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Canary in the forest?—Tree mortality and canopy dieback of western redcedar linked to drier and warmer summers

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Abstract

Aim: Forest dieback is increasing from unfavourable climate conditions. Western redcedar (WRC)—a culturally, ecologically and economically important species—has recently experienced anomalously high mortality rates and partial canopy dieback. We investigated how WRC tree growth and dieback responded to climate variability and drought using tree-ring methods.

Location: Pacific Northwest, USA.

Taxon: Western redcedar (*Thuja plicata*).

Methods: We collected tree cores from three tree health status groups (no canopy dieback, partial canopy dieback, and dead trees) at 11 sites in coastal (maritime climate) and interior (continental climate) WRC populations. From growth rates, we computed four growth indices that assessed the resilience to drought and estimated the year of death.

Results: Warmer and drier climate conditions in May/June that extended the annual July-to-September dry season reduced radial growth in 9 of 11 sites (1975–2020). WRC trees recovered growth to pre-drought rates within 3 years when post-drought climate conditions were cooler/wetter than average. However, recovery from drought was slower or absent when warmer/drier conditions occurred during the post-drought recovery period, possibly leading to the recent and widespread mortality across the coastal population. WRC mortality was portended by 4–5 years of declining growth. Annually-resolved mortality in coastal populations predominately occurred in 2017–2018 (80% of sampled dead trees), a period that coincided with exceedingly hot temperatures and the longest regionally dry period from May to September (1970–2020). In interior populations, mortality was dispersed among years but associated with warmer and drier conditions from August to September.

Main conclusions: Our findings forewarn that a warming climate and more frequent and severe summer droughts, especially in consecutive years, will likely increase the vulnerability of WRC to canopy dieback and mortality and possibly other drought-sensitive trees in one of the world's largest forest carbon sinks.

KEYWORDS
climate change, drought, forest decline, forest die-off, *Thuja plicata*, tree mortality

1 | INTRODUCTION

Forest dieback is increasing in many forest biomes (Hammond et al., 2022; McDowell et al., 2020). Tree mortality and partial canopy dieback can result from individual abiotic and biotic stressors or the interaction among multiple stressors (e.g. the 'decline spiral' of Franklin et al., 1987, Manion, 1991), complicating the identification of proximate causes and increasing the difficulty of predicting dieback (Allen et al., 2015; Trugman et al., 2021). Tree mortality is an essential and natural component of forest ecosystems, but extensive losses of forest cover have substantial implications for forest structure and composition (Anderegg et al., 2012), climate regulation (Bonan, 2008; Pan et al., 2011), water cycles (Mikkelson et al., 2013), and cultural management (Armstrong et al., 2022). Developing long-term strategies to adapt to climate change requires a stronger understanding of the proximate causes of forest dieback (abiotic versus biotic agents; Hennon et al., 2020).

More severe and frequent drought and heat events are key drivers of recent forest dieback (Allen et al., 2015; Anderegg et al., 2019; Sommerfeld et al., 2018), often interacting with other agents (e.g. bark beetle outbreaks; Raffa et al. 2008). Warmer and drier climate conditions reduce soil moisture availability, increase atmospheric drought, and elevate heat stress, which may result in failure of tree hydraulic systems and dehydration of tissues (Adams et al., 2017; Arend et al., 2021; McDowell et al., 2022). If unfavourable conditions persist, partial canopy dieback or mortality may occur. Climate models predict increases in temperature and shifts in drought characteristics (e.g. frequency and intensity) during some seasons, indicating that most trees will need to survive multiple drought or heat events to persist (Hammond et al., 2022). New tree canopy dieback events in forested regions where no dieback events were previously reported may help foreshadow broader-scale forest vulnerability to dieback under climate change (i.e. canary in the coal mine).

In temperate forests, annual tree growth rings record the response to multiple abiotic and biotic conditions (e.g. climate variability, competition) over decades to centuries and are helpful for identifying potential causes of partial canopy dieback and mortality (Camarero et al., 2015; Hennon et al., 2020). For example, prolonged decreases in tree radial growth (years to decades) can result from non-lethal insect attacks and slowly increasing environmental stress, such as from shading or decadal shifts toward unsuitable climate conditions. In contrast, abrupt termination of growth is more commonly caused by disturbances (e.g. lethal bark beetles or fire) or acute climate events (Cailleret et al., 2017; Puchi et al., 2021). Prior to tree death, the response of annual growth to drought events (e.g. resistance or resilience) can be used as evidence of climate conditions that induce tree stress (Bigler et al., 2004; Lloret et al., 2011). Interestingly, coexisting trees of the same species within a population may differ in their response to stressors and susceptibility to dieback (Camarero et al., 2015; Serra-Maluquer et al., 2021). Retrospective analyses of tree-rings that examine the response of forest demographic processes, such as growth and mortality, to climate

variability and extreme climatic events are needed to inform species' vulnerability to climate change (Clark et al., 2016; Lévesque et al., 2013), particularly for taxa and geographies of ecological, global and cultural significance (e.g. Bradshaw et al., 2020; Case et al., 2021).

Forests of the Pacific Northwest (PNW) region of western North American (including the states of Washington, Oregon, and Idaho, USA and the province of British Columbia, Canada) play an outsized role in global climate regulation because they sequester and store large quantities of carbon (Buotte et al., 2020; Waring & Franklin, 1979). Within the last decade, western redcedar (*Thuja plicata* Donn ex D. Don; hereafter, WRC) has experienced anomalously high mortality and partial canopy dieback (hereafter, dieback) throughout much of its distribution in the PNW (Goodrich et al., 2022; WA DNR, 2020). WRC trees are a culturally, economically, and ecologically critical species and canopy dieback has generated widespread concern (Hebda & Mathewes, 1984; Klinka et al., 2009; Sutherland et al., 2016). With respect to mortality agents, no known native, lethal bark beetle species are recognised as primary drivers of WRC tree mortality (USDA, 2010), and WRC trees are more tolerant to many root pathogens compared to co-occurring conifer species (Morrison et al., 2014). As such, longer and hotter summer drought conditions are hypothesised as the likely cause of the recent WRC tree dieback in the PNW (Seebacher, 2007), with climate effects on dieback likely varying between the disjunct interior (drier, continental climates) and coastal populations (more mesic, maritime climate; Michalet et al., 2021). Compared to its common tree associates in the PNW region (e.g. Douglas-fir, *Pseudotsuga menziesii*), WRC is an understudied species and no peer-reviewed studies to date have examined WRC tree canopy dieback.

We investigated how WRC tree radial growth and dieback responded to climate variability and drought in coastal and interior populations in the PNW. To identify characteristics of radial growth that may relate to higher likelihood of survival, while controlling for other biophysical conditions, co-existing WRC trees within 11 sites in the PNW were sampled in three health status groups based on canopy condition: no canopy dieback (<40% canopy dieback; hereafter, *healthy*), partial canopy dieback (>40% and <100% canopy dieback; hereafter, *unhealthy*), and trees that were found dead and presumably died in the last three decades (no green canopy; hereafter, *dead*). We addressed four research questions. (1) How did the growth of unhealthy or dead trees differ from that of neighbouring healthy trees in the last three decades? (2) How did tree growth responses to climate vary by tree health status and population from 1975 to 2020 (or 1975 to year of mortality)? (3) When pre-drought climatic conditions and drought severity were similar, did radial growth responses to drought differ between warm/dry and cool/wet post-drought conditions during the recovery period, and did this relationship vary by tree health status and population? (4) How was annually-resolved tree mortality affected by intra- and interannual variability in weather and climate conditions?

2 | MATERIALS AND METHODS

2.1 | Study area

We studied WRC tree dieback in six sites in coastal and five sites in interior populations (Table 1; Table S1; Figure 1). WRC trees inhabit a broad gradient in annual precipitation from temperate rainforests (>500 cm year^{-1}) of the coast and windward slopes of the Cascade and Olympic Mountains to considerably drier rainshadows in coastal forests and dry and cold interior forests (ca. 70 cm year^{-1}; Minore, 1983). Both populations experience a relatively wetter and cooler period (October–June) followed by an extended warm and dry summer season (July–September) during which soil moistures drop precipitously (Baker et al., 2019; Franklin & Dyrness, 1973). Traits that contribute to WRC's broad distribution and long lifespan (>1000 years) include high rates of survival under unfavourable conditions (e.g. high shade, nutrient-poor soils, and wet conditions), high resistance to biotic agents of mortality (due to high concentration of terpenes) and slow growth (i.e. dense wood; Antos et al., 2016). Common tree-species associates of WRC trees vary from wetter forests of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Sitka spruce (*Picea sitchensis* (Bong.) Carrière) and red alder (*Alnus rubra*) to drier forests of Douglas-fir, grand fir [*Abies grandis* (Dougl. ex D. Don) Lindl.] and bigleaf maple (*Acer macrophyllum* Pursh; Minore, 1983). Since European colonisation, nearly all forests within WRC's distribution have been heavily logged on public and private lands and some portions of its range have been converted to agricultural and urban areas.

2.2 | Field sampling

In summer 2021, we located areas in the field that were mapped as WRC dieback prior to 2020 and subsequently published in Goodrich et al. (2022). We selected sampling areas to span a range of climatic moisture deficit (CMD) and climate conditions (Table 1; Table S2; Wang et al., 2012). Potential sites were excluded if we observed evidence of recent forest management (e.g. thinning in the last 30 years), recent disturbance (e.g. wind, fire) or human development.

In an area with WRC dieback, we used a targeted sampling approach to identify 10 neighbouring triplets of healthy, unhealthy and dead dominant or co-dominant trees (see Figure 1 for example photos) or pairs when dead trees were not present at the site (20–30 trees per site) (Table 1; Figure 1), following similar recent studies (Camarero et al., 2015; Comeau et al., 2019). At each site, triplets (or pairs) were matched for similar tree size (DBH, diameter at breast height) and tree height, and all trees within a site were in a similar abiotic (e.g. aspect and site moisture availability) and biotic (e.g. stand basal area) environment.

For each tree, we extracted two tree cores (increment core diameter: 0.5 mm) at breast height (ca. 1.4 m) with the bark and outer most ring intact (i.e. no rot). Then, we recorded the following tree attributes: DBH, height, health status (healthy, unhealthy, dead), percent canopy dieback (0–100% in 10% classes), tree crown symptoms (top kill, branch dieback, thinning crown), and pest and pathogen damage (e.g. bark beetles, root disease, heartwood decay). We observed no evidence of insect damage in the cambium of dead WRC trees. Additionally, no consistent biotic damage agent of mortality was found in 148 field site visits with WRC tree dieback in Washington and Oregon (Goodrich et al., 2022), though no roots were destructively sampled for pathogens. The sampled area differed by site (ca. 0.5–2 ha) due to the density and extent of mortality and partial canopy dieback symptoms. Topographic descriptors, location, and stand structure and composition were recorded at each site (Table S1).

2.3 | Tree core processing and development of tree-ring chronologies

We processed WRC tree cores following standard dendroecological procedures (Speer, 2010) and measured scanned cores (2400 dpi) with a precision of 0.01 mm (CooRecorder; Maxwell & Larsson, 2021). For each site, healthy and unhealthy ring-width series were crossdated using marker rings and time-shifted correlation coefficients, which were used to date floating ring-width series from dead trees ('dplR' package in R; Bunn, 2010; R Core Team, 2022). We successfully crossdated 90% of all the sampled cores (493 of 547 cores), together representing 94% of the sampled trees (263 of 281; Table 1). For dead trees, the year of the outermost partial or full ring was estimated as the year of tree death (Bigler & Rigling, 2013). Ring-width timeseries from multiple cores were averaged for any overlapping years. We calculated basal area increment (BAI) using measurements of raw ring-width and the trees' DBH (Biondi, 1999).

To test climate-growth relationships, we constructed tree ring chronologies by tree health status for each site from 1975 to 2020 ('dplR' package), a period with >15 trees per site in the chronology (Figure S1). Ring-width series were detrended using a cubic smoothing spline (50% frequency cutoff, 30-year wavelength; Klesse, 2021) to account for the decline in absolute ring-width associated with increasing tree bole diameter. Because of our interest in examining interannual-scale variation in climate-growth relationships, temporal autocorrelation in detrended ring-width series was removed with autoregressive models (i.e. prewhitening). Ring-width series were averaged using the Tukey's biweight robust mean (unaffected by outliers) to construct residual site chronologies for all trees and each tree health status group (Figure S2). For the site tree-ring chronologies, we report mean inter-series correlation (i.e. MSI, the correlation among all ring-width series) and expressed population signal (i.e. EPS, variance explained by the sample trees) of detrended ring-width series (Wigley et al., 1984).

2.4 | Climate and drought datasets

To characterise drought conditions, we calculated standardised precipitation evaporation index (SPEI) by month, season and water

TABLE 1 Characteristics of the 11 sampled sites, tree size and sample depth, and descriptors of tree ring-width chronologies (1975–2020) for western redcedar in the northwestern United States.

Pop.	Site	Site				Trees				Ring-width chronologies				
		Elev. (m)	CMD (mm)	BA (m²/ha)	Init. (yrs)	DBH (cm)	Healthy	Unhealthy	Dead	RW (mm)	BAI (mm²)	MSI	AR1	EPS
Interior	RG	1080	160	34.8	>150	88 (53–151)	10 (10)	10 (10)	0	1.06 (0.12)	2741 (267.4)	0.58	0.32	0.92
	HG	1315	250	51.0	>150	104 (84–129)	11 (11)	11 (11)	0	1.62 (0.12)	5062 (412.5)	0.59	0.16	0.94
	SL	715	350	28.8	<150	42 (32–71)	4 (4)	6 (6)	5 (5)	1.98 (0.20)	2481 (336.0)	0.53	0.20	0.85
	MP	1034	420	29.4	<150	46 (33–93)	10 (10)	10 (10)	0	2.05 (0.13)	2914 (363.9)	0.54	0.22	0.90
	LI	762	500	37.1	<150	42 (28–92)	10 (9)	10 (9)	9 (9)	2.58 (0.14)	3091 (348.4)	0.55	0.35	0.93
Coastal	BW	308	195	25.6	<150	58 (34–108)	10 (10)	10 (10)	10 (10)	2.28 (0.17)	3665 (396.4)	0.48	0.37	0.90
	LM	158	240	26.6	<150	50 (33–83)	10 (10)	10 (9)	10 (8)	2.91 (0.22)	3622 (343.4)	0.49	0.46	0.91
	IC	875	300	32.4	>150	64 (46–105)	10 (10)	10 (9)	0	1.06 (0.10)	2201 (268.4)	0.56	0.32	0.91
	TR	140	340	25.3	<150	50 (28–97)	10 (10)	10 (10)	10 (10)	3.02 (0.16)	3467 (306.2)	0.54	0.31	0.92
	RF	59	420	17.7	<150	67 (30–106)	10 (10)	10 (10)	10 (10)	2.65 (0.22)	4550 (546.2)	0.54	0.35	0.93
	MR	202	430	23.0	<150	86 (33–122)	10 (10)	10 (10)	10 (8)	3.68 (0.27)	7967 (781.2)	0.52	0.22	0.93

Note: Site characteristics include elevation (Elev.), modelled site climate moisture deficit (CMD; 1980–2010 normals Wang et al., 2012.) stand basal area (BA; estimated by averaging estimates of basal area at each sampled tree), estimated stand initiation (<150 or >150 years; based on tree ages in Figure S1). Tree characteristics include diameter at breast height (DBH mean and (range)) and number of sampled (and successfully crossdated trees) by tree health status group (healthy, unhealthy, dead). Descriptors of ring width chronologies (1975–2020) include ring width (RW mean (standard error)), basal area increment (BAI mean (standard error)), mean series intercorrelation (MSI), series mean first-order autocorrelation (AR1), and expressed population signal (EPS).

Abbreviations: BW, Barlow Wayside; HG, Hobo Grove; IC, Icicle Creek; LI, Lindsey; LM, Little Mountain; MP, McCroskey Park; MR, Mount Richmond; RF, Ramirez Farm; RG, Roosevelt Grove; SL, Slate; TR, Trillium.
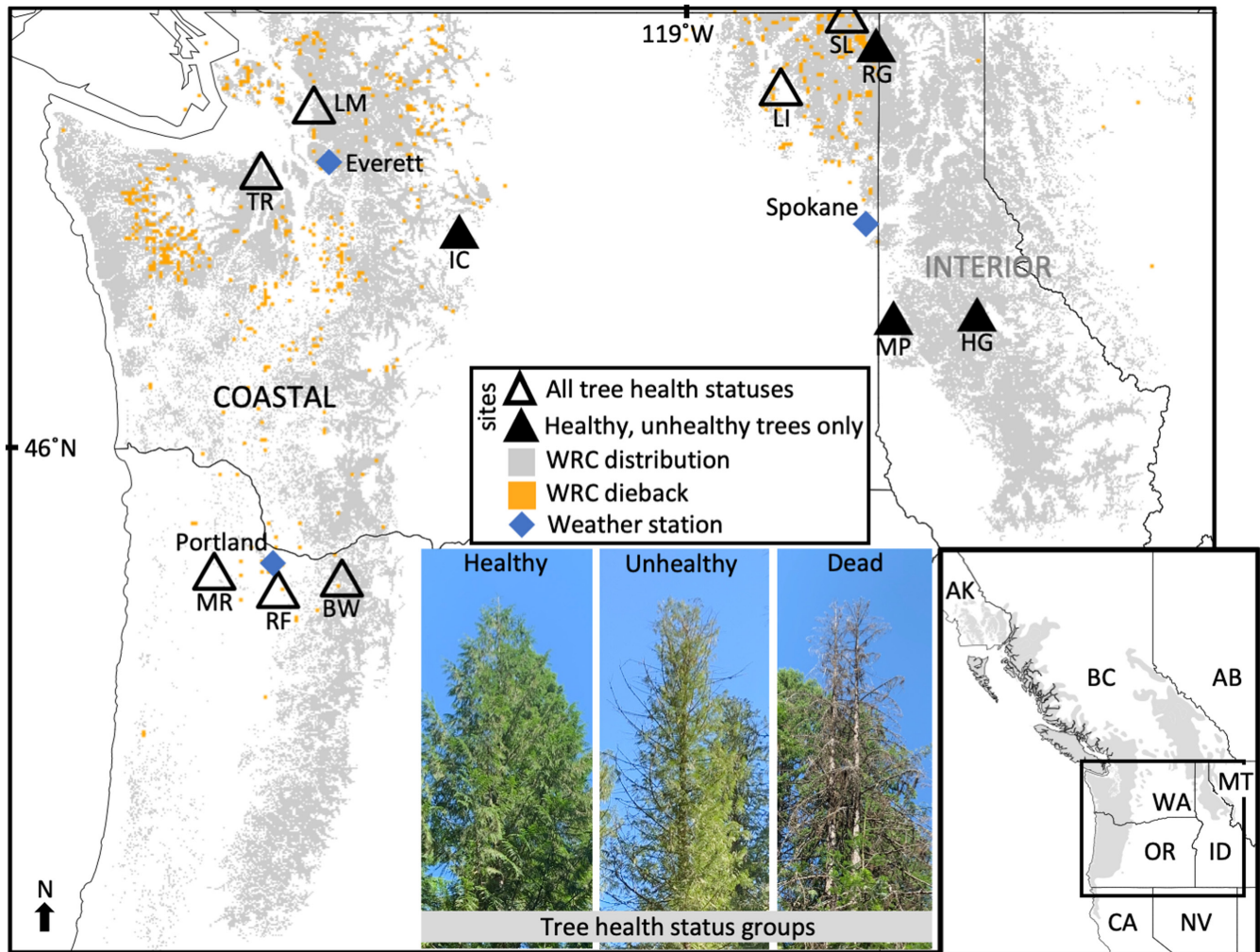
FIGURE 1 Locations of the 11 sampled sites (triangles) with western redcedar dieback and mortality (orange; USDA Forest Service 2021) within the modelled distribution of western redcedar (grey; *Thuja Plicata*; Ellenwood et al. 2015) in the northwestern United States (map, Mercator projection) and western North America (map inset, Mercator projection; Little 1971)). Photos show examples of trees in three tree health status categories: healthy (<40% canopy dieback), unhealthy (>40% and <100% canopy dieback) and dead (no green canopy).

year (October–September) from 1900 to 2020 ('spei' package in R; Beguería & Vicente-Serrano, 2017) using monthly precipitation and air temperature (PRISM, 2022). SPEI is a widely used multiscalar drought index representative of soil moisture availability. To assess the possible influence of weather conditions on tree mortality, we downloaded instrumental daily weather data for three representative locations in the study area (Figure 1), including Everett, WA (USW00024222), Spokane, WA (USW00024157), and Portland, OR (USW00024229; NOAA, 2022). We computed two weather indices expected to affect tree mortality by month from May to September (1970–2020): (1) maximum temperature index (MTI; the number of days that monthly maximum daily air temperature exceeded the 90th percentile) and (2) dry period index (DPI; the longest consecutive period of days with <1.0 mm of precipitation).

2.5 | Statistical analysis

2.5.1 | Tree radial growth preceding tree death and during canopy dieback (Question 1)

We expected that unhealthy and dead trees would experience several years of reduced tree growth prior to death or 2020 (the last full ring sampled from unhealthy and healthy trees) compared to healthy trees. We calculated the annual growth ratio (30 most recent years) for co-located pairs of (1) dead and healthy and (2) healthy and unhealthy trees in each site (Cailleret et al., 2017). Ratios were calculated annually per tree pair by dividing a dead or unhealthy tree's BAI by the paired healthy tree's BAI. Annual growth ratios less than one indicate that healthy trees grew more in that year than dead or unhealthy trees. In the field, we matched trees of similar size to control

for size effects on tree growth. The DBH of the healthy trees was within 7 cm DBH of the unhealthy or dead tree to maximise available samples for each pair (41 tree pairs for dead-healthy and 56 tree pairs for unhealthy-healthy). As annual growth ratios were similar among sites within populations, we computed and present population averages and 95% confidence intervals of annual growth ratios for interior and coastal populations ('boot' package in R; Canty & Ripley, 2022).

2.5.2 | Tree radial growth response to interannual climate variability (Question 2)

We expected that reduced radial growth would be correlated with below-average soil moisture availability during the growing season as indicated by low spring and summer precipitation and high spring and summer temperature (Brubaker, 1980) and that radial growth of unhealthy and dead trees would be more strongly related to climate variability than healthy trees (Cailleret et al., 2019). Because warming and overall atmospheric aridity trends increased significantly across the western US, including the PNW, starting in the year 2000 (e.g. Abatzoglou & Williams, 2016), we conducted separate correlation function analyses for two periods, 1975–1999 and 2000–2020. The effects of period of analysis and tree health status had negligible effects on climate-growth relationships for either period (Figures S3–S7) and were excluded from further analysis. We tested correlations from 1975 to 2020 between tree-ring site chronologies (all tree health status groups; 'treeclim' package in R; (Zang & Biondi, 2015)) and three site climate variables: (1) monthly maximum air temperature, (2) monthly total precipitation, and (3) monthly SPEI. Correlations were tested from April of year prior to ring formation (lagged effects) to September of ring formation year. To focus on regional response of growth to climate, we only interpret statistically significant results ($\alpha = 0.05$) for multiple sites in the same month.

2.5.3 | Tree radial growth response to drought events (Question 3)

We expected that warmer/drier climate conditions in the post-drought period (3 years) would increase the time required to reach pre-drought growth rates and reduce post-drought compared to pre-drought growth rates (i.e. resilience; Lloret et al., 2011), especially for unhealthy and dead trees (i.e. differential post-drought resilience; DeSoto et al., 2020). For each site, we compared radial growth responses to two exemplary drought years from 1975 to 2015 (period with >5 samples in each tree health status group per site, Figure S1). We defined drought years as May–June SPEI < −1.0 based on the important influence of May–June SPEI on annual tree radial growth on both populations (see results for Question 2). While both drought years had similar pre-drought and drought year May–June SPEI, post-drought conditions were warm/dry or cool/wet (Figures S8 and S9). We selected the 2015 regional drought year (lowest or second lowest May–June SPEI from 1975 to 2020 for all sites), which was followed by

three years of warm/dry conditions in spring and summer (i.e. multi-year drought; Figures S8 and S9). For the second drought year, we selected a site-specific drought year based on the lowest May–June SPEI (other than 2015) from 1975 to 2014. These site-specific drought years all occurred prior to 2004 and were followed by 3 years of notably cooler/wetter conditions in spring and summer (i.e. single-year drought; see Figure S8 for drought years by site).

To characterise radial growth responses to drought events, we extracted three growth metrics from each tree's detrended ring-width index to calculate four resilience indices (Lloret et al., 2011; Schwarz et al., 2020; Thurm et al., 2016). For each tree, the growth metrics were as follows: *Dr* was the mean annual growth during the drought year, *PreDr* was the mean annual growth for the 3 years before the drought year, and *PostDr* was the mean annual growth for the 3 years after the drought year. For trees that died less than 3 years after the drought year, we calculated PostDr from the years prior to death, excluding partial rings. We also recorded the number of years post-drought required to return to *PreDr*. For each tree and drought event, we computed the following resilience indices:

1. Resistance (Rt) = $Dr/PreDr$.
2. Recovery (Rc) = $PostDr/Dr$.
3. Recovery period (Rp) = Number of years post-drought required to reach pre-drought growth rates.
4. Resilience (Rs) = $PreDr/PostDr$.

The three-year period for the resilience indices was based on the average length of the recovery period when drought was followed by cool/wet conditions. Unhealthy and healthy trees (57% or 107 of 189 trees) that were still in their recovery period from the 2015 drought year in 2020 (last full ring) were assigned a recovery period of 6 years (i.e. the minimum period for recovery).

We tested for differences in radial growth responses to warm/dry and cool/wet post-drought climate conditions by tree health status and population using linear mixed models (LMM; Pinheiro et al., 2022) for each of four resilience indices (response variables). We included the following predictor variables: drought year (drought occurring prior to 2004 with cool/wet post-drought conditions or 2015 drought with warm/dry post-drought conditions), tree health status, population, the interaction between drought year and tree health status, and the interaction between drought year and population. We included a random effect of trees within site to account for repeated measures of individual trees in two droughts and potential differences among sites in resilience indices. Model residuals were checked, and model fit was assessed using the conditional and marginal r^2 ('MuMin' package in R; Bartoń, 2018).

2.5.4 | Effect of climate and weather variability on tree mortality (Question 4)

To assess whether WRC tree mortality corresponded with warm/dry spring and summer climate and weather conditions, we graphically

compared annually resolved dates of WRC tree mortality to climate (SPEI) and daily weather indices (DPI and MTI) from 1970 to 2020. For SPEI, we selected May to September SPEI for coastal populations and August to September SPEI for interior populations after comparing monthly and water year SPEI (1970–2020) to mortality years (Figure S10).

3 | RESULTS

3.1 | Tree radial growth preceding tree death and during canopy dieback (Question 1)

Trees that died (dead) and partial canopy dieback trees (unhealthy) experienced a period of reduced radial growth prior to death or 2020, respectively, compared to healthy trees (Figure 2; Figures S11 and S12). Average annual growth ratios of dead trees' BAI (compared to healthy trees') were notably lower for 4 years (interior) and 5 years (coastal) prior to tree death (95% confidence interval <1.0; Figure 2a), with similar annual growth ratios for the prior ca. 25 years (−30 to −5 years). The timing and duration of the reduction in annual growth ratios of dead compared to healthy trees was highly variable among individuals but consistent within populations (Figures S11 and S12). Radial growth of dead trees was lowest in the last full year of growth, with an average reduction in annual growth ratios of 112% in interior (range in individuals, 0–262%) and 78% in coastal populations compared to healthy trees (range of individuals, 96–191%; Figure 2; Figure S12). Findings for unhealthy/healthy tree pairs were similar to dead/healthy pairs in coastal populations, that is the lowest annual growth ratio in 2020 (68%; range in individuals, 90–248%), while tree pairs in interior populations showed no difference by site (e.g. MP, HG; Figure S12) or more modest (ca. 40%) reductions in growth of unhealthy compared to healthy trees (e.g. Figure 2b, SL, RG; Figure S12).
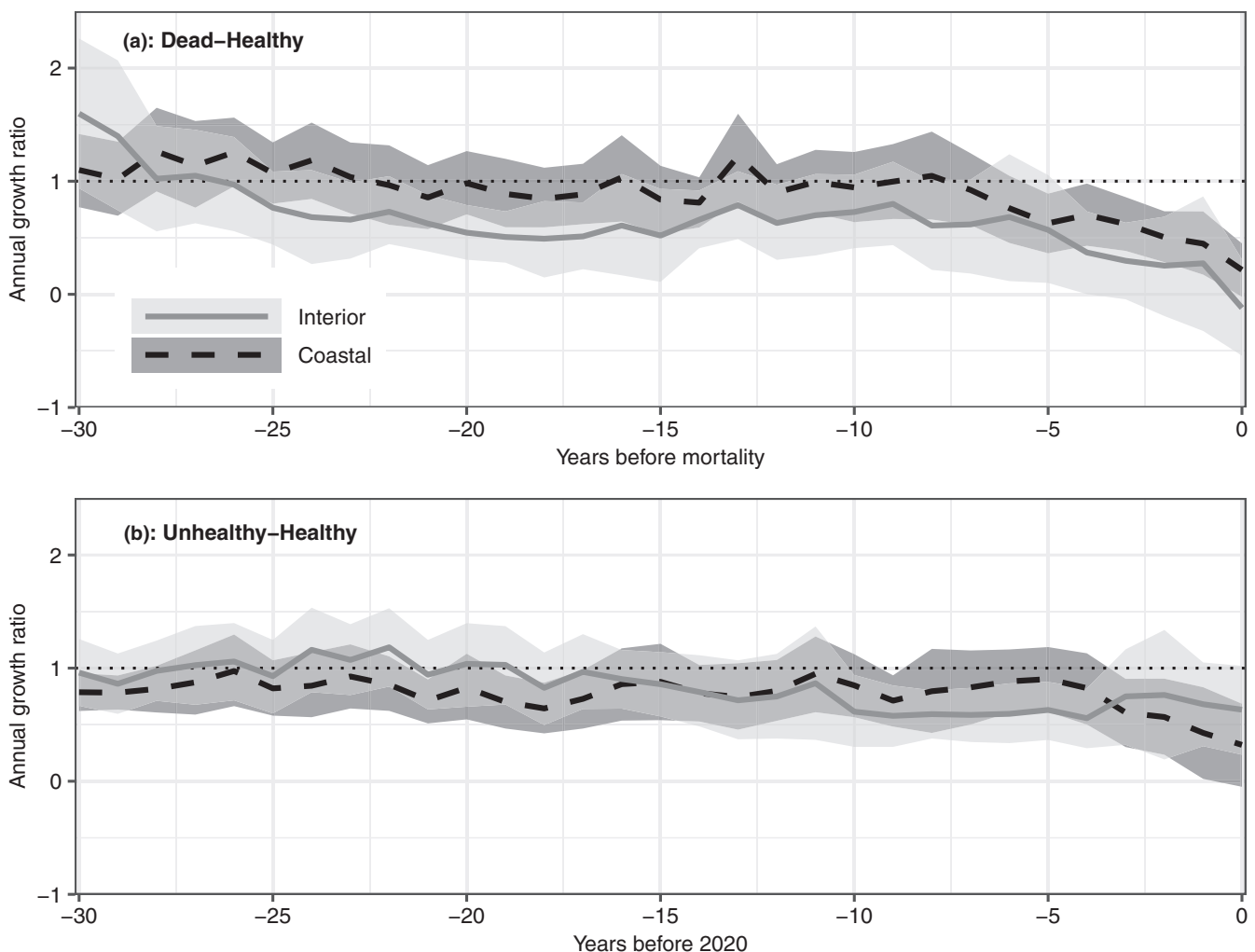

FIGURE 2 Annual growth ratios for (a) dead-healthy tree pairs (7 sites; 41 tree pairs) and (b) unhealthy-healthy tree pairs (9 sites; 56 tree pairs) computed from the most recent 30 years of western redcedar tree growth (basal area increment) in the northwestern United States. The grey and dashed black lines are the means, and the light and dark grey shaded ribbons are the 95% confidence intervals of all trees in the interior and coastal populations, respectively. An annual growth ratio significantly less than one indicates that healthy trees grew more than their paired, co-located dead or unhealthy trees in that year (or the opposite, if ratio >1).

3.2 | Tree radial growth response to interannual variability in climate (Question 2)

Tree-ring chronologies were relatively well correlated from 1975 to 2020 for all site pairs in coastal populations on the westside of the Cascade Mountains (Spearman's rho >0.36, $p<0.01$ for 'all trees' in coastal sites except IC) and for sites in interior populations (Spearman's rho >0.30, $p<0.05$ for 'all trees' in interior sites; Figures S2 and S13).

Tree ring chronologies were also correlated to the interannual variability in monthly maximum temperature, total precipitation, and SPEI for some months from April of the year prior to ring formation to September of the growth year (1975–2020; Figure 3). In coastal populations, radial growth in three or more sites increased under the following conditions: cooler maximum June temperatures in the growth year ($p<0.05$ for 3 of 6 sites), higher total May or June precipitation in the growth year ($p<0.05$ for 6 of 6 sites), and higher May or June SPEI in growth year ($p<0.05$ for 6 of 6 sites; Figure 3). In interior populations, the two high-elevation sites with lower climate moisture deficits were relatively unaffected by interannual climate variability (1 of 54 and 2 of 54 correlation tests with $p<0.05$ at HG and RG, respectively). In the remaining three interior sites (SL, LI, MP), radial growth increased under the following conditions: warmer January maximum temperatures in growth year ($p<0.05$ for 3 of 3 sites), higher June SPEI in growth year ($p<0.05$ for 2 of 3 sites), higher July SPEI in year prior to ring formation ($p<0.05$ for 2 of 3 sites) and lower SPEI in November prior to ring formation ($p<0.05$ in 2 of 3 sites).
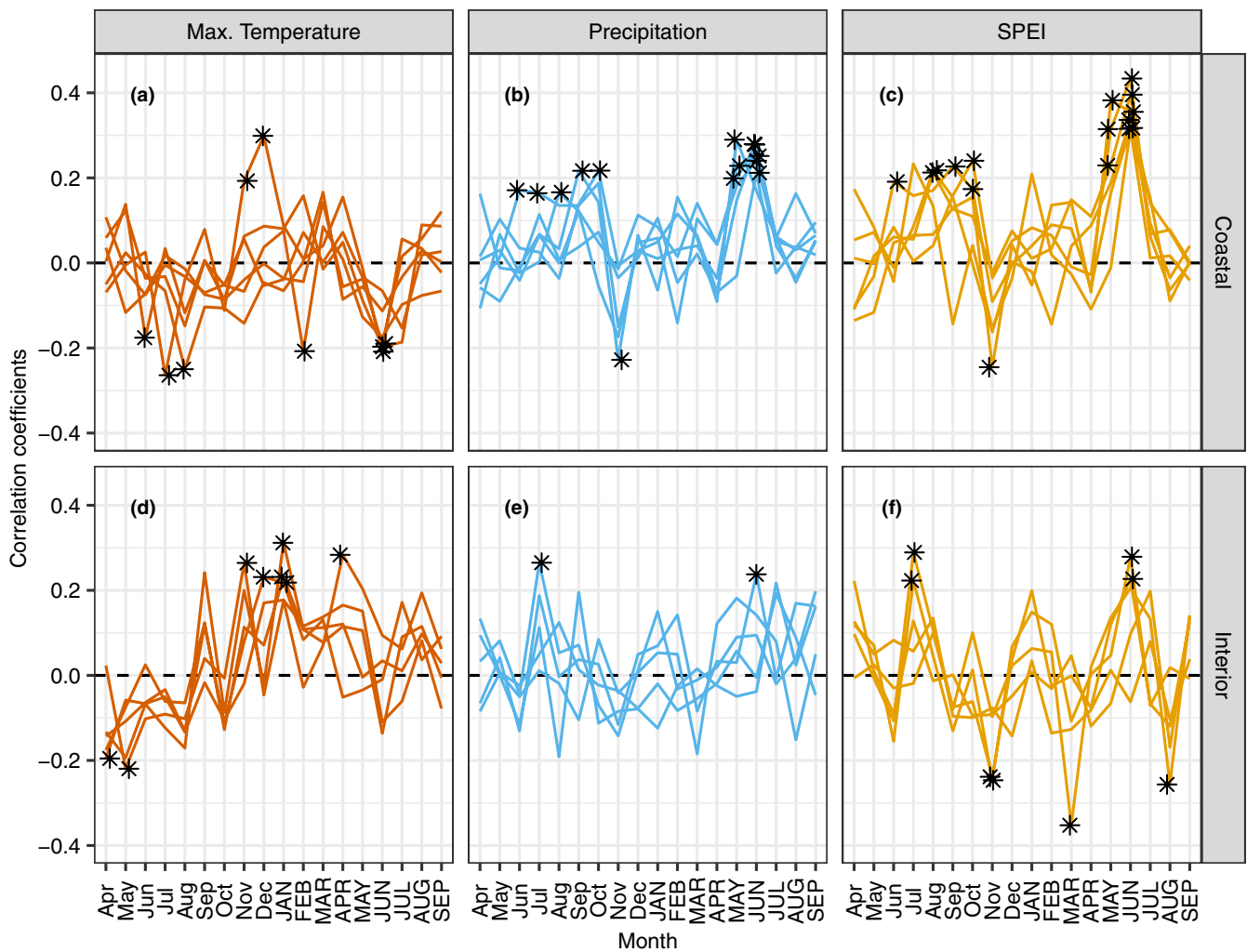

FIGURE 3 Correlation coefficients between the site tree ring chronologies and monthly climate variables from 1975 to 2020 for coastal and interior populations of western redcedar in the northwestern United States. Climate variables included monthly (a, d) maximum temperature, (b, e) total precipitation, and (c, f) Standardised Precipitation Evaporation Index (SPEI) from the year prior to growth (lower case) to the growth year (upper case). Positive values of SPEI indicate cooler, wetter conditions and negative values indicate warmer, drier conditions. Stars indicate significant relationships ($p<0.05$). See Figures S3–S5 for negligible effect of tree health status group on climate-growth relationships.

3.3 | Tree radial growth response to drought events (Question 3)

For trees in all health status groups, annual growth rates were 12.6% (mean, SE 1.1%) lower during the two drought years by site compared to the average of the prior 3 years (i.e. resistance index, Rt; Figure 4a,b). The resistance index (Rt) LMM did not indicate differences in resistance by drought year, tree health status, population or the interaction of drought year and tree health status (Table 2). In contrast, WRC trees in the interior population were notably more resistant to the 2015 drought (mean growth reduction −8.3%, SE 1.9%; Figure 4b) than trees in the coastal population (mean −20.2%, SE 1.5%; Figure 4a), as demonstrated by the Rt LMM ('Population (interior)*Drought yr. (2015)' variable in Rt model, Table 2). However, the 2015 drought was also slightly less severe at sites in the interior population (May–June SPEI median −1.37) compared to the coastal population (median −1.82; Figure S9).

The recovery period, recovery index and resilience index all indicated slower recovery of growth rates when the post-drought period was warm/dry (2015 drought) compared to cool/wet (site specific drought year; 'Drought (2015)' variable in Rp, Rc and Rs LMMs, Table 2, Figure 4c–h). For example, the time required to return to pre-drought growth rates (i.e. recovery period) was significantly longer when post-drought conditions were warm/dry (mean 3.6 years, SE 0.2) compared to cool/wet (mean 2.6 years, SE 0.2) for interior and especially coastal populations ('Drought (2015)' variable; Table 2). However, there were important differences by tree health status and population. Trees that died following the 2015 drought recovered more rapidly during cool/wet post-drought conditions and more slowly during warm/dry post-drought conditions compared to unhealthy and healthy trees ('Drought (2015)*Status (dead)' variable in Rc LMM; Table 2). Additionally, growth rates of trees in interior populations were more resilient to droughts than those in coastal populations, especially when drought was followed by warm/dry conditions ('Population (interior)' and 'Population (interior)* Drought (2015)' variables in Rs LMM, Table 2).

3.4 | Effects of climate variability on tree mortality (Question 4)

In coastal populations, 80% of sampled WRC tree mortality occurred in 2017 or 2018, though mortality occurred in all years from 2015 to 2020 (Figure 5d). Years with WRC tree mortality in coastal populations occurred during exceptionally warm/dry climate conditions as indicated by May to September SPEI of −1.5 in 2015, −0.6 in 2016, −1.0 in 2017 and −1.8 in 2018 (Figure 5a) and confirmed by daily weather conditions (Figure 5b,c). From 1970 to 2020, the MTI indicated exceeding hot conditions in 2015 and 2018 (Figure 3b) and the DPI indicated the longest dry periods in 2017 (Everett, WA) or 2018 (Portland, OR; Figure 5c). Mortality in coastal populations occurred during the same years as exceptionally hot/dry summer conditions (2017, 2018) which was preceded by exceptionally warm/

drier conditions in 2015 and 2016. During the years with WRC tree mortality, October to September was average to cooler/wetter (SPEI mean 0.46, range −0.68-1.31; Figure S10).

In interior populations, intermittent, low-level mortality (1–3 sampled trees per year) was reconstructed since the late 1980s, but the majority (57%) of sampled WRC tree mortality occurred from 2012 to 2018 (Figure 5d). Years with WRC tree mortality were warmer/drier from August to September as evidenced by SPEI < −0.9 for 7 of 9 mortality years (Figure 5; Figure S10). Daily weather conditions indicated that most mortality years (7 of 9) co-incided with warmer/drier than average conditions from May to September (Spokane; Figure 5b,c), as evidenced by the MTI (mean 13 days) and DPI (mean 38 days) above their respective mean during mortality years from 1970 to 2020 (Figure 5b,c). Climate conditions from October to September during the years with mortality were warmer/drier (4 of 9 years; Figure S10), but also cooler/wetter (5 of 9 years).

4 | DISCUSSION

We found that trends in radial growth corroborated the reported decline in canopy condition of WRC trees (Figure 1) and indicated a period of reduced growth prior to mortality that varied by population (Figure 2). Radial growth sensitivity to the interannual variability climate (Figure 3) and resilience to drought events (Figure 4) further implicate warm/dry conditions as likely agents of increased physiological stress. Indeed, multiple consecutive years (2015–2018) of anomalously warm/dry summer conditions were associated with WRC tree mortality in coastal populations and most mortality in interior populations (Figure 5). By investigating the varied responses of WRC tree growth and canopy dieback to climate variability, our findings offer insightful cues for understanding the implications of climate change for an iconic PNW species.

As expected, tree death was portended by several years of radial growth decline that culminated in the lowest growth the year prior to death relative to neighbouring healthy trees, a new finding for WRC trees. Reductions in tree growth in association with canopy dieback can be a key indicator of unrepairable hydraulic failure and a higher likelihood for mortality (Bigler & Bugmann, 2004; Klesse et al., 2022). Similar reductions in radial growth prior to death were also observed for many other gymnosperms, including Alaskan cedar (*Callitropsis nootkatensis*; Comeau et al., 2019), though the period and magnitude of decline varies widely by species (Cailleret et al., 2017). WRC trees with partial canopies and trees that died endured from multiple decades to just a few years of reduced tree growth (relative to comparable surviving trees), suggesting no evidence for a single regional climate event as the 'inciting' factor for mortality during the 2015–2019 period. Assessment of the interannual variability in growth prior to death by site, coupled with eco-physiological measurements, for trees that survived and died may produce more accurate predictors of future tree mortality than the timing of tree growth decline (Cailleret et al., 2019).
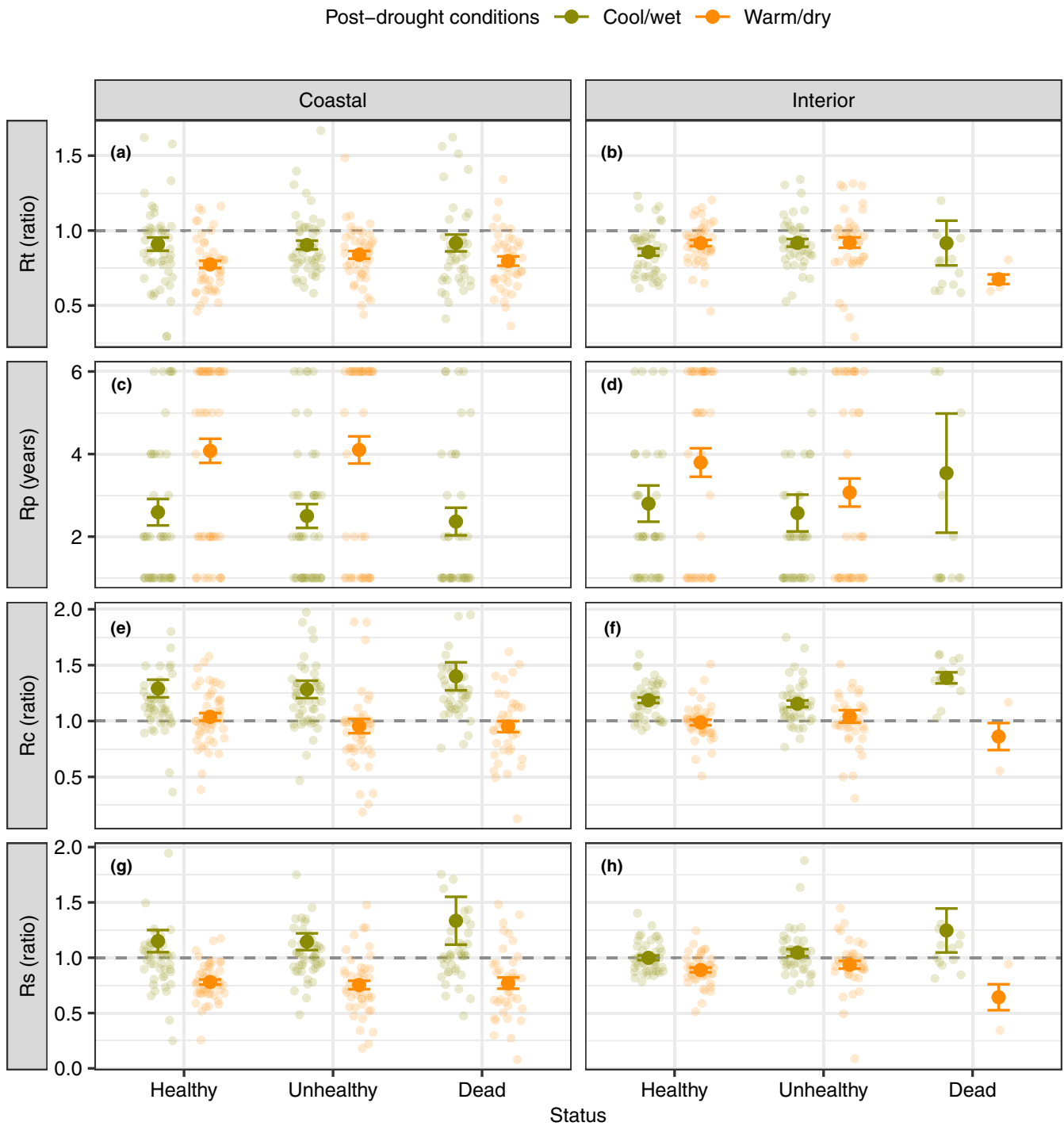
FIGURE 4 Mean (standard error) of four resilience indices characterizing the response of radial growth to drought years with warm/dry (multi-year summer drought starting in 2015; orange) or cool/wet (site specific single-year summer drought; green) post-drought conditions by tree health status group for coastal and interior populations of western redcedar in the northwestern United States (see Table S3 for statistically significant differences among populations and tree health status groups). Pre-drought climate conditions and drought severity were similar for both drought years (Figure S8). The resistance index (Rt) is the annual growth during the drought year divided by the average of growth in the 3 years pre-drought. The recovery period (Rp) is the number of years necessary post-drought to return to the average of growth in the 3 years pre-drought. The recovery index (Rc) is the average of growth 3 years post-drought divided by annual growth during the drought year. The resilience index (Rs) is the average of growth in the 3 years pre-drought divided by the average of growth in the 3 years post-drought.

Our findings that drier/warmer conditions in May/June reduced tree growth (9 of 11 sites; Figure 3) and slowed recovery from drought (Table 2; Figure 4) in coastal and interior populations addresses key uncertainties about the response of WRC

TABLE 2 Summary of four linear mixed effects models for resistance index (Rt), recovery period (Rp), recovery index (Rc), and resilience index (Rs) of western redcedar radial growth in the northwestern United States.

Response	Predictor	β	SE	DF	t	p	SD (residual)
Rt							
Fixed	Intercept	0.83	0.03	229	27.03	**<0.01**	
	Drought (2015)	−0.02	0.02	201	−0.86	0.39	
	Status (dead)	−0.04	0.03	229	−1.31	0.19	
	Status (unhealthy)	0.03	0.03	229	1.19	0.24	
	Population (interior)	0.06	0.04	9	1.44	0.18	
	Drought (2015)×Status (dead)	0.03	0.04	201	0.65	0.52	
	Drought (2015)×Status (unhealthy)	0.00	0.04	201	0.04	0.97	
	Population (interior)×Drought (2015)	0.10	0.03	200	2.93	**<0.01**	
Random	Site						0.06
	Tree/site						0 (0.17)
Trees/sites	242/11						
R^2m/R^2c	0.05/0.15						
Rp							
Fixed	Intercept	2.85	0.35	179	8.07	**<0.01**	
	Drought (2015)	1.23	0.35	179	3.55	**<0.01**	
	Status (unhealthy)	−0.21	0.35	177	−0.60	0.55	
	Population (interior)	−0.20	0.41	9	−0.47	0.65	
	Drought (2015)×Status (unhealthy)	−0.16	0.49	179	−0.32	0.75	
	Population (interior)×Drought (2015)	−0.85	0.49	178	−1.74	0.08	
Random	Site						0.56
	Tree/site						0 (0.23)
Trees/sites	189/11						
R^2m/R^2c	0.06/0.11						
Rc							
Fixed	Intercept	1.16	0.03	228	38.02	**<0.01**	
	Drought (2015)	−0.15	0.03	183	−4.75	**<0.01**	
	Status (dead)	0.09	0.04	228	2.44	**0.02**	
	Status (unhealthy)	0	0.03	228	0.03	0.98	
	Population (interior)	0.02	0.03	9	0.46	0.66	
	Drought (2015)×Status (dead)	−0.15	0.05	183	−2.72	**0.01**	
	Drought (2015)×Status (unhealthy)	−0.05	0.04	183	−1.13	0.26	
	Population (interior)×Drought (2015)	−0.02	0.04	182	−0.47	0.64	
Random	Site						0.04
	Tree/site						0 (0.20)
Trees/sites	242/11						
R^2m/R^2c	0.20/0.23						
Rs							
Fixed	Intercept	0.94	0.02	228	39.82	**<0.01**	
	Drought (2015)	−0.14	0.03	178	−5.3	**<0.01**	
	Status (dead)	0.06	0.03	228	1.67	0.10	
	Status (unhealthy)	0.03	0.03	228	1.25	0.21	
	Population (interior)	0.07	0.02	9	3.06	**0.01**	
	Drought (2015)×Status (dead)	−0.05	0.05	178	−1.1	0.27	
	Drought (2015)×Status (unhealthy)	0.00	0.04	178	−0.11	0.91	
	Population (interior)×Drought (2015)	0.11	0.04	177	3.13	**<0.01**	

(Continues)

TABLE 2 (Continued)

Response	Predictor	β	SE	DF	t	p	SD (residual)
Random	Site						0.02
	Tree/site						0.04 (0.17)
Trees/sites	241/11						
R^2m/R^2c	0.19/0.23						

Note: For fixed effects, values are estimates of coefficients (β), standard error (SE), degrees of freedom (DF) and *p*-values (*p*). For random effects, values are standard deviations (SD) of intercept and residual error. The following predictors were tested: tree health status group (healthy, unhealthy, dead), drought (2015 drought with warm/dry post-drought conditions or single-year drought with cool/wet post-drought conditions), WRC tree population (interior or coastal), the interaction between tree health status group and drought, and the interaction between drought and population. $p < 0.05$ were considered statistically significant (bold).

tree growth to climate, with direct implications for carbon sequestration. The amount of precipitation and the temperatures in May and June likely regulates the availability of soil moisture for photosynthesis, carbon gain, and radial growth during the growing period (mid-May to mid-July) and the rate that soil moisture is depleted during the subsequent dry period from July to September (Baker et al., 2019). Higher precipitation and cooler conditions in May and June prolong the period of ample soil moisture for tree growth further into the summer months, whereas warm/dry climate conditions in May and June increases the length of the summer soil moisture drought, potentially increasing tree stress and susceptibility to canopy dieback and mortality. In summary, our finding for WRC trees, that growth is limited by late spring and early summer moisture availability, is consistent with findings from coastal populations of WRC trees in southern British Columbia, Canada (Seebacher, 2007; Walters & Soos, 1963) and multiple other conifer species in the PNW region, such as western hemlock (Brubaker, 1980; Nakawatase & Peterson, 2006).

Most WRC trees (>65%) in our study were still in the process of recovering radial growth from the 2015 drought when two consecutive years of warmer, drier late spring and summer climate conditions occurred in 2017 and 2018 (i.e. compounded drought; Peltier et al., 2016). Consequently, radial growth rates required longer to recover (Rp) and were notably less resilient (Rs) when drought was followed by warm/dry (2015 drought) compared to cool/wet conditions (Table 2). WRC trees close their stomata to limit water loss during periods of low soil moisture availability (Grossnickle et al., 2005) and are more vulnerable to cavitation for some organs (e.g. branches) and can have smaller root systems than co-occurring species (e.g. Douglas-fir; Mcculloh et al., 2014). Warm and dry conditions during the recovery period may have slowed recovery of water transport capacity (due to cavitation) and lengthened the period of stomatal closure, thereby lowering photosynthesis and reducing carbon gain, as has been observed for other conifers (Brodribb & Cochard, 2009; Trugman et al., 2018).

Our findings support the hypothesis that populations exposed to moderate climate conditions (coastal) are more susceptible to changes in climate than those populations adapted to more variable, continental climate (interior; Bonebrake & Mastrandrea, 2010). Compared to coastal populations, radial growth rates of WRC trees in interior populations were more resistant and resilient to drought

(Figure 4; Table 2), though drought severity was slightly lower at sites in interior populations in 2015 (Figure S9). The higher growth resistance of WRC trees in interior relative to coastal populations is consistent with their greater water use efficiency and drought tolerance, specifically osmotic potential and relative water content at turgor loss point (Grossnickle & Russell, 2010). North to south within WRC populations, genetic variation is minimal (Shalev et al., 2022). However, differences between populations in their physiological and growth response to drought may indicate that interior populations are better adapted to continued warming and drying summer conditions and may be a potential source for seeds for assisted migration of coastal populations (Grossnickle & Russell, 2010). Acclimation in growth and physiological responses to hotter and drier environmental conditions through adjustment in foliar anatomy has also been demonstrated within a WRC population (Tomaszewski, 2022), but the capacity of acclimation and/or adaptation to enable survival of WRC under expected future climate change remains an unresolved question.

Spatial and temporal synchrony in hot/dry conditions and tree mortality over ca. 400 km in 2017 and 2018 in the coastal population is strong evidence that climate was the proximate cause of recent WRC canopy dieback (Figure 5). The hot/dry conditions associated with mortality in both populations likely resulted in low soil moisture availability, high evaporative demand, and a greater chance for hydraulic failure (McDowell et al., 2022). Additionally, favourable climate conditions for growth prior to the 2015–2018 period (multiyear summer drought) may have acclimated hydraulic structures to cool/wet conditions and increased vulnerability to hydraulic failure during the subsequent multi-year summer drought period (i.e. structural overshoot, Jump et al., 2017). Interestingly, the timing and quantity of mortality and the specific climate conditions associated with mortality differed between populations. WRC tree mortality in sampled coastal populations was episodic (80% of dead trees sampled died in 2 years, 2017–2018), whereas mortality in interior populations occurred over a longer period with fewer deaths of sampled trees per year (Figure 5). In coastal populations, WRC tree mortality was associated with anomalously warm/dry late spring and summer climate conditions from 2015 to 2018–including exceedingly high maximum summer temperatures and the longest summer dry period from 1970 to 2020 (i.e. hot drought). Similar warm and dry conditions in consecutive years may not have occurred since the
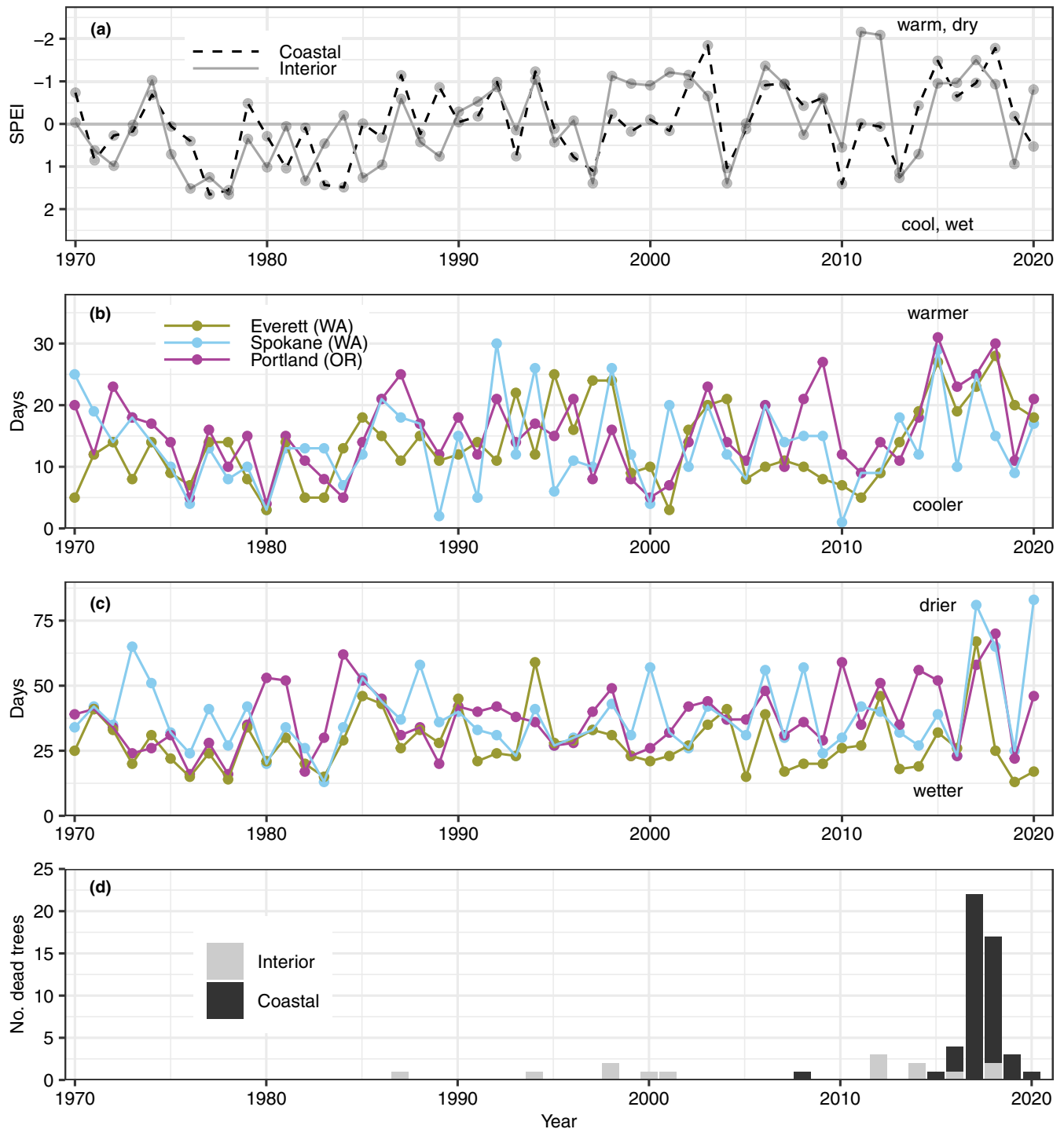
FIGURE 5 (a) Standardised Precipitation Evaporation Index (SPEI) averaged for individual years from 1970 to 2020 by sites in interior (dashed black, August–September SPEI) and coastal (solid black May–September SPEI) western redcedar populations (y-axis is inverted) in the northwestern United States. (b) The Maximum temperature index (MTI) or the number of days maximum monthly temperature exceeded the 90th percentile (May–September) at three weather stations with long-term climate data near the study sites (Figure 1). (c) The dry period index (DPI) or the longest consecutive period of days with <1.0 mm of precipitation (May–September). (d) The number of dead trees by site and year from 1970 to 2020.

1930s (as indicated by SPEI, Figure S8), and nearly all dead WRC trees that we sampled in coastal populations likely germinated after the 1940s (Figure S1) or were shaded by overstory trees during the 1930s warm/dry period. In interior populations, WRC tree mortality

was limited but associated with warm/dry conditions in late summer (August to September). In summary, WRC trees appear vulnerable to widespread mortality from multiple, consecutive years of extended hot/dry summer conditions.

In the context of climate change, our results indicate that seasonal rather than annual shifts in temperature and precipitation may have the greatest effect on WRC tree growth and dieback. Projected decreases in summer precipitation (Mote & Salathé, 2010) would reduce growth of WRC trees in lower elevations in both populations (present study) and in high elevation habitats in the Cascade Mountains (Ettinger et al., 2011). However, of greatest concern for the persistence of WRC trees and possibly other co-occurring species is the increasing trend in growing season climate water deficits, decreasing trend in summer soil moisture availability, and the forecasted increase in the annual maximum consecutive days with <3 mm of precipitation of nine additional days by mid-century in the PNW region (Kunkel et al., 2013; Rogers & Mauger, 2021). Such conditions were associated with recent WRC tree dieback in lower elevation habitats in interior and coastal population (Figure 5). WRC tree dieback may be a 'canary in the forest' as dieback of three common associates (western hemlock, Douglas-fir, grand fir, and bigleaf maple) in the last decade and over a smaller area than WRC dieback may also be related to unfavourable climate conditions (WA DNR, 2020, Betzen et al., 2021; but see Bennett et al., 2023). For WRC trees, our results imply that more frequent warmer/drier summer climate conditions would further reduce tree growth and elevate the risk of canopy dieback.

Our findings need to be considered in the context of where we sampled. In coastal populations, recent WRC dieback was observed and sampled in low elevation, warmer/drier forests with relatively young WRC trees (<150 years; except IC site). Wetter locations that we explored (e.g. Cascade and Olympic Mountains, coastal temperate rainforest) had old, partial canopy dieback (e.g. spike tops), but no evidence of dieback in the last two decades and we did not sample these areas. In interior populations, we sampled lower and higher elevation sites with younger (<150 years) and older WRC trees (>150 years), but a relatively small sample size of dead trees. Further research is needed that explores how WRC tree- (e.g. tree size, age and height as well as root pathogens) and stand-scale (e.g. tree density, soils, topography and location within the distribution of WRC) factors may increase vulnerability to dieback (Hennon et al., 2020).

5 | CONCLUSION

By exploring WRC as a 'canary in the forest', our findings are an early warning that warming climate and multi-year hot droughts during the summer will likely increase the vulnerability of WRC trees, and possibly accompanying shade-tolerant species, to canopy dieback. Global syntheses of tree mortality indicate no or very few tree mortality events from hot droughts in the PNW, and we show a direct effect of climate and weather on tree mortality in low elevation, mesic forests in the PNW region in the absence of fire or primary biotic mortality agent. Continued loss of WRC trees

may shift tree species composition to species more tolerant of current and future climate conditions, such as Douglas fir. In the context of adapting forests to future climate conditions, WRC trees in the interior population appear more drought-resistant and less vulnerable to widespread, episodic canopy dieback than coastal populations. Selecting seeds from provenances or genotypes in interior populations may help sustain WRC trees in coastal populations and assist with migrating WRC trees to match the rapid changes in global climate.

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BIOSKETCH

Robert Andrus studies climate effects on forest demographic processes and disturbance ecology in the western US. This work is a product of his postdoctoral research at the Washington State University and includes collaborators from local universities and state and federal agencies.

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SUPPORTING INFORMATION

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