the three conifers and in the top four for high growth for *P. edulis*, *P. ponderosa*, and *Q. douglasii*. A few lagged winter and summer precipitation variables emerged in the top five for low growth for all four species

Low- and high-growth classification variable importance

FIGURE 3 | Variable importance plots produced by the climate-only random forest (RF) classification models for four species associated with the top-performing models (see Table 2): (A) QUDO, (B) PSME, (C) PIPO, and (D) PIED, along with two species associated with relatively poor performing models: (E) PIEN and (F) POTR. Only the top 10 most important predictor variables are shown and ordered (along y-axes) based on the low-growth classification RF model. Variable importance values for each variable are shown for the low-growth (black symbols) and high-growth (green) classification RF models. Cold-season ("winter") climate variables are denoted by filled (closed) symbols and warm-season ("summer") by open symbols; non-seasonal climate variables are denoted by an "×". Species codes are defined in Table 1. Climate variables are coded as varXseason, where var = ppt (precipitation), vpd (maximum VPD), or tmean (temperature); X is the lag year ($X = 0$ for current year, …, $X = 4$ for 4 years prior); season = cold or warm (see Table S1).

(Figure 3A–D); lagged VPD was generally of low importance for predicting low growth, except for *P. edulis*. A greater number of lagged moisture-related variables (precipitation and VPD) ranked in the top 10 for predicting high growth compared to low growth (Table S5).

Temperature conditions, regardless of season or timing (current or lagged), were generally of little importance for predicting extreme growth, except for winter temperature during the current year (*P. menziesii* and *P. ponderosa*) and three years prior (*Q. douglasii*) for low growth (Table S5B). Site-level climate (MAP or MAT) was not important for predicting low growth in the three conifers, but it ranked sixth most important for *Q. douglasii* (Figure 3A and Table S5B). Conversely, for high growth, MAP ranked most important (*Q. douglasii* and *P. menziesii*) or in the top five (*P. edulis* and *P. ponderosa*) (Table S5C). For low growth, current winter precipitation, along with either current winter VPD or prior year's winter precipitation, accounted for 31%–50% of the total variable importance, which was mostly attributed to the strong importance of current winter precipitation (Table S5B). In contrast, the top two climate predictors for high growth only accounted for 18%–24.5% of the total variable importance (current winter precipitation along with either current summer precipitation or site-level MAP; Table S5C).
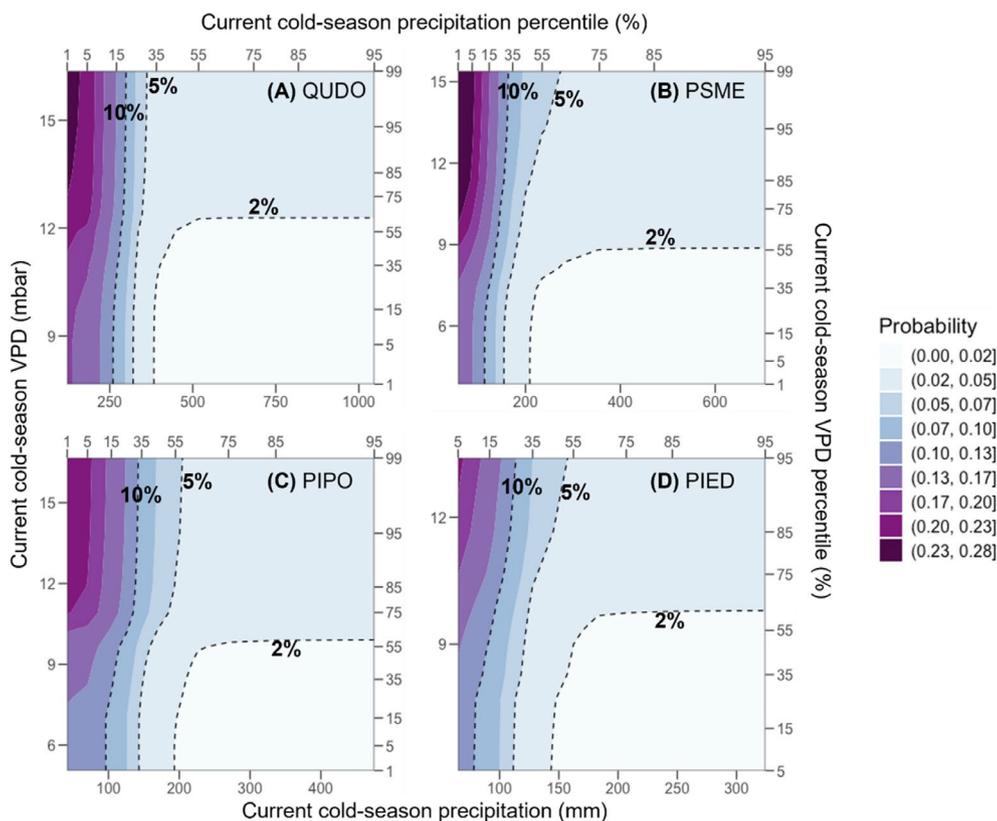
FIGURE 4 | Contours represent the predicted probability of extremely low growth as a function of current cold-season ("winter") precipitation and VPD for: (A) QUDO, (B) PSME, (C) PIPO, and (D) PIED. The *x*- and *y*-axis limits vary by species such that winter precipitation values span the 1st to 95th percentiles (see top axis labels) and winter VPD values span the 1st to 99th percentiles (see right axis labels), with the percentiles determined separately for each species. The dashed contour lines denote conditions leading to a 2%, 5%, and 10% chance of low growth; probabilities exceeding 0.1 (10%) are deemed to represent a high chance of low growth. The distribution of winter precipitation and VPD values observed for each species is overlaid on the contour plots in Figure S7. Species codes are defined in Table 1.

For comparison with the classification RF results, variable importances for the regression RF models are summarized in the supporting materials (Text S2; Figures S3 and S4), which tend to align better with the low- compared to the high-growth classification rankings (Tables S4 and S5).

3.4 | Predicted Probabilities of Extreme Growth

Predicted probabilities of extreme-growth years as a function of key climate variables lend insight into asymmetric responses (Q2) and species-specific responses (Q3). For *Q. douglasii*, *P. menziesii*, *P. ponderosa*, and *P. edulis*, a dry winter preceding ring formation is associated with a higher probability of extreme low growth (Figures 4 and S5), whereas a wet winter results in a higher probability of extreme high growth (Figure S6). Partial dependence plots (Figures 5 and 6) summarize how this probability of extreme growth varies in relation to pairs of important climate variables: there is at least a 20% chance of low growth when current winter precipitation is below its 20th to 25th percentile (50–100 mm; Figures 4, 5, and S5). Such relationships between the probability of extreme growth and current winter precipitation were sometimes influenced by interacting climate variables (Figures 4–6). For example, the negative impact of a current dry winter is exacerbated if accompanied by high winter VPD (higher probability of low growth; Figures 4 and S5) or if the preceding winter was also dry (as for *Q. douglasii*; Figures 5B

and S7A). For example, if current winter precipitation and VPD exceed their 5th and 90th percentiles, respectively, then there is at least a 20% chance of low growth (Figure 4), a frequency that mirrors the impacts of severe, regional-scale droughts.

Wetter and drier sites had differing responses to climate. That is, site-level MAP governed the relationship between the probability of extremely high growth and seasonal climate (Figures 5A and S6). The probability of high growth increases with increasing current winter precipitation, but this relationship is greatly modified by MAP such that wetter sites (MAP exceeding its 75th percentile [~400–600 mm]) have an overall lower probability of high growth. Conversely, drier sites (MAP below its 50th percentile [~400–500 mm]) have an overall higher probability of high-growth years, and the probability of high growth nearly doubles following a wet winter (current winter precipitation exceeding 300–500 mm) relative to a dry winter (< 300 mm). Conversely, the effect of current winter precipitation on the probability of low growth is relatively independent of MAP; regardless of site-level MAP, the probability of low growth approaches 25% for abnormally dry winters and drops to 1%–2% for abnormally wet winters (Figure 4).

For two of the Southwest conifers (*P. ponderosa* and *P. edulis*), current summer precipitation also affects the probability of extreme growth, but only in dry years. On average, higher summer rainfall results in a higher (lower) probability of high (low)
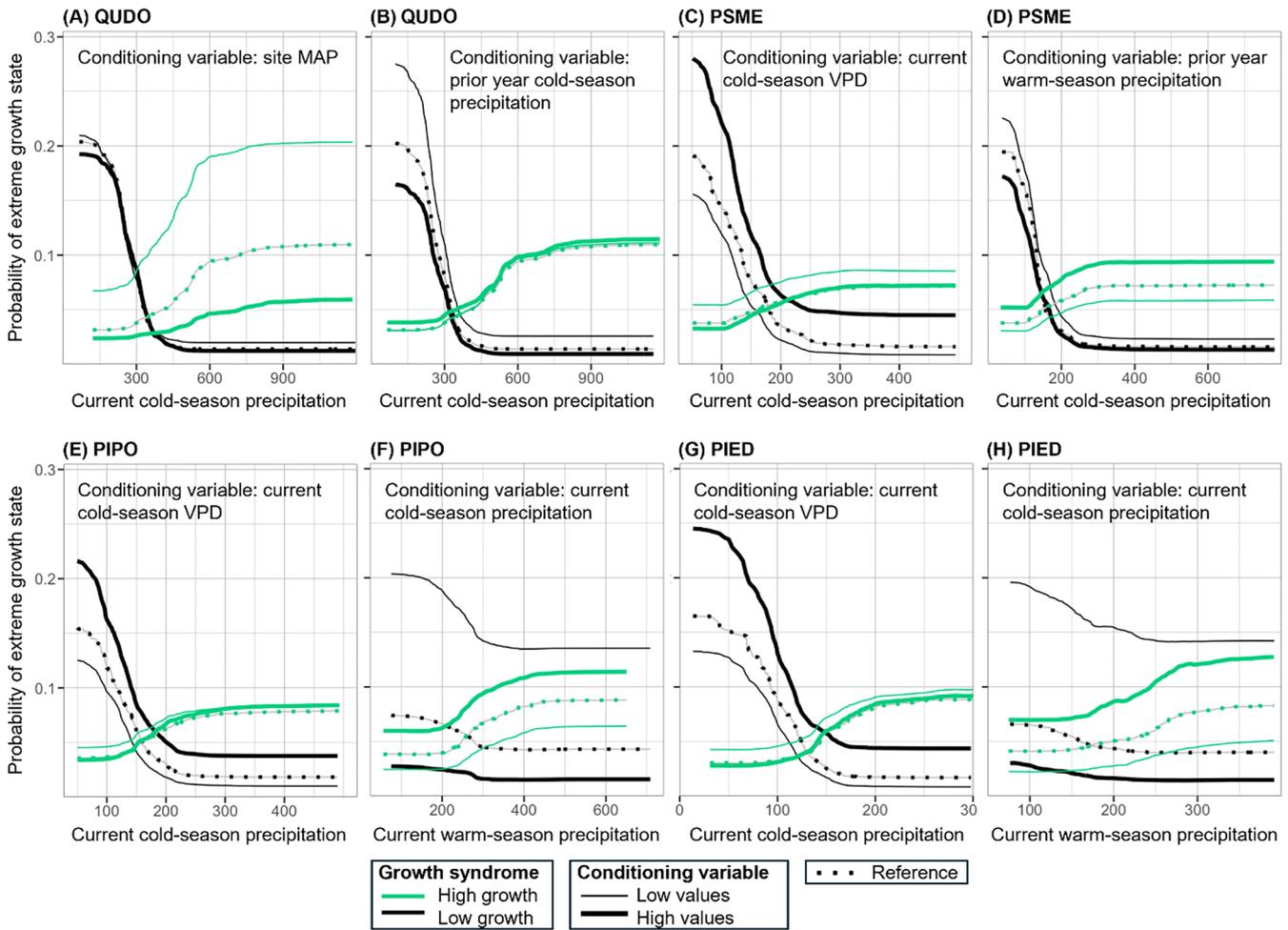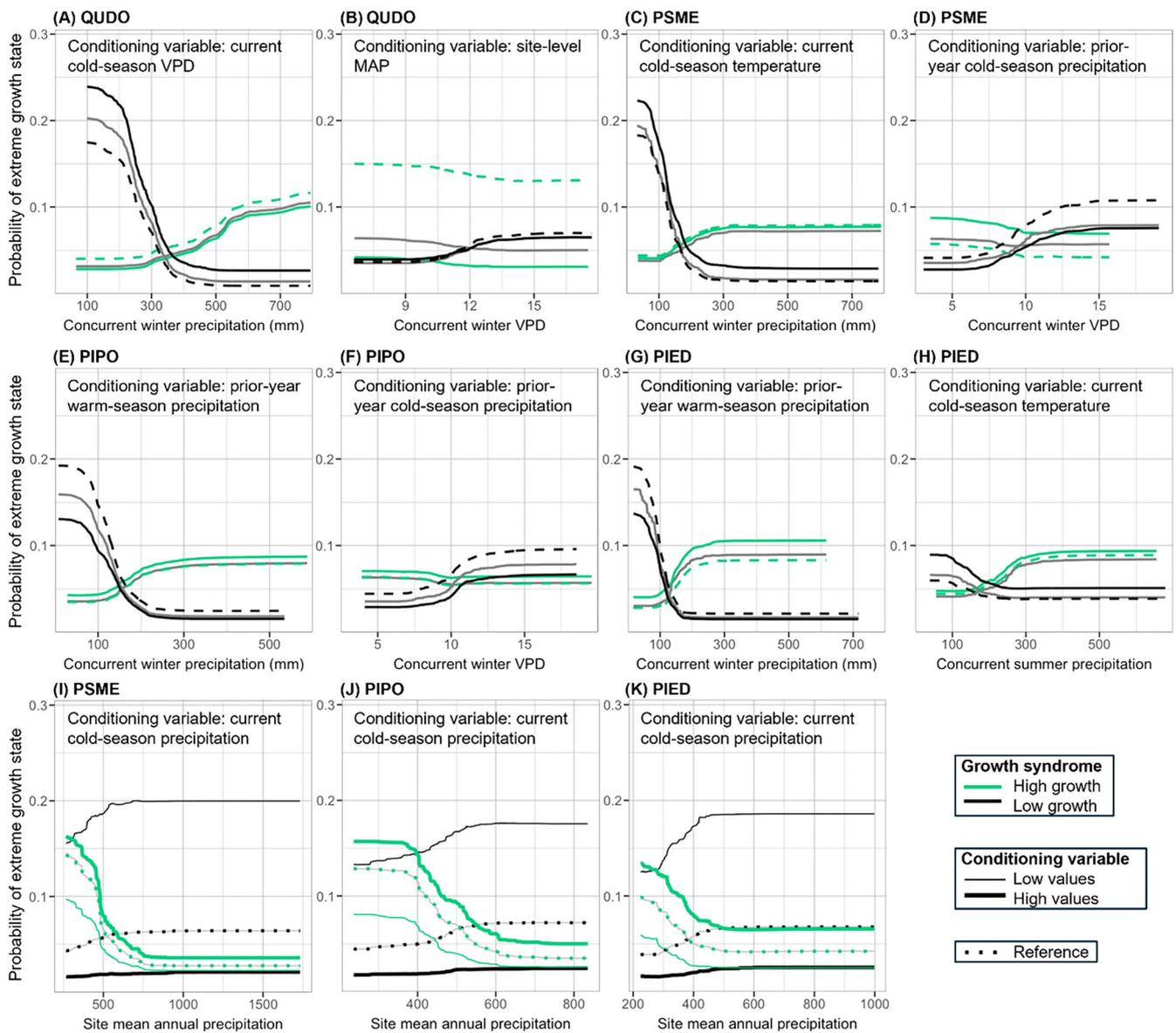
FIGURE 5 | Partial dependence plots produced by the climate-only low- and high-growth classification random forest (RF) models for four species associated with the top-performing models (see Table 2). The plots show the predicted probability of extreme growth (high growth = green; low growth = black) as a function of an important climate variable (*x*-axis), conditioned on two levels of another important climate variable. The high (thick lines) and low (thin lines) values of the conditioning variable are based on the variable's 97.5th and 2.5th percentile, respectively; the reference curve corresponds to the unconditional probability as a function of the focal variable (*x*-axis) given (marginalizing over) observed values of *all* other covariates, including the conditioning variable. Two examples are shown for each species: (A) QUDO, conditioning variable (cv) = site-level MAP, (B) QUDO, cv = prior-year cold-season ("winter") precipitation, (C) PSME, cv = current winter precipitation, (D) PSME, cv = prior-year warm-season ("summer") precipitation, (E) and (F) PIPO, cv = current winter precipitation, (G) PIED, cv = current winter VPD, and (H) PIED, cv = current winter precipitation. Species codes are defined in Table 1.

growth (Figures 5F,H and S7B,C). However, preceding winter conditions modify the relationship between the probability of extreme growth and current summer rainfall. For both *P. ponderosa* and *P. edulis*, if the current summer is preceded by a wet winter (high current cold-season precipitation), then the probability of low growth is low (< 5%) regardless of summer rainfall amount. Conversely, if the preceding winter was abnormally dry, then the probability of low growth varies from about 20% (dry summer) to 13%–14% (wet summer).

3.5 | Climatic Conditions During Extreme Growth Years

To understand extreme climate conditions from a tree's perspective (Q4), we compared the climate conditions associated with extreme-growth years, focusing on variables that consistently emerged as important predictors of extreme growth

for *Q. douglasii*, *P. menziesii*, *P. ponderosa*, and *P. edulis*. The distributions describing climate conditions during low-, nominal-, and high-growth years were significantly different from each other for 57 of the 60 comparisons (3 pairwise comparisons × 4 species × 5 variables; Figures 7 and S8). While many of the distributions overlap for a given climate variable, the large number of significant comparisons is likely a result of the large sample sizes. We focus on the variables that show the greatest difference among extreme- and nominal-growth years. In particular, current winter precipitation showed the greatest dissimilarity: 97% of low-growth years had winter precipitation amounts that were less than the mean winter precipitation received during nominal-growth years, and 79% of high-growth years had winter precipitation that was greater than the nominal mean. Current winter VPD also differed significantly, with VPD being shifted to higher (lower) values during low-growth (high-growth) years. The most notable difference for current summer precipitation was a shift towards

FIGURE 6 | Additional partial dependence plots produced by the climate-only low- and high-growth classification RF models for four species associated with the top-performing models (Table 2). The plots show the predicted probability of extreme growth (high growth = green; low growth = black) as a function an important climate variable (x-axis), conditioned on two levels of another important climate variable; see Figure 5 for additional details.

higher precipitation in high-growth years. Prior year's winter and summer precipitation showed a trend towards high-growth years being associated with slightly higher antecedent precipitation.

In general, correlation analyses demonstrated that high-growth years are characterized by a combination of conditions, while low-growth years are characterized by extreme values of individual climate variables. Of the 180 pairwise correlations (3 pairwise comparisons [low vs. high, low vs. nominal, high vs. nominal] × 15 climate variable pairs × 4 species), 49 were significantly different from each other ($p < 0.05$) and 18 were marginally different ($0.05 \leq p < 0.1$) (Figure 8). The largest number of significant differences occurred for *P. menziesii* (26 at $p < 0.05$; Figure 8B) and the least occurred for *Q. douglasii* (2 at $p < 0.05$; Figure 8A). Sample size likely impacted the number of significant differences (see N sites,

Table 1), but the number of significant differences (49) is much greater than what would be expected by chance (9 at $\alpha = 0.05$).

Summarizing across all four species, notable differences in the strength of the correlations emerged (i.e., based on differences in r between extreme- and nominal-growth years that were either marginally significant, $p < 0.1$, or the magnitude of the difference was greater than > 0.1). Of the 60 low- versus nominal-growth comparisons, 24 correlations became weaker and only 10 became stronger during low-growth years (Figure 8). Conversely, 19 correlations became stronger and only 12 became weaker during high-growth years (Figure 8). During high-growth years, stronger correlations emerged between prior winter precipitation and current winter temperature and between winter and summer precipitation (paired by current or prior year). During low-growth years,
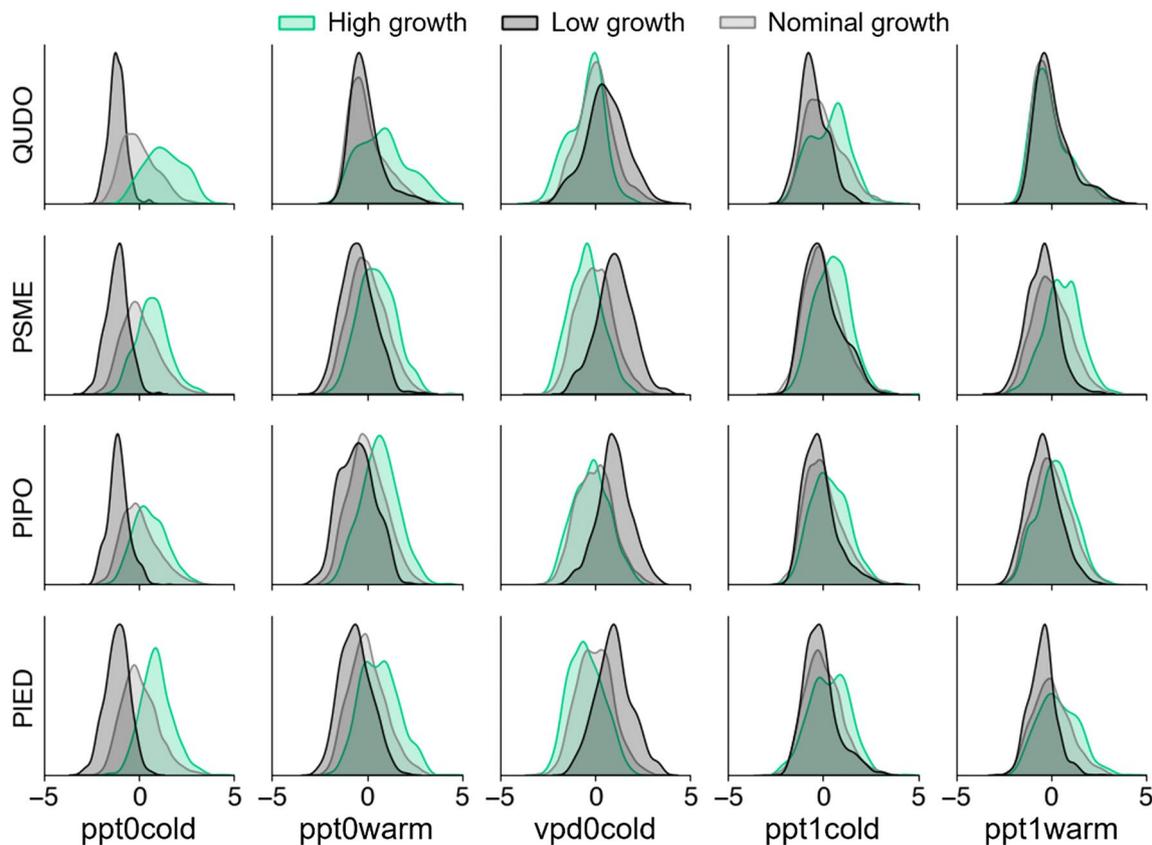
FIGURE 7 | Density plots of important climate variables (see Figure 3) representative of low- (black/gray), high- (green), and nominal- (dark gray/gray) growth years, summarized across all sites for each species. Density plots are produced for the four species associated with the top-performing models (see Table 2), that is, species for which climate is predictive of low- and high-growth years. Density plots are for standardized climate values, z, such that for climate variable x, $z = (x - \bar{x})/sd_x$, where x is the value of the variable in a given year and site, $\bar{x}$ and sd_x are the site-level mean and standard deviation for each species. See Table 1 for species codes and Figure 3 and Table S1 for definitions of the climate variables. Kolmogorov–Smirnov tests that compared distributions between low-, high-, and nominal-growth years within each species-climate variable group indicate all distributions were significantly different ($p < 0.05$) from each other, except for QUDO ppt1warm (low- vs. high-growth), QUDO ppt1warm (high- vs. nominal-growth), and PSME ppt1cold (low- vs. nominal-growth).

weaker correlations generally emerged among various pairs of precipitation-related variables.

4 | Discussion

Our study identified the conditions leading to extreme growth in trees occurring in the western USA. Across species, high-growth years were generally less synchronous across space (Q1, see §4.1.2), more difficult to predict than low-growth years (except in *A. lasiocarpa*), and variables unrelated to seasonal climate were more important for predicting the occurrence of high-growth years (Table S4). Seasonal climate variables were strong predictors of extreme growth in four generally low- to mid-elevation species (*Q. douglasii*, *P. menziesii*, *P. ponderosa*, and *P. edulis*), but were trivial for predicting extreme growth in three relatively high-elevation species (*A. lasiocarpa*, *P. engelmannii*, and *P. tremuloides*) (Q3, see Section 4.2). Of the four species for which climate was predictive of extreme growth, there was evidence for symmetric responses to current winter precipitation as a single predictor, but when conditioned on other climate variables, asymmetric responses emerged (Q2, see Section 4.1). From an ecological perspective (Q4, see Section 4.3), high growth appears

to require a combination of good conditions, while low growth primarily emerges from dry winters, particularly if followed by dry summers for certain species. Despite this, the univariate distributions of climate conditions for low- and high-growth years were overlapping for all climate variables, suggesting extreme growth is implicitly multivariate, emerging from combinations of favorable or unfavorable conditions.

4.1 | Climate Responses Are Largely Asymmetric

While the response to a few key climate covariates, such as current winter precipitation, was somewhat symmetric (Figure 5), the combination of conditions that produced high-growth extremes suggests tree responses to climate are largely asymmetric (Dannenberg et al. 2019; Wise and Dannenberg 2019). To our knowledge, asymmetric temperature and VPD responses have not been widely documented (but see Gantois 2022). For the four focal species for which climate was predictive of extreme growth (*Q. douglasii*, *P. menziesii*, *P. ponderosa*, and *P. edulis*), dry winters preceding ring formation were associated with a high probability of low growth, whereas wet winters were associated with a high probability of high growth, suggesting a
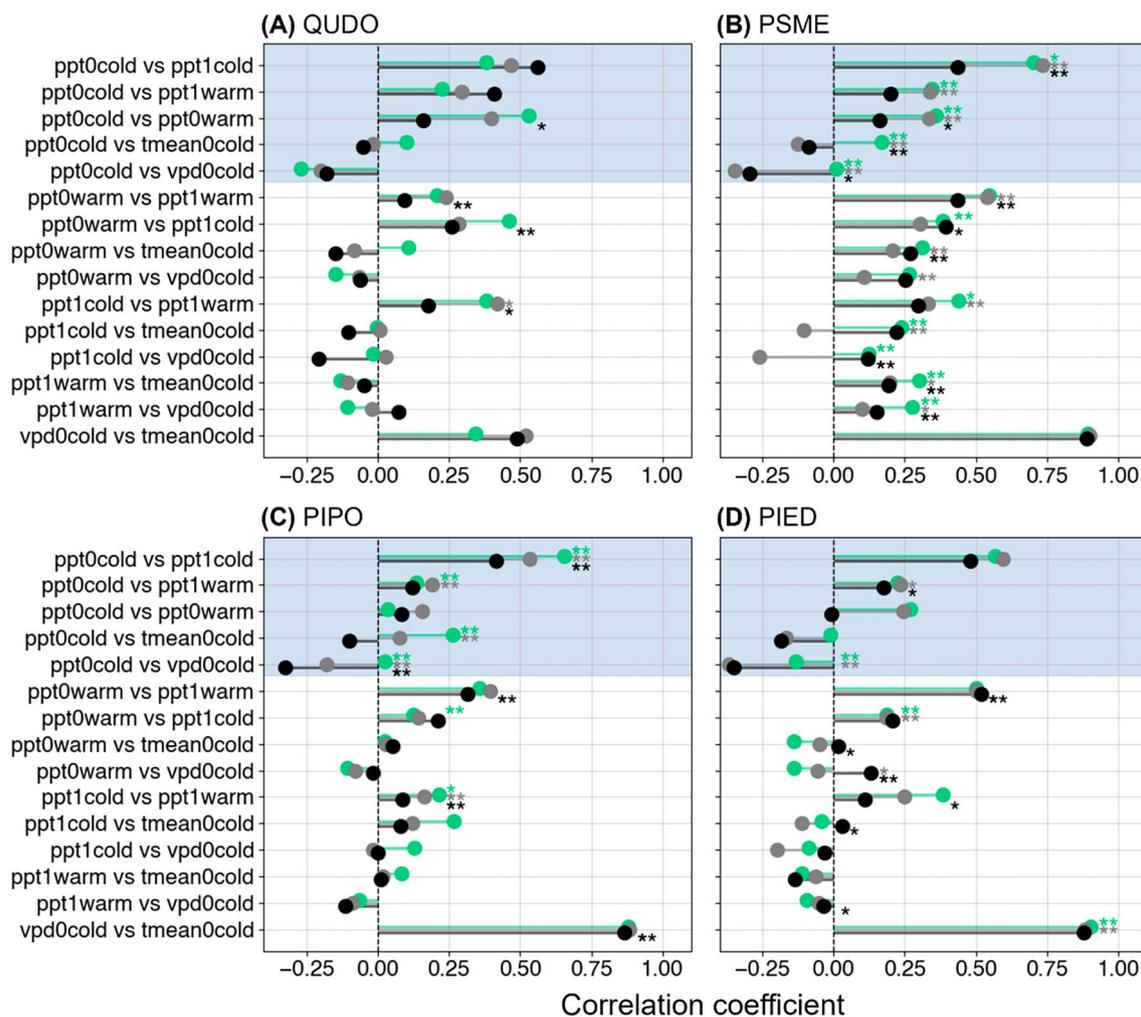
FIGURE 8 | Bivariate Pearson correlations between climate variables that emerged as the most important predictors (see Figure 3) of low- and high-growth years for four species associated with the top-performing models (see Table 2): (A) QUDO, (B) PSME, (C) PIPO, and (D) PIED. Correlations were computed for low-growth (black), high-growth (green), and nominal-growth (gray) years. The vertical dotted line indicates a correlation of zero. Asterisks denote correlations that differ at the $**p < 0.05$ and $*p < 0.1$; green asterisks compare high- to nominal growth; black asterisks compare low- to nominal growth; gray asterisks compare low- to high-growth. The blue shaded region denotes correlations involving current cold-season (winter) precipitation (ppt0cold). Species codes are defined in Table 1. See Figure 3 and Table S1 for definitions of the climate variables.

"symmetric" response. The importance of winter precipitation preceding ring formation is not surprising given existing understanding of ring-width–climate correlations in North America (St. George 2014) and the predominance of sites in the ITRDB selected to reconstruct aspects of hydroclimate in the Southwest (Nehrbass-Ahles et al. 2014). However, predicting high growth was more nuanced, where wet winter impacts were contingent upon other climate factors, and current winter moisture conditions were generally less influential on high- compared to low-growth years (Table S4B,C). Climate interactions were more important for high growth, where, for example, the positive effect of winter precipitation was weaker in wetter sites (high MAP; Figure S6) or if the prior summer (Figure 5D) or prior winter (Figure S7B,C) were relatively dry. In short, high-growth years are not simply anomalously wet, but are the result of combinations of "favorable" conditions, conditions that may be less likely under future climate (Williams et al. 2022).

Moisture supply (i.e., precipitation) and demand (i.e., VPD) variables, however, emerged as important predictors of both

growth extremes, whereas temperature variables were relatively unimportant. Compared to other regions, forests in most of the western USA—such as the region encompassing our *Q. douglasii*, *P. menziesii*, *P. ponderosa*, and *P. edulis* sites—experience strong seasonal moisture limitation and high atmospheric demand, particularly recently (Ficklin and Novick 2017; St. George 2014; Williams et al. 2022). Current winter temperature, however, ranked relatively high for predicting low growth in the three conifers (*P. edulis*, *P. ponderosa*, and *P. menziesii*). This could reflect the negative impact of freezing temperatures and winter drought ("frost drought") on hydraulic function (Delapierre et al. 2024; Mayr et al. 2006; Pittermann and Sperry 2006), which could reduce carbon metabolism and growth during the subsequent growing season (e.g., Charrier et al. 2021). This could also be an artifact of winter temperature and VPD being highly correlated (Figure 8), as the current winter VPD ranked highly for low growth (Figure 5). For all four focal species, however, seasonal temperature variables were not important for predicting high growth, providing additional evidence of asymmetric temperature responses. This

may be because a majority of the ring width is determined by earlywood formation (Björklund et al. 2017; Miina 2000; Pichler and Oberhuber 2007), which takes place early in the growing season, before temperatures peak, and is generally more reliant on winter moisture (Belmecheri et al. 2018). We elaborate on the unique, hence asymmetric, climate relationships of extreme low (Section 4.1.1) and high growth (Section 4.1.2) below.

4.1.1 | Low Growth is Strongly Coupled to Recent Winter Climate

Moisture conditions during the winter immediately preceding ring-formation were critical for predicting low growth for all four focal species. An exceptionally dry winter (low precipitation) could result in a 20%–30% chance of extreme low growth, especially if accompanied by high moisture demand (high VPD; Figures 4 and 5C,E,G). While other analyses of ring-width data suggest that climate over multiple past years continues to influence tree growth (Anderegg et al. 2015; Bond-Lamberty et al. 2014; Ogle et al. 2015), antecedent climate had comparatively little influence on the probability of low growth. These results point to the critical importance of winter precipitation for replenishing soil moisture and facilitating tree growth the following growing season (Fritts 1974; St. George 2014). Moreover, both sufficient moisture inputs and comparatively low evaporative demand during the current winter are critical to successful ring production in our focal species (Figure 4). Winter moisture stress likely governs the probability of low growth through its impact on cell turgor at the start of the growing season (Lockhart 1965; Vieira et al. 2020), which impacts cellular expansion and ring formation (Cabon et al. 2020; Peters et al. 2021). Similarly, freezing-induced cavitation is exacerbated by winter drought, both in terms of precipitation deficits and high VPD (Delapierre et al. 2024; Mayr et al. 2006; Pittermann and Sperry 2006), which can delay growth (Charrier et al. 2021). Longer snow-free periods in winter may also increase the likelihood of root freezing, which may divert subsequent carbon allocation away from radial growth towards repair (Tierney et al. 2001). Given that current winter precipitation and VPD are the dominant factors underlying low growth, this further points to the importance of winter drought in governing periods of growth depression in the western USA (St. George 2014; Truettner et al. 2018).

In the Southwest, the North American Monsoon is a major driver of summer climate (Adams and Comrie 1997), and summer rainfall can be important for tree growth and physiological function (Peltier and Ogle 2019a; Strange et al. 2023), particularly in more southern sites (Therrell et al. 2002). But the influence of monsoonal precipitation can be complex, topographically idiosyncratic, and contingent upon other factors such as temperature, VPD, and prior winter precipitation (Belmecheri et al. 2018; Boos and Pascale 2021; Szejner et al. 2016). We found that current summer precipitation was only moderately important for predicting the occurrence of low growth in the three focal conifers, and the effect of a dry summer was contingent upon the preceding (current) winter. For example, if the current winter was dry, a subsequent dry summer (a dry year overall) could lead to a high (~20%) probability of low growth (Figure 5F,H). However, if a dry summer during the prior year was followed

by a wet winter, then the dry summer had little impact on the probability of low growth (< 5%, Figure 5F,H). These results are consistent with the notion that a strong summer monsoon can rescue trees from a winter drought in parts of the Southwest (Peltier and Ogle 2019a; Strange et al. 2023), thus extending the season of wood formation. Additionally, failed monsoons can halt wood formation early (Morino et al. 2021), but high monsoon precipitation alone is not sufficient to support high growth. Concurrent summer VPD emerged as an important predictor of low growth in *P. ponderosa* and *P. edulis*, which is consistent with the major role of monsoon storms in reducing evaporative stress for these low- to mid-elevation species that occupy relatively dry regions of the Southwest (Figure 1A,B).

4.1.2 | High Growth Is Less Predictable and Asynchronous Across Space

Droughts tend to have large, relatively homogeneous spatial footprints at landscape scales in the Southwest (Cole et al. 2002), while anomalously high precipitation may be more heterogeneous, for example, when associated with atmospheric rivers (Borkotoky et al. 2023; DeFlorio et al. 2024). While low-growth years are generally the result of one major factor (i.e., poor winter moisture conditions immediately preceding ring formation), high-growth years are less predictable because their occurrence depends on either multiple coinciding climate factors or a wider array of climate conditions. In short, our analysis revealed a compounding effect of sequential favorable conditions such that high growth is impacted by climate experienced over multiple seasons and years (Figure 8). Of the top 7–11 climate variables that accounted for 50% of the total variable importance for high growth in the four focal species, over half were lagged climate variables (Table S4C). The majority (74%) of the important lagged variables represented winter moisture (precipitation or VPD) conditions during the previous 1–4 years; prior summer moisture conditions were also important, but to a lesser extent (26% of the lagged variables). This is somewhat consistent with prior work suggesting long (positive) legacies of extreme wet years (Jiang et al. 2019), but our results further imply that multiple sequential good years are required to produce high growth. Given more frequent drought conditions, along with a trend towards aridification (Koppa et al. 2024; Williams et al. 2022), both of which will reduce the likelihood of sequential years of favorable conditions, extreme high growth will likely be less common under future climate in the Southwest (Williams et al. 2013). Our results also suggest that some caution may be warranted when using high growth to predict past climate conditions, given that high growth results from combinations of conditions.

Site-level climate history (MAP and, to some extent, MAT) is important for predicting the occurrence of high-growth years (Table S4C), which tend to be associated with drier sites (lower MAP) (Figure S6). Notably, MAP ranked the most important in predicting high growth for *Q. douglasii* and *P. menziesii* (Table S4C). While raw ring widths may generally be wider in wetter sites (higher MAP, e.g., Bowman et al. 2011), our definition of extreme growth is based on ring-width index (RWI) percentiles. Drier, more stressed sites are often preferred for climate reconstructions because they yield more variable

(less complacent) ring widths compared to wetter sites (Fritts et al. 1965). Thus, we would expect more frequent extreme growth years at drier sites, especially given that our definition of low- and high-growth years is based on RWI percentiles determined across all sites for a given species. Thus, given greater RWI variability in drier sites, they are more likely to have occurrences of annual RWI values that exceed the 95th percentile. In fact, drier sites are associated with an overall higher probability (~12%–20%) of high-growth years compared to wetter sites (~4%–8%) following a wet winter (Figures 5A, 6I–K, and S6). While drier sites are more likely to support high-growth years, the magnitude of that growth (i.e., biomass accumulation or ring width) is likely smaller than in a wetter site.

4.2 | Species-Specific Responses to Climate May Reflect Disturbance or Decline

Widespread aridification of forests in the western USA began in the late 1990′s and early 2000′s, while long-term fire suppression has produced forests of densely stocked, stressed trees (Parks et al. 2025; Williams et al. 2022). Tree growth extremes in such forests may only be weakly driven by climate, and instead related to competition or disturbance, for example, from ongoing beetle-kill in spruce and fir or dieback in trembling aspen (Raffa et al. 2008; Worrall et al. 2010). We expected current and lagged seasonal climate variables to be predictive of extreme growth states in all seven species that we studied, given that prior studies have shown sufficiently strong relationships between ring widths (raw widths or RWI values) and various climate variables (Adams and Kolb 2005; Bigler et al. 2007; Fritts 1976; Harvey et al. 2020; Kelsey et al. 2018; McCullough et al. 2017; Rodman et al. 2024; Wilmking et al. 2020). However, our findings suggest that climate only served as a good predictor of RWI values (Table S3 and Text S2) and extreme growth (Table 2) for some tree species (*Q. douglasii*, *P. menziesii*, *P. ponderosa*, and *P. edulis*) but not others (*A. lasiocarpa*, *P. engelmannii*, and *P. tremuloides*). We considered 30 climate variables, so it might be surprising that none were useful for predicting growth in the latter three species. These species generally occur at higher elevations, and many subalpine forests across the western USA are dense, and have been in a state of decline due to rapid warming and disturbance impacts (Anderegg et al. 2015, 2022; Ayres and Lombardero 2000; DeRose et al. 2013; Kelsey et al. 2018).

Such decline, disturbance effects, historic fire exclusion, or more mesic conditions might explain the weak importance of climate for our three higher elevation species. Widespread decline in *P. tremuloides* stands across the western USA from 2000 to 2010 was attributed to fungal pathogens, fire exclusion, and drought (Singer et al. 2019; Worrall et al. 2013). Since the early 2000′s, *A. lasiocarpa* populations have been declining in abundance and basal area across 60% of its range in the western USA, also linked to insect (bark beetle) epidemics and fire (Bigler et al. 2007; Perret et al. 2023). Likewise, from 1997 to 2013, 2.5 million ha of spruce forests in Alaska and the western USA experienced severe decline and mortality due to spruce beetle (*Dendroctonus rufipennis*) outbreaks (Kelsey et al. 2018; Pettit et al. 2019). Most of the tree-ring data for these species pre-dates these events, but land management, particularly fire exclusion practices, may have produced conditions that promoted such die offs. Extreme low-growth states, in particular, could be characteristic of dense forests under relatively mesic regimes, such that the role of climate would likely be masked by competition or decline signals. Additionally, these high-elevation species may exhibit differing, or opposite, climate sensitivities across sites depending on landscape position or other topographic features (Coulthard et al. 2021). Finally, the range of some of these species also includes portions of the Pacific Northwest, where growth is less interannually variable compared to the Southwest. Such patterns suggest future tree growth in certain forests or species may become less predictable if disturbances or non-climate stressors drive more variation in tree growth than climate.

The four species for which climate was predictive of extreme growth are typically found (or historically sampled) in lower-density stands, which are more likely to be moisture-limited. For *Q. douglasii*, only three variables accounted for 50% of the total importance for low growth, whereas the three conifers required 6–7 climate variables to achieve 50% total importance (Table S5B). The smaller number of variables needed for *Q. douglasii* may reflect the smaller area over which the sites occurred, such that the sites likely shared more similar climate and edaphic conditions compared to the wider region over which the conifers were sampled. In particular, *Q. douglasii* grows in a narrow range of elevations in a ring around the central valley in California, and experiences relatively homogeneous moisture conditions associated with large frontal storms. In contrast, *P. menziesii* and *P. ponderosa* occupy areas that span a wide range of climatic contexts, across a range of elevations, topographic positions, soils, and moisture regimes (e.g., winter versus summer precipitation dominated). Differences across these species may also reflect different moisture use strategies and traits. For example, *Q. douglasii* occurs in a Mediterranean climate, characterized by wet winters and dry summers, and is deciduous with ring-porous wood (Gil-Pelegrín et al. 2017; Nixon 2002). Thus, *Q. douglasii* is reliant on a less complex moisture source (no monsoon), and the bulk of each annual ring is formed in the spring using stored carbon reserves, finishing growth before summer drought (Barbaroux and Breda 2002). In contrast, most conifers in the Southwest sustain ring growth over the summer through a combination of stored carbohydrates and new photosynthate, supported by both winter and summer precipitation (Belmecheri et al. 2018; Morino et al. 2021).

4.3 | Drought From a Tree's Perspective

Our analysis of extreme low-growth years allows us to evaluate drought conditions from a tree's perspective. For the three focal conifers in the Southwest (*P. menziesii*, *P. ponderosa*, and *P. edulis*), if current winter precipitation falls below the 20th to 30th percentile representative of a species' range, there is at least a 10% chance of a low-growth year (Figure 4). Moreover, correlations between current winter precipitation and other key climate variables were weaker during low-growth years, except for current winter VPD, which was more strongly correlated with current winter precipitation during low-growth years (Figure 8). This points to the dominant importance of current winter moisture conditions for governing the occurrence of low growth. If current winter VPD falls above its 85th to 90th percentile and winter precipitation falls below its 5th to 10th percentile for a

given species, there is a very high chance that such winter moisture stress will lead to extreme low growth (Figure 4). That is, a combination of supply- and demand-related moisture stresses leads to extremely low growth, and such compounded drought conditions are becoming more common (e.g., Mukherjee and Mishra 2021).

5 | Conclusions

Our study evaluated the drivers of extreme growth states in trees, thus informing extreme climate conditions from a tree's perspective. Our machine-learning approach enabled a systematic assessment of the drivers of growth extremes across major tree species in the western USA, suggesting major risks to future forests. The western USA is becoming more arid (Koppa et al. 2024), and favorable years are becoming less frequent (Hall et al. 2024; Jones and Gutzler 2016). Climate conditions favoring high growth arise from a combination of favorable conditions occurring over multiple years, and such conditions will be less likely in the future. These high-growth years may be important for future demography (Hacket-Pain et al. 2024, 2025; Shriver et al. 2022) if they drive interannual variability in reproductive effort and recruitment success. Similarly, low-growth years may increase the probability of future mortality (Cailleret et al. 2017; Ogle et al. 2000) and are likely to increase in frequency because winter moisture stress is expected to increase with climate change in the western USA (Hall et al. 2024; Jones and Gutzler 2016). The combination of these factors implies shrinking populations of some tree species, particularly conifers in the western USA, consistent with recent widespread mortality (Andrus et al. 2021; Fettig et al. 2019; Wang et al. 2021).

Author Contributions

Kiona Ogle: conceptualization, funding acquisition, investigation, project administration, visualization, writing – original draft, writing – review and editing. **Jarrett J. Barber:** formal analysis, funding acquisition, methodology, writing – review and editing. **Brandon M. Strange:** conceptualization, formal analysis, writing – review and editing. **Rohan D. Boone:** data curation, formal analysis, visualization, writing – review and editing. **Alicia M. Formanack:** writing – review and editing. **Drew M. P. Peltier:** conceptualization, funding acquisition, writing – review and editing.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The low-, high-, and nominal-growth class data and associated climate data used in this study, along with the code for implementing the classification random forest (RF) models, are available on GitHub via Zenodo (https://zenodo.org/records/15635985; DOI: 10.5281/zenodo.15635984). PRISM climate data were originally downloaded from https://prism.oregonstate.edu/terms/ (see also https://doi.org/10.17616/R3S62R) and ITRDB were originally downloaded from https://www.ncei.noaa.gov/access/paleo-search/?dataTypeId=18 (see also https://doi.org/10.25921/c3qh-2h10). The additional *P. tremuloides* data were obtained directly from Ireland (Ireland et al. 2014).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.