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Photoperiod cues and patterns of genetic variation limit phenological responses to climate change in warm parts of species' range: Modeling diameter-growth cessation in coast Douglas-fir

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Abstract

The phenology of diameter-growth cessation in trees will likely play a key role in mediating species and ecosystem responses to climate change. A common expectation is that warming will delay cessation, but the environmental and genetic influences on this process are poorly understood. We modeled the effects of temperature, photoperiod, and seed-source climate on diameter-growth-cessation timing in coast Douglas-fir (an ecologically and economically vital tree) using high-frequency growth measurements across broad environmental gradients for a range of genotypes from different seed sources. Our model suggests that cool temperatures *or* short photoperiods can induce cessation in autumn. At cool locations (high latitude and elevation), cessation seems to be induced primarily by low temperatures in early autumn (under relatively long photoperiods), so warming will likely delay cessation and extend the growing season. But at warm locations (low latitude or elevation), cessation seems to be induced primarily by short photoperiods later in autumn, so warming will likely lead to only slight extensions of the growing season, "reflecting photoperiod limitations on phenological shifts. Trees from seed sources experiencing frequent frosts in autumn or early winter tended to cease growth earlier in the autumn, potentially as an adaptation to avoid frost. Thus, gene flow into populations in warm locations with little frost will likely have limited potential to delay mean cessation dates because these populations already cease growth relatively late. In addition, data from an abnormal heat wave suggested that very high temperatures during long photoperiods in early summer might also induce cessation. Climate change could make these conditions more common in warm locations, leading to much *earlier* cessation. Thus, photoperiod cues, patterns of genetic variation, and summer heat waves could limit the capacity of coast Douglas-fir to extend its growing season in response to climate change in the warm parts of its range.

KEYWORDS

cambial growth, climate change, day length, diameter growth, genecology, phenology, *Pseudotsuga menziesii* var. *menziesii*, secondary growth

1 | INTRODUCTION

An organism's phenology allows it to align periods of physiological activity with favorable climatic conditions and impacts individual fitness, species distributions, interspecific interactions, community assembly, and ecosystem function (Chuine, 2010; Forrest & Miller-Rushing, 2010; Richardson et al., 2013; Wolkovich & Cleland, 2014). The relationships between phenology and climate will therefore mediate the impacts of climate change on a wide range of ecological processes. In temperate and boreal trees, numerous efforts have documented and modeled the effects of climate on spring budburst (e.g., Cannell & Smith, 1983; Hänninen & Kramer, 2007; Harrington, Gould, & St. Clair, 2010; Laube et al., 2014; Polgar & Primack, 2011; Romberger, 1963; Sarvas, 1974; Vegis, 1964) and have illuminated how this particular phenological event might mediate climate change impacts on trees in important and sometimes surprising ways (e.g., Cannell & Smith, 1986; Chuine, 2010; Hänninen, 2006; Harrington & Gould, 2015). However, phenological events associated with the end of the growing season in the autumn and events associated with organs other than buds have received far less attention despite their similar degree of importance for trees and forests (Delpierre et al., 2016; Gallinat, Primack, & Wagner, 2015; Hänninen, 2016; Rossi et al., 2016).

In particular, the cessation of tree diameter growth in the autumn is a phenological event that has large impacts on individual performance and forest ecosystem function, but is very poorly understood. The timing of diameter-growth cessation helps determine the length of the growing season, the ability of trees to repair and expand vascular connections between roots and leaves, wood properties, ecosystem productivity, and rates of carbon sequestration. In models of tree and ecosystem functioning, this phenological event is depicted in rudimentary ways due to lack of data, poor understanding of environmental and genetic drivers, and the absence of quantitative models for the cessation process, leading to potentially unrealistic characterizations of how diameter-growth-cessation timing will mediate impacts of climate change on processes such as growth, survival, and net primary production (reviewed by Delpierre et al., 2016). A common expectation is that growth-cessation events will occur later in the year under climate change, a response that would allow trees to extend their growing seasons and take advantage of newly favorable warm conditions in late autumn (e.g., Jeong, Ho, Gim, & Brown, 2011; Menzel & Fabian, 1999; Rossi et al., 2016; Vitasse et al., 2011). But this might not always be the case due to environmental and genetic limitations on the capacity of trees to shift growth-cessation timing to later in the year. Thus, we can gain valuable insight into the impacts of climate change on trees and forests by identifying these limitations and producing robust models of the diameter-growth-cessation process.

Three of the most important unanswered questions about diameter-growth-cessation phenology are as follows: (1) What are the interactive effects of temperature and photoperiod? (2) How does genetic variation influence this event? (3) How might responses to climate change differ across a species' range?

Question 1: Knowing the extent to which diameter-growth cessation is determined by temperature versus photoperiod is critical in determining how this phenological event will shift in the future, because temperatures will likely change drastically while photoperiod will not. The more photoperiod dependent an event is, the more limited an organism will likely be in terms of responding to higher temperatures with phenological shifts (see Körner & Basler, 2010 and response by Chuine, Morin, & Bugmann, 2010). Budburst in temperate and boreal trees is generally more strongly influenced by temperature (both cool temperatures to satisfy chilling requirements and warm temperatures to trigger budburst) than photoperiod, but these sensitivities vary among species and photoperiod effects sometimes become stronger under warmer conditions (i.e., photoperiod may have little effect under cool winter/spring conditions, but under warm conditions, long photoperiods can promote budburst and compensate for low chilling) (Hänninen, 2016; Laube et al., 2014). Low temperatures (Begum et al., 2016; Peltola, Kilpelainen, & Kellomaki, 2002; Rossi, Morin, Deslauriers, & Plourde, 2011) and short photoperiods (Delpierre et al., 2016) have both been posited as cues for diameter-growth cessation, but results from observational studies along elevational gradients are equivocal as to which mechanism predominates (Moser et al., 2010; Oladi, Pourtahmasi, Eckstein, & Braeuning, 2011; Prislan, Gricar, De Luis, Smith, & Cufar, 2013; Takahashi & Koike, 2014). Modeling the joint effects of temperature and photoperiod could help clarify the apparent confusion in the literature, as this interaction is known to be important in determining the timing of bud set and cessation of shoot elongation (Tanino, Kalcsits, Silim, Kendall, & Gray, 2010), and could provide more realistic projections of climate change impacts than approaches focused on one cue or the other.

Question 2: There is often genetic variation in phenological traits along climatic gradients that likely reflects local adaptation (Aitken, Yeaman, Holliday, Wang, & Curtis-McLane, 2008) and can alter phenological responses to climate change in important ways (Alberto et al., 2013; Clark, Melillo, Mohan, & Salk, 2014; Clark, Salk, Melillo, & Mohan, 2014; St. Clair & Howe, 2007). For example, genotypes from seed sources that experience greater summer drought have been observed to burst bud earlier in the spring compared to other genotypes, potentially as an adaptation that allows trees to increase the amount of time spent growing under favorable moist conditions (Gould, Harrington, & St. Clair, 2011; St. Clair, Mandel, & Vance-Boland, 2005). If local populations currently have genetic predispositions toward phenological traits that might become unfavorable under future climates (e.g., late budburst or early diameter-growth cessation), then gene flow from populations having more favorable traits for the changed environment (e.g., those in dry locations with predispositions toward earlier budburst) might improve climate change resilience. But where local populations already possess the most favorable values of a phenological trait, the opportunities for improving climate change resilience via gene flow will be relatively limited. Although there is evidence for genetic variation in diameter-growth-cessation timing (Gould, Harrington, & St. Clair, 2012), how these traits relate to the climate of a tree's genetic source remains poorly understood.

Question 3: Geographic patterns in temperature, photoperiod, and genetic trait values could lead to important differences in the response of diameter-growth-cessation timing to climate change across a species' range. These types of spatial patterns have been identified for budburst and diameter-growth initiation, with trees in cool locations (high latitude/elevation) exhibiting strong shifts in initiation to earlier in the year (likely a favorable response to climate change), while trees in warmer locations (low latitude/elevation) exhibit much weaker shifts or even initiate growth later in the year due to low chilling (likely an unfavorable response) (Ford, Harrington, Bansal, Gould, & St. Clair, 2016; Harrington & Gould, 2015; Murray, Cannell, & Smith, 1989). These patterns in phenological responses are likely to influence geographic patterns in resilience to climate change and range shift dynamics (Amano et al., 2014; Chuine et al., 2010; Morin, Viner, & Chuine, 2008). Similar analyses for diameter-growth cessation across major portions of a species' range are lacking (but see Rossi et al., 2011 for an example of potential geographic variations within a species' range).

In light of the literature on diameter-growth cessation and other growth-phenology events, we developed the following hypotheses related to environmental and genetic drivers of diameter-growth cessation, and geographic patterns in responses to climate change. (1) We hypothesized that cool temperatures *or* short photoperiods could induce growth cessation and that these effects would be compensatory. In other words, the probability of cessation would be more sensitive to decreases in temperature under long photoperiods (so that cool temperatures could trigger cessation even under long photoperiods) and more sensitive to decreases in photoperiod under warm conditions (so that short photoperiods could trigger cessation even under high temperatures). (2) We developed two hypotheses about genetic effects on the timing of growth cessation: (i) Trees from locations with frequent frosts in autumn and early winter would cease growth earlier in the autumn to avoid exposing vulnerable actively growing tissues to frost. (ii) Trees from locations with poor climatic conditions for growth (due to cool temperatures, low soil moisture, or both) would cease growth later in autumn to ensure adequate growth rates and competitive ability. (3) We hypothesized that trees would respond to warming by ceasing growth later in the year in cool parts of the region (high latitudes/elevations) where cool temperatures are the dominant cue for cessation, but that this response would be muted in warmer parts of the range (low latitudes/elevations) where short photoperiods are the prevailing cue for cessation and will limit shifts in cessation timing.

To test these hypotheses, we studied the environmental and genetic influences on the timing of diameter-growth cessation across a broad environmental gradient for coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco), a foundation tree species in forest ecosystems of the Pacific Northwest region of North America and timber economies throughout the world (Franklin & Dyrness, 1988). We did this by collecting high-frequency data on tree diameter growth over multiple years in a set of common gardens planted in climatically disparate environments with trees from a wide range of seed sources. We then fit statistical models to the data and projected expected dates of autumn growth cessation across the region under current and future climates. Also, in 1 year at our warmest site, most of the trees ceased growth in the early summer around peak photoperiod in conjunction with an abnormal heat wave. We sought to take advantage of this rare but potentially informative event and modeled the possibility of very high temperatures leading to premature cessation in the summer, and how the existence of such a tipping point might lead to surprising shifts in cessation timing in response to climate change in some parts of the coast Douglas-fir range.

2 | MATERIALS AND METHODS

2.1 | Study description

The high-frequency diameter-growth data for this study came from a representative subset of the trees and sites in the Douglas-fir Seed-Source Movement Trial, a large-scale common garden trial covering a wide range of site and seed-source environments. The trees used in this particular study were grown from seed collected from 25 parent trees in 16 different wild stands in distinct physiographic subregions throughout the coast Douglas-fir range in California, Oregon, and Washington (one or two parent trees per stand; Figure 1, Table 1). The parent trees were randomly selected dominant or

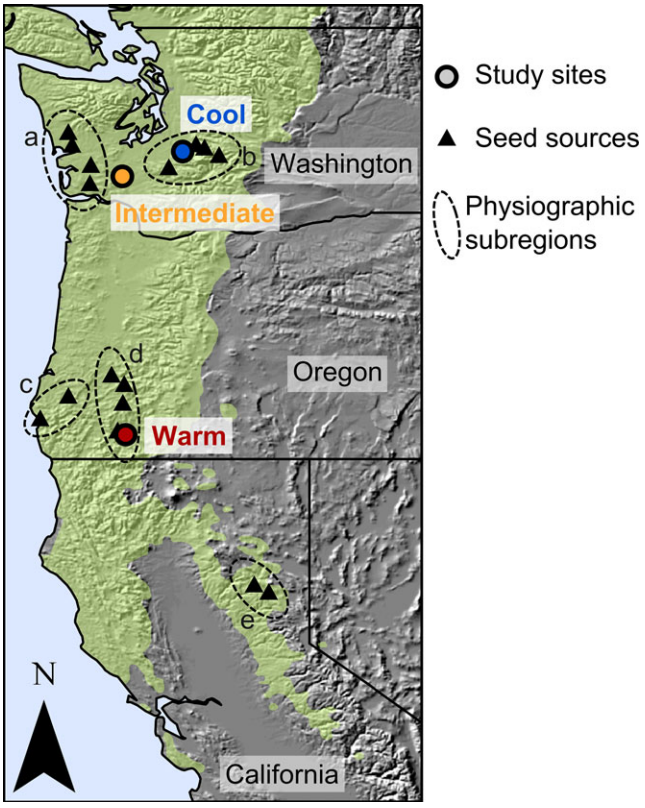

FIGURE 1 Study sites (cool, intermediate, warm), seed sources, and the physiographic subregions of the seed sources (identified by the letters) shown with the range of coast Douglas-fir (Little, 1971) [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Seed sources. See Figure 1 for outlines of physiographic subregions. MAT (mean annual temperature) and MAP (mean annual precipitation) are the normals for the 1981–2010 time period, as estimated by ClimateWNA (Wang et al., 2012)

Physiographic subregion	Latitude	Longitude	Elevation (m)	Parent trees	MAT (°C)	MAP (mm)
a	47.32°N	123.91°W	142	2	9.8	3,100
a	47.11°N	123.85°W	93	2	10.0	2,522
a	46.78°N	123.55°W	160	1	10.0	2,158
a	46.48°N	123.56°W	484	1	9.1	3,222
b	47.11°N	121.84°W	1,017	1	6.2	1,962
b	47.06°N	121.70°W	1,076	2	6.0	1,803
b	46.94°N	121.47°W	1,416	2	4.2	1,714
b	46.74°N	122.28°W	836	1	7.5	2,214
c	43.04°N	123.92°W	439	2	11.1	1,762
c	42.67°N	124.37°W	750	2	11.7	4,391
d	43.38°N	123.21°W	314	1	11.5	1,231
d	43.22°N	123.01°W	601	1	11.2	1,431
d	42.92°N	123.03°W	454	2	11.9	1,022
d	42.47°N	123.12°W	540	1	11.9	676
e	39.97°N	120.90°W	1,149	2	11.1	1,039
e	39.85°N	120.66°W	1,683	2	8.7	1,238

TABLE 2 Study sites

Site	Latitude	Longitude	Elevation (m)	MAT (°C)[a]	Years observed	Cessation observations
Cool	46.95°N	122.01°W	860	8.3 (6.9–9.7)	2011–2015	90
Intermediate	46.55°N	122.99°W	240	9.9 (8.9–11.3)	2010–2015	105
Warm	42.35°N	122.94°W	415	11.7 (10.7–12.8)	2010–2012, 2015	74

[a]Mean annual temperature for the years with diameter-growth-cessation observations, with the minimum and maximum annual temperatures during the study in parentheses.

codominant individuals. Seeds were germinated in spring 2007 and transplanted into the soil at the field sites after two growing seasons. The three sites are at different latitudes and elevations, so they experience different combinations of climate and photoperiod regimes (Figure 1, Table 2). The "cool" site was situated near the species' local upper elevation limit, the "intermediate" site in the range core, and the "warm" site in an inland basin below the species' local lower elevation limit. We recorded hourly air temperature using on-site weather stations equipped with HOBO U30 data loggers and smart sensors from Onset Computer Corporation, Pocasset, Massachusetts, USA.

We used electronic dendrometers to observe diameter-growth cessation. These sensors measured and recorded stem diameter at the base of each tree every 30 min, which allowed us to precisely determine the date when annual diameter growth ceased. We used DEX dendrometers from Dynamax (Houston, TX, USA) and DR dendrometers from Ecomatik (Munich, Germany) and recorded measurements to a Campbell CR10X or CR1000 data logger (Campbell Scientific, Logan, UT, USA). We observed diameter growth at two or three of the sites each year from 2010 to 2015, for a total of 15 site-by-year combinations, 113 unique trees, 269 instances of diameter-growth cessation, and 97,992 observations of daily tree growth status (see Table S1 for the number of trees monitored from each physiographic subregion at each site in each year).

2.2 | Seed-source climate

To quantify the typical frequency of autumn and early winter frost exposure at the seed-source locations, we estimated the median number of hours with temperatures ≤ -2°C (hard frost events that could be damaging—Bigras, Ryyppö, Lindström, & Stattin, 2001) in September–December at the location of each seed source (parent tree) during the 1981–2010 time period. We did this using hourly temperature recordings from 420 weather stations in the region and climate estimates from ClimateWNA (Wang, Hamann, Spittlehouse, & Murdock, 2012) (see Ford et al., 2016, for details of temperature estimation methods).

To characterize the climatic quality of the growing conditions at seed-source locations, we calculated actual evapotranspiration (AET) values for a standard hypothetical vegetation layer under the current climate (1981–2010) for each of the seed sources. This formulation of AET is a well-established metric of the simultaneous availability of energy and water for plant functioning and is therefore a useful indicator of the climatic favorability of an environment for growth

(Stephenson, 1990, 1998). Following Lutz, Van Wagtendonk, and Franklin (2010), we used a Thornthwaite-type water balance model to calculate AET, an approach considered most appropriate when reliable measures of humidity and wind speed are not available (Dingman, 2002), as with this study. The monthly estimates of mean temperature and precipitation needed to run the model came from ClimateWNA, while the required data on soil water-holding capacity came from the USDA Natural Resources Conservation Service STATSGO2 Database (NRCS, 2015).

2.3 | Modeling two distinct diameter-growth-cessation pathways for autumn and summer

The trees in our study exhibited two distinct modes of diameter-growth cessation which we analyzed separately. The vast majority of growth-cessation events (97%) occurred during the autumn (later than September 1) when photoperiods were relatively short and temperatures generally cool. Thus, we were able to characterize the effects of photoperiod and temperature on growth-cessation timing in autumn with a relatively high degree of confidence. However, at the warm site during the hottest year (2015), nine of the 12 trees stopped growing in mid- to late June under long photoperiods and very high temperatures. All these trees survived and exhibited normal diameter-growth initiation and budburst in the following spring (2016). Because it appeared that the physiological mechanisms behind cessation at this site in this year were distinct from the mechanisms behind the rest of the observed cessation events, we analyzed these events separately. As these summer cessation events were so rare, the strength of the inferences that we can draw from their analysis is limited. However, the events highlight possible pathways to growth cessation that are currently rare but could become more prevalent with climate change, leading to surprising and important phenological responses to warming.

2.4 | Statistical models for diameter-growth cessation in autumn

We fit statistical models to characterize the effects of environmental drivers and seed-source climate on diameter-growth-cessation timing in autumn. These were generalized linear mixed-effects models with a logit link function and a beta-binomial error distribution. The observations used to fit the models were the proportion of trees in each group (all individuals from a particular physiographic subregion, see Figure 1, for a particular site and year) ceasing growth on a given day out of all the trees growing the day before. This was determined for each group for each day from June 21 (typical date of the summer solstice) until all trees in the group ceased growth for the year. We included group identity as a random effect to account for the repeated observations within groups of individuals with similar seed-source climates, growing at the same site in the same year. These models allowed us to estimate the daily probability of a tree within a particular group ceasing growth given the state of the environmental drivers and the seed-source climate. We then fit several candidate models that differed by which environmental and seed-source climate variables (fixed effects) were included in the model to evaluate our hypotheses on how these factors influence diameter-growth cessation. The variables related to environmental conditions were daily mean temperature and photoperiod, while the variables related to seed-source climate were frost exposure during the autumn/early winter and AET. See Appendix S1 for the mathematical description of the models.

We fit the models using hierarchical Bayesian methods with Markov chain Monte Carlo (MCMC) simulations, assigning noninformative prior distributions to all model parameters. We ran each model with three MCMC chains and confirmed the chains had converged using the Gelman–Rubin statistic and visual inspection of the chains and posterior parameter distributions. For each candidate model, we calculated the value of the information criterion based on approximate leave-one-out cross-validation (LOOIC) for Bayesian models using the LOO software package (Vehtari, Gelman, & Gabry, 2016) to assess model predictive accuracy and determine which explanatory variables to include in our final (most parsimonious) model. We implemented the models in Stan using the RSTAN package (Stan Development Team, 2016) in R version 3.3.0 (R Core Team, 2016).

2.5 | Projections for diameter-growth cessation in autumn across the region

We used the final autumn-cessation model to project climate change-induced shifts in the expected date of diameter-growth cessation in the autumn across the range of coast Douglas-fir in the Pacific Northwest. For input climate data, we used estimates of hourly temperatures across the region under the current climate (1981–2010) based on weather station data and ClimateWNA, and estimates of changes in temperature by the end of the century (2071–2100) based on ensemble climate model projections using the RCP8.5 climate change scenario (IPCC, 2013), a high-warming scenario that we chose to span a wide range of potential temperature changes (see Ford et al., 2016, for details of temperature estimation methods). We then used our growth-cessation model and these temperature estimates to predict the timing of when 50% of trees would stop growing at each map grid cell (1 arc-min resolution) under the current and future climates, given the seed-source climate at that grid cell for the current time period (1981–2010).

We also made a separate set of projections to show expected growth-cessation date for different genotypes experiencing the same environmental conditions, thus illustrating genetic effects on diameter-growth-cessation timing in autumn. To do this, we calculated the expected date of cessation at each map grid cell in the range of coast Douglas-fir in the region with our final model using the conditions at that grid cell to estimate the tree's seed-source climate (frost exposure—see Results section), but using the environmental conditions (daily mean temperature and photoperiod—see Results section) from the centroid of this geographic area under the current climate (1981–2010).

2.6 | Statistical models and projections for diameter-growth cessation in summer

We fit statistical models to quantify the effects of environmental drivers on diameter-growth-cessation timing in summer. These were generalized linear models with a logit link function and beta-binomial error distribution, which we fit using maximum-likelihood methods and the *optim* function in R version 3.3.0 (R Core Team, 2016). The observations used to fit the models were the proportion of trees ceasing growth on a given day out of all trees growing the day before for each group of trees (all individuals from a particular physiographic subregion for a particular site and year) for each day from May 11 (latest observed date of diameter-growth initiation) until September 1 for all study sites and years with data. The models allowed us to estimate the daily probability of a tree within a particular group ceasing growth given the state of the environmental drivers. Mixed models with group identity as a random effect that were implemented with hierarchical Bayesian methods did not converge due to the lack of summer cessation in most groups. The absence of a hierarchical variance structure in the models that did converge adds to the caution needed in interpreting the predictions of these models. We also did not consider genetic effects on summer cessation due to the limited number of seed sources that experienced these events. We evaluated candidate models that differed by which environmental variables and interaction effects were included as predictors. These variables were daily maximum temperature, photoperiod, and volumetric soil moisture content at 10 and 50 cm depth. For each model, we calculated AIC_c (Akaike's information criterion with a second-order bias correction) to assess model predictive accuracy and selected the model with the best (most parsimonious) AIC_c value as our final summer cessation model. We used the final fitted models for both autumn and summer cessation to project changes in the expected date of diameter-growth cessation (the date by which 50% of trees in a population are expected to have ceased growth) across the range of coast Douglas-fir in the Pacific Northwest under the current (1981–2010) and future (2071–2100, RCP8.5) climate.

3 | RESULTS

3.1 | Diameter-growth cessation in autumn—model evaluation

For our analysis of diameter-growth cessation in autumn, we found that daily mean temperature, photoperiod, and their interaction, as well as seed-source frost exposure, led to improved model predictive accuracy, while seed-source AET did not (Table 3). For our final model, predictions of cessation timing generally matched observations (Figure 2, Figs S1–14). The correlation between predicted and observed dates of when 50% of trees in a group ceased growth produced an r^2 value of .66, while the correlation between predicted and observed proportion of trees within a group still growing on each day produced an r^2 value of .92.

3.2 | Diameter-growth cessation in autumn—model predictions

Our final model suggested that both cooler temperatures and shorter photoperiods led to a greater probability of growth cessation and that these two variables had compensatory effects on cessation probability, owing to the nature of their interaction effect (Figure 3, Table S2). Also, trees from seed-source locations that had a higher frequency of frost exposure in the autumn and early winter tended to stop diameter growth earlier than those with a lower frequency of frost exposure (i.e., seed-source frost exposure had a positive effect on cessation probability; Table S2).

The modeled timing of diameter-growth cessation varied by site, year, and seed source (Figure 4). The changes in predicted proportion of trees that had ceased growth by a particular date were erratic early in the autumn, especially at the cool site, due to fluctuations in temperature (Figure 4). At this time of year, photoperiods are relatively long and expected cessation probability would have been relatively sensitive to fluctuations in temperature (Figure 3). But in mid- to late autumn, the changes in predicted proportion of trees that had ceased growth became far more consistent (Figure 4). At this time of year, photoperiods are relatively short and

TABLE 3 Comparison of candidate models for diameter-growth cessation in autumn. ΔLOOIC is the difference in LOOIC (the information criterion based on approximate leave-one-out cross-validation) between the given model and the model with the lowest LOOIC, with lower values implying greater predictive accuracy. The term "temp × photo" refers to the interaction effect of temperature and photoperiod

Rank	Model	ΔLOOIC
1	Temperature + Photoperiod + temp × photo + $Frost_{seed\text{-}source}$	0.00
2	Temperature + Photoperiod + temp × photo + $Frost_{seed\text{-}source}$ + $AET_{seed\text{-}source}$	1.20
3	Temperature + Photoperiod + temp × photo	2.89
4	Temperature + Photoperiod + temp × photo + $AET_{seed\text{-}source}$	3.37
5	Temperature + Photoperiod	16.97
6	Photoperiod	22.51
7	Temperature	220.37
8	Null	543.68

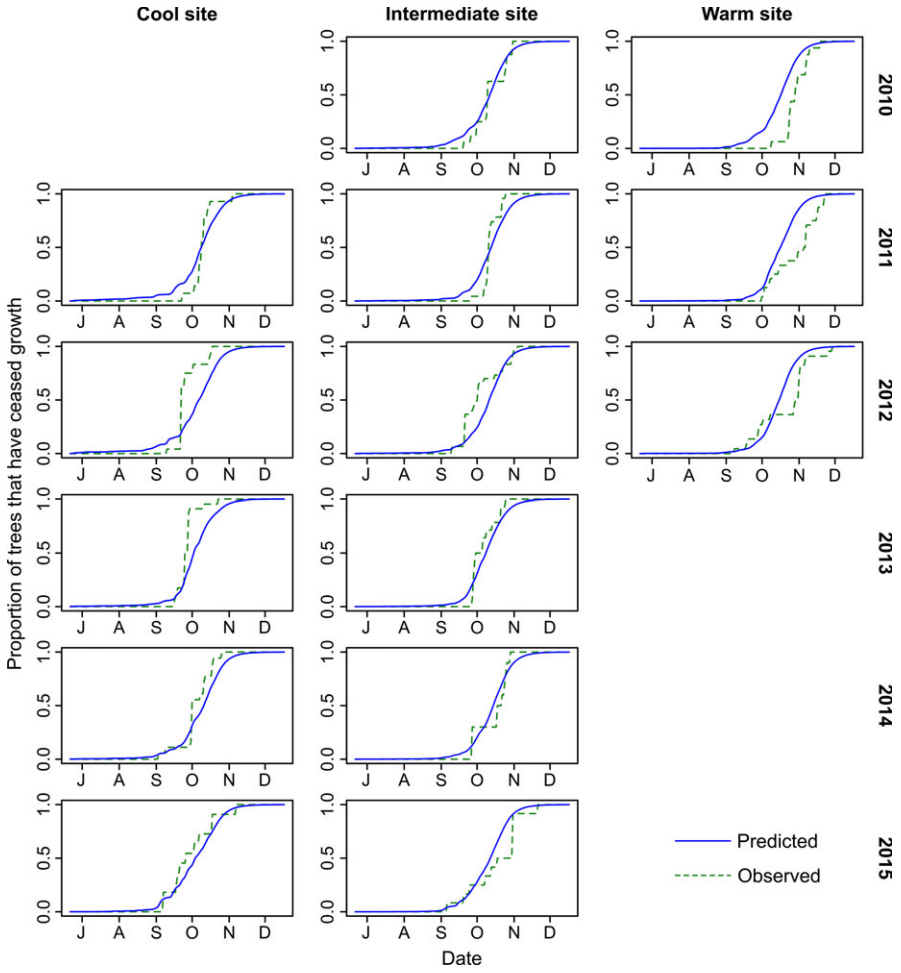

FIGURE 2 Comparison of predicted and observed values of the proportion of trees that had ceased diameter growth over time for each year at each site in the study, according to the autumn diameter-growth-cessation pathway [Color figure can be viewed at wileyonlinelibrary.com]

expected cessation probability becomes more sensitive to the consistent changes in photoperiod (Figure 3).

To limit the effects of model artifacts on predictions outside the observed ranges of temperatures and photoperiods, and to produce biologically plausible predictions, we constrained the model predictions to always exhibit the positive (but saturating) effects of cooler temperatures and shorter photoperiods on growth-cessation probability that were observed in our study. These constraints did not reduce the accuracy of the predicted values for our observed data and actually led to a very slight improvement (root-mean-square errors of 0.1011 vs. 0.1016). The constraints only affected a very small portion of the geographic range where we made predictions (predicted date of cessation differed between constrained and unconstrained predictions in 0.25% of map grid cells under the current climate, and none of the cells under the future climate scenario). See Appendix S2 for details on these prediction constraints.

The influences of temperature, photoperiod, and seed-source climate led to variation in predicted dates of diameter-growth cessation in autumn across the coast Douglas-fir range in the region, as well as differences in responses to climate change (Figure 5). Under the current climate, the model predicted later cessation dates at lower latitudes and elevations where there were warmer temperatures, longer photoperiods following the September equinox (though shorter photoperiods prior to the equinox), and/or less seed-source frost exposure (Figure 5a). This geographic pattern is maintained for projections based on the future climate scenario, but cessation is predicted to be later in the year due to warmer temperatures (Figure 5b). However, the magnitude of this change in cessation date varied strongly across the region, with smaller shifts toward lower latitudes or elevations (Figure 5c). Variation in seed-source climate also led to differences in expected timing of growth cessation, with trees from higher latitude and elevation seed sources that experience greater frost exposure predicted to cease growth earlier than those from other seed sources (Figure 5d).

3.3 | Diameter-growth cessation in summer

Our analysis of diameter-growth cessation during the summer suggested that these events were associated with abnormally high temperatures (>40°C) coinciding with long photoperiods (>15 hr; Figure 6). However, there was no evidence that low soil moisture was associated with these particular events, as the best model (based on AIC_c) did not include soil moisture as an explanatory variable. The summer cessation model implies that very little of the range of coast Douglas-fir in the region experiences summer growth cessation in a typical year under the current climate (1.6% of the

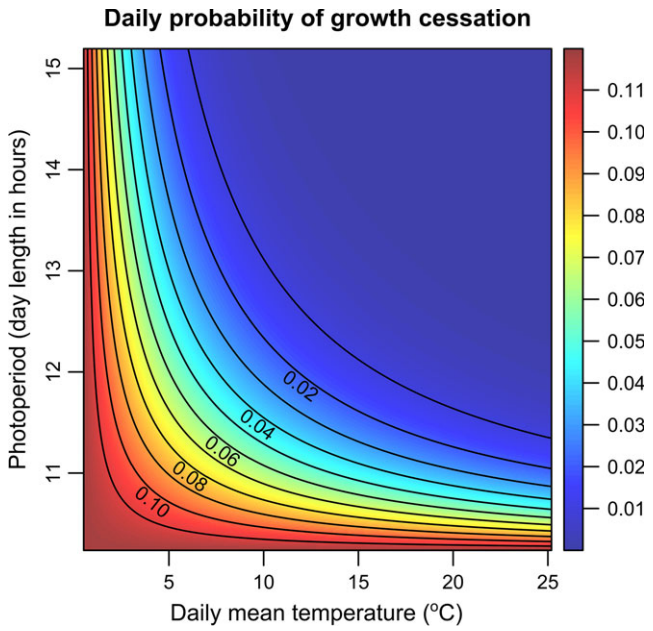

FIGURE 3 For diameter-growth-cessation events in the autumn, the probability of a tree ceasing growth increased with reductions in daily mean temperature and photoperiod. Furthermore, the effects of temperature and photoperiod were contingent on each other: Growth-cessation probability was most sensitive to changes in temperature under long photoperiods and most sensitive to changes in photoperiod under high temperatures. Thus, the model suggested compensatory effects of low temperatures and short photoperiods for increasing cessation probability. Very cool temperatures led to high cessation probability even under long photoperiods, and very short photoperiods led to high cessation probability even under warm temperatures, although cessation probability was greatest under cool temperatures and short photoperiods. The plot shows the expected growth-cessation probabilities based on the mean genetic effect of the study trees pooled across seed sources

range in the region, Figure 7a), but under a high-warming scenario (RCP8.5, 2071–2100), these events could become much more prevalent (occurring on 38.5% of the range in the region in a typical year, Figure 7b). In locations with cool summers (high latitudes or elevations, and areas near the coast), the models predicted that cessation will still occur in autumn under climate change, and at a later date due to warmer autumn temperatures (Figure 7c–e). But where summer temperatures are already high (low-latitude and low-elevation areas away from the coast), cessation was predicted to begin occurring in the summer in typical years due to higher summer temperatures, leading to much earlier cessation in the future (Figure 7c–e).

4 | DISCUSSION

4.1 | Limitations on autumn phenology responses to climate change across the coast Douglas-fir range

Warmer autumn temperatures brought by climate change will likely promote later diameter-growth cessation in coast Douglas-fir, but the magnitude of this shift may be limited by the effects of short photoperiods and the genetic composition of local populations, with these limitations being strongest in the warm portions of the range. Higher autumn temperatures were associated with later growth cessation (Figure 3), so future autumn warming will likely lead to growth cessation occurring later in the year across the range (Figure 5a–c). The magnitude of this expected change in cessation date is greatest at high latitude and elevation locations (Figure 5c) where temperatures are currently low and the sensitivity of cessation probability to changes in temperature is high (Figure 3). But at lower latitudes or elevations which currently experience moderate-to-warm autumn temperatures, shifts in cessation date are expected to be small (Figure 5c) because cessation probability under these conditions is relatively insensitive to differences in temperature and is instead sensitive to differences in photoperiod (Figure 3). Therefore, our model suggests that cessation date in these locations will shift very little because it will continue to be determined primarily by the annual photoperiod cycle which is unaffected by climate change (and which might have a clearer effect on cessation timing than temperature—Table 3).

Geographic patterns in genetic effects on diameter-growth-cessation timing suggest that the potential for gene flow to facilitate shifts in cessation timing in response to climate change will likely vary across the range of coast Douglas-fir. Populations at low latitudes or elevations currently exhibit the strongest genetic predispositions toward late cessation, likely reflecting local adaptation to these low-frost environments where there is little risk in extending the growing season late into autumn (Figure 5d). The ability of gene flow to promote evolution of later cessation in these populations is likely to be limited because there are few other populations which could be the source of gene flow that have genotypes which promote even later cessation. However, gene flow may facilitate later cessation in high latitude and elevation populations that currently cease growth relatively early (likely reflecting local adaptation to high historic levels of frost exposure, Figure 5d), because of the potential for gene flow from low-latitude or low-elevation populations.

Thus, photoperiod cues and patterns of genetic variation will likely allow for coast Douglas-fir to phenologically track climate change in the cool parts of the range by extending the growing season later into autumn, but will also limit its ability to do so in the warm parts, which might lead to its growth period becoming decoupled from the timing of suitable growing conditions. These geographic patterns in projected phenological shifts are similar in principle to those expected for growth-initiation events (budburst and diameter-growth initiation) in coast Douglas-fir. Initiation events are expected to occur earlier in the year with warming at high latitudes and elevations, allowing trees to capture newly favorable conditions in the early spring and track climate change, but to occur at similar or later times of the year toward low-latitude and low-elevation range limits, so that shifts in growth-initiation phenology lag behind climate change (Ford et al., 2016). Together, these findings suggest that growth-phenology shifts will likely improve climate change resilience in the cooler parts of the range, but might reduce

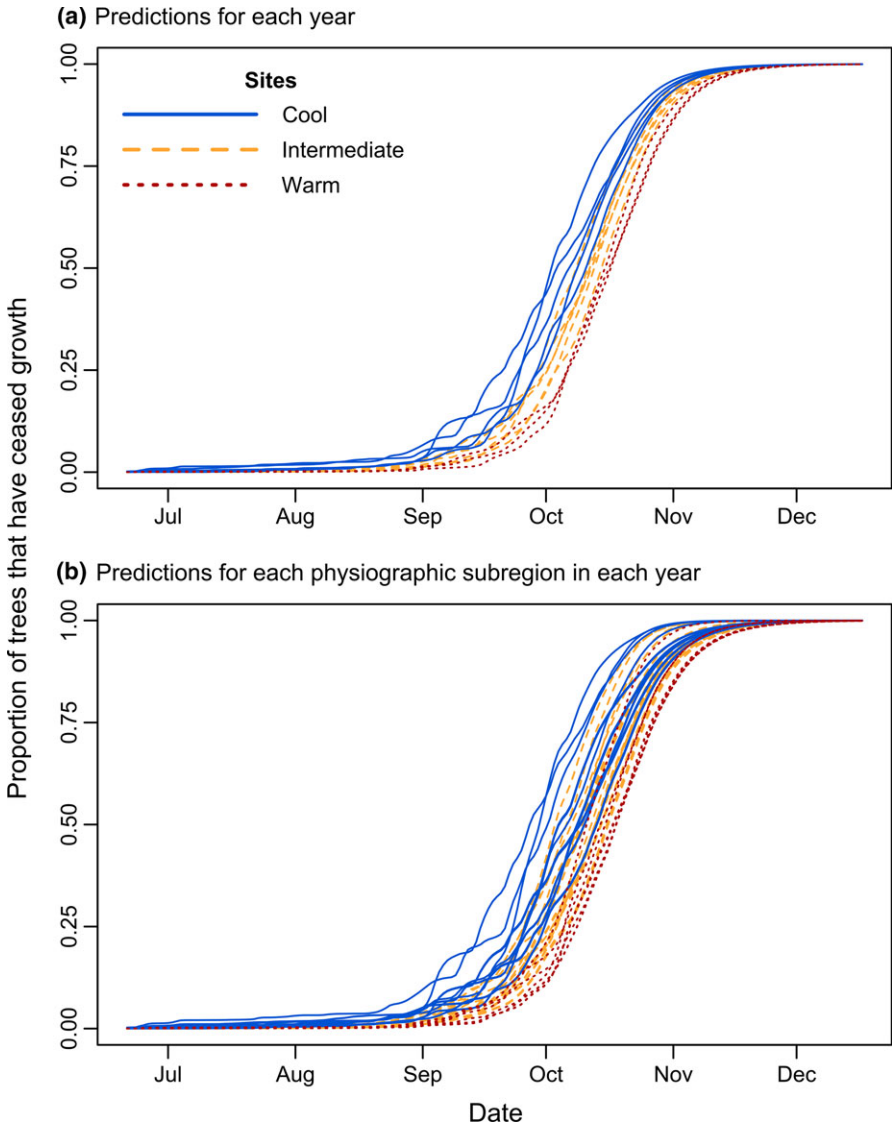

FIGURE 4 Modeled timing of diameter-growth cessation in autumn varied by site, year, and genetic source. (a) Each curve represents predictions for a particular year at the given site, averaged over all trees. Figure 2 shows how these predictions compared to the observations. (b) Each curve represents the predictions for a particular seed-source physiographic subregion, for a particular year at the given site. Figs S1–14 show how these predictions compared to the observations

it in the warmer parts. If co-occurring species in these warm parts of the range (either current residents or newly arrived migrants) better track climate change phenologically, they could gain a competitive advantage over coast Douglas-fir (Cleland et al., 2012; Harrington & Gould, 2015), which could be one factor contributing to possible range contractions along the warm edges of the species' distribution (also see Amano et al., 2014; Chuine, 2010; Morin et al., 2008). These unfavorable shifts in growth phenology may also exacerbate growing season drought stress, which is likely to increase in the future and could reduce growth rates in warm parts of the coast Douglas-fir range (Littell, Peterson, & Tjoelker, 2008; Restaino, Peterson, & Littell, 2016). However, the relatively small delays in diameter-growth-cessation timing in the warm parts of the range may help trees avoid exposing actively growing tissues to frost, which will still occur in the future despite warming, and may only come at a small cost to growth potential because photoperiods are short and insolation is weak at this time of the year (creating suboptimal conditions for photosynthesis even under warm temperatures).

4.2 | Physiological mechanisms underlying diameter-growth cessation in autumn

Multiple physiological processes influence the timing of diameter-growth cessation and are likely sensitive to both temperature and photoperiod. Diameter growth in trees is primarily a function of wood production (xylogenesis), which ceases with the end of cell division and expansion in the cambium and xylem. Declining temperatures have been shown to correspond with the cessation of both cell division and expansion in these tissues (Begum et al., 2016). However, trees along elevational gradients experiencing very different temperatures but similar photoperiod regimes can still exhibit similar diameter-growth-cessation timing (Moser et al., 2010; Takahashi & Koike, 2014), suggesting that temperature is not the sole determinant of cessation and that photoperiod might play an important role. How photoperiod influences xylogenesis cessation is poorly understood (Delpierre et al., 2016), but likely involves trees sensing changes in light conditions through their leaves, leading to

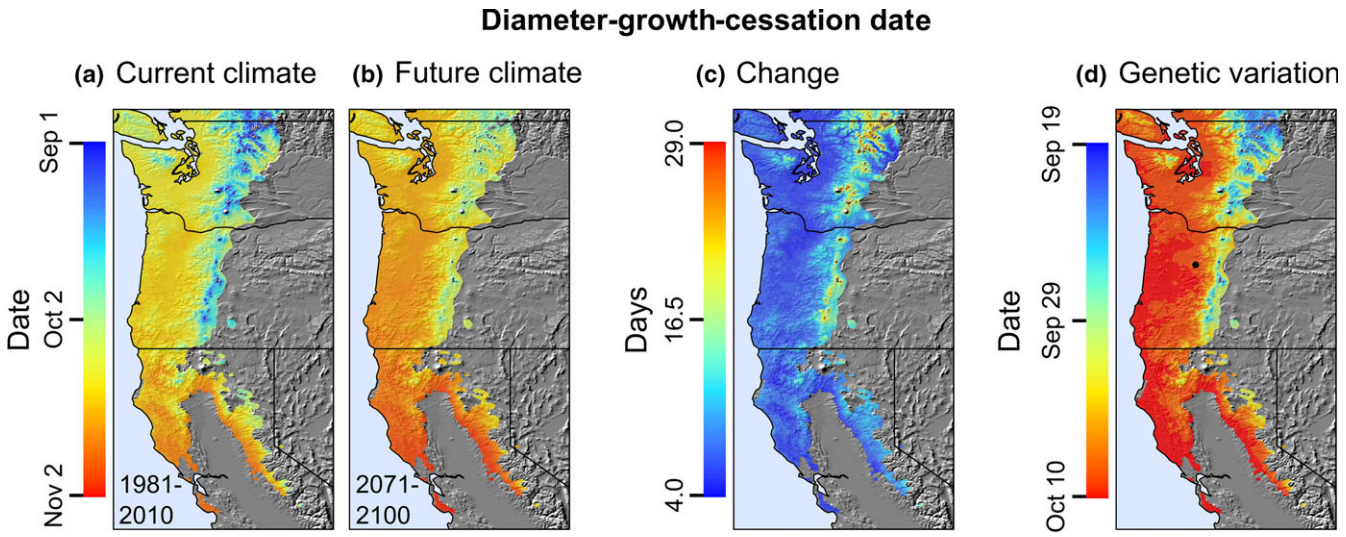

FIGURE 5 The expected date of diameter-growth cessation (according to the autumn-cessation model) and the shift in this date under climate change depend on the environment where the tree grows and the climate of the seed source. (a) Expected dates of when 50% of trees at a given location would cease diameter growth under the current climate (1981–2010) and (b) a future climate scenario (RCP8.5, 2071–2100). For both "a" and "b," the genetic (seed-source) effect on cessation date was based on frost exposure under the current climate (1981–2010) of the given location (map grid cell). (c) The change in expected cessation date between the two time periods shown in "a" and "b" (the positive values indicate that future growth cessation occurs later in the year). (d) The expected cessation dates for trees from the seed sources at the given locations (map grid cells) experiencing the same environmental conditions (the conditions at the centroid of the coast Douglas-fir range shown on the map [*dot*])

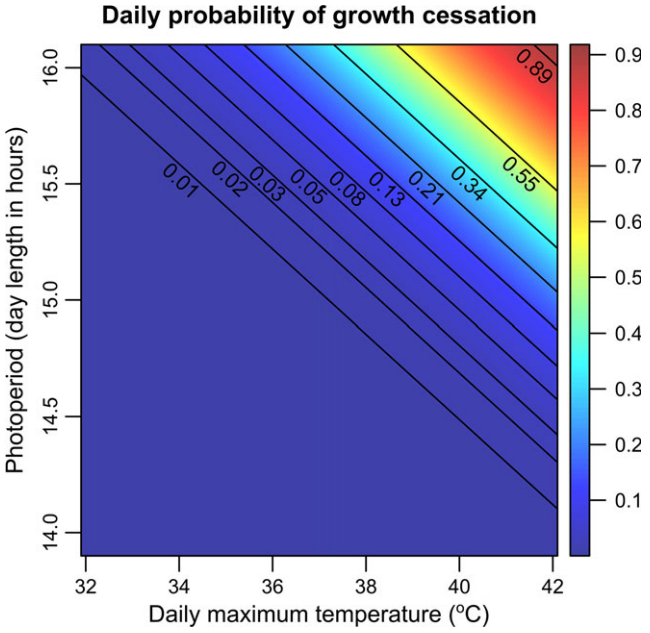

FIGURE 6 Modeling based on data from a rare early summer heat wave suggested that the probability of a tree ceasing diameter growth during the summer increased with higher daily maximum temperatures and longer photoperiods. Our analysis did not detect an interactive effect between photoperiod and temperature, or an effect of soil moisture

changes in the production of plant hormones in the leaves and transport of those hormones to the cambium and xylem (Jackson, 2009; Taiz & Zeiger, 2010).

The physiological mechanisms underlying any interactive effects of temperature and photoperiod on diameter-growth cessation are even more poorly understood. However, recent studies with *Arabidopsis thaliana* suggest that phytochromes—a group of pigments that function as light-sensing photoreceptors and play key roles in several phenological events (Taiz & Zeiger, 2010)—can also act as thermosensors (Jung et al., 2016; Legris et al., 2016). Although these studies were conducted on a short-lived herbaceous species, phytochromes are found in trees and all other higher plants. The ability of phytochromes to sense both light and temperature suggests that they could play an important role integrating photoperiod and temperature cues for diameter-growth cessation (and other phenological events).

Our data set was well suited to evaluating possible interactive effects of temperature and photoperiod on diameter-growth cessation. The two variables showed a relatively weak positive correlation on the daily temporal scale used in our analyses (r^2 = .29) despite their inherently strong seasonal correlation. Thus, we had the opportunity to distinguish potential temperature, photoperiod, and interaction effects under natural conditions, avoiding the artifacts of manipulated-environment experiments which may not accurately reflect phenological responses to real climate change (Wolkovich et al., 2012). However, these types of manipulative experiments do allow for more control of environmental conditions and provide an important and complementary approach that would further improve understanding of the environmental drivers behind diameter-growth-cessation phenology (Clark, Melillo, et al., 2014; Clark, Salk, et al., 2014; Hänninen, 1995).

To analyze the data in this study, we used statistical models that directly relate environmental variables (temperature and

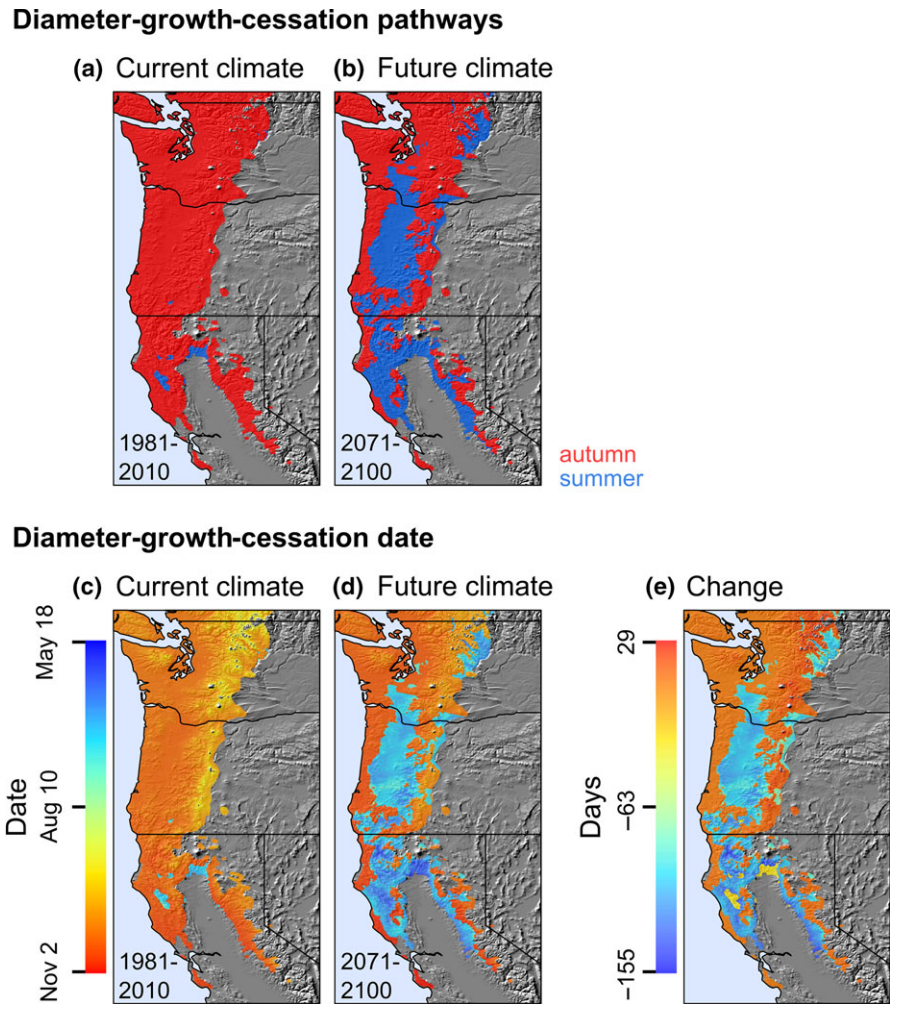

FIGURE 7 The expected date of diameter-growth cessation and the shift in this date under climate change differed drastically across the range depending on the predicted cessation pathway that trees follow under current and future climates. We characterized two possible pathways: (1) the "autumn" pathway in which low mean temperatures and short photoperiods increase the probability of cessation, typically leading to cessation in the autumn months, and (2) the "summer" pathway in which high maximum temperatures and long photoperiods increase the probability of cessation, typically leading to cessation in the summer months. (a) The expected pathway responsible for the cessation of most trees in a typical year under the current climate (1981–2010) and (b) under a future climate scenario (RCP8.5, 2071–2100). (c) Expected dates of when 50% of trees at a given location would cease diameter growth under the current climate and (d) under the future climate scenario. (e) The change in expected cessation date between the two time periods shown in "c" and "d"

photoperiod) to the occurrence of a phenological event (diameter-growth cessation), as opposed to process-based models that relate environmental variables to a phenological event indirectly via mathematical functions assumed to represent physiological processes within the organism that determine how environmental cues translate into phenological responses. While they do have limitations, process-based models for growth-initiation events in trees (primarily budburst) have been able to illuminate important potential impacts of climate change owing to the biological realism of these models (e.g., Chuine, 2010; Ford et al., 2016; Hänninen, 2016; Hänninen & Kramer, 2007). As our understanding of growth-cessation processes in trees continues to improve, researchers will have the opportunity to develop process-based models of this phenological event, potentially leading to additional insights into the effects of climate change.

Although the literature suggests that temperature and photoperiod are the primary environmental determinants of diameter-growth cessation in autumn (Begum et al., 2016; Delpierre et al., 2016; Peltola et al., 2002; Rossi et al., 2011), other environmental factors could also play a role. For example, studies of autumn leaf phenology have found that precipitation, insolation (independent of photoperiod), and growth-initiation timing can affect the timing of autumn events (Fu et al., 2014; Liu et al., 2016). It is possible that these factors and others could also influence diameter-growth-cessation timing to some degree.

4.3 | Evolutionary mechanisms underlying diameter-growth cessation in autumn

Several processes have the potential to influence evolutionary changes in diameter-growth-cessation timing in coast Douglas-fir in response to climate change. Some evolutionary changes will likely occur gradually through gene flow via natural pollen and seed dispersal, and selection within populations for individuals with alleles that promote later cessation. This process could be accelerated by assisted gene flow (human movement of genotypes thought to be better adapted to future climates than the local genotypes; Aitken & Bemmels, 2016). Coast Douglas-fir exhibits high levels of genetic variability in some phenological traits (St. Clair et al., 2005), which may promote genetic adaptation in response to climate change (Aitken et al., 2008) and may make it possible to select for phenological traits that improve resilience to climate change in progeny trials (Anekonda, Lomas, Adams, Kavanagh, & Aitken, 2002; Jayawickrama, 2005; St. Clair & Howe, 2009). However, the effects of genetic variation on diameter-growth-cessation timing in our study were weak

compared to the effects of environmental variation, suggesting that this trait has high phenotypic plasticity (Table 3, Table S2), so the capacity for genetic changes to counter large temperature shifts may be limited. In addition, some of the effects of seed-source climate observed in this study may be due to maternal effects (as opposed to genetic effects) that might not persist as the trees age.

4.4 | Potential for surprises: Could warming shift diameter-growth cessation from autumn to summer?

The diameter-growth-cessation events observed during an abnormal heat wave in early summer at our warmest site highlight the possibility of growth-cessation pathways that are currently rare but could become prevalent with climate change and lead to surprising phenological responses that are difficult to forecast. Although warm temperatures and long photoperiods were typically conducive to growth in our study (Figure 3), the combination of very high temperatures with long photoperiods appeared to create a stressful environment that induced the cessation of diameter growth (Figure 6). Duchesne, Houle, and D'Orangeville (2012) also observed abnormal diameter-growth cessation in conjunction with an early summer heat wave for balsam fir (*Abies balsamea*). These results suggest two distinct pathways to cessation: an autumn pathway in which low temperatures and short photoperiods induce cessation, and a summer pathway in which exceptionally high temperatures and long photoperiods induce cessation. Although our analyses imply that the summer pathway is very rarely realized under current conditions (Figure 7a), climate change could make it more common by increasing daily maximum temperatures (Figure 7b). The summer pathway is most likely to become prevalent in areas currently experiencing high summer maximum temperatures that may be near thresholds for diameter-growth cessation when photoperiods are long. Thus, trends toward later cessation brought by moderate warming could be sharply reversed if severe warming causes temperatures to cross important tipping points, resulting in trees ceasing growth in summer instead of autumn.

The existence of two distinct pathways to cessation implies the possibility of divergent phenological responses to climate change across the coast Douglas-fir range. In areas with mild summer temperatures (high latitudes or elevations, or coastal locations), trees are expected to continue to follow the autumn pathway, with cessation occurring later in the year due to warmer autumn temperatures (Figure 7). But in areas with high summer temperatures (low-latitude and low-elevation locations away from the coast), trees might begin to follow the summer pathway, with cessation occurring much earlier in the year than it currently does as a result of higher summer temperatures inducing cessation around peak photoperiods (Figure 7). This severe curtailing of the growing season would likely limit the total amount of wood produced during the year and, in particular, decrease the proportion of latewood, which plays a critical role in limiting embolism damage in the xylem and maintaining water conductance under hot and dry conditions (Domec & Gartner, 2002). Thus, summer cessation of diameter growth could drastically reduce coast Douglas-fir's resilience to climate change by both shortening its growing season and increasing its susceptibility to drought stress, which will likely become more prevalent and severe in the future.

The results highlight the need for further research into the potential for high temperatures and long photoperiods to induce diameter-growth cessation in the summer (which might be best conducted with growth chamber experiments), as well as examination of the underlying physiological mechanisms. The conditions that led to summer cessation in this study did not appear to result in immediate tissue death because all trees that stopped growth in summer 2015 survived and resumed growth the following spring. Cambial tissue death generally does not occur until temperatures are ~50°C (Körner, 2006; Larcher, 2003), and temperatures in our study never reached those levels. However, mitosis tends to cease around 40°C (Francis & Barlow, 1988; Rao & Engelberg, 1965). These temperatures were realized at our hottest site in conjunction with the early summer cessation events of 2015, but were also realized late in the summer during other years when growth continued into autumn. Thus, it is possible that photoperiod mediates the effects of high temperatures on growth cessation. One way this could occur is if more heat-shock proteins accumulate in the leaves on hot days with long photoperiods (and thus longer periods of thermal stress) compared to days with shorter photoperiods but the same maximum temperatures (Bray, Bailey-Serres, & Weretilnyk, 2000). The greater heat-shock protein concentration could reduce transport of plant hormones such as auxins or strigolactones (Agusti et al., 2011) from leaves to cambium, inhibiting the resumption of mitosis when temperatures cool (Larson, 1994). Stopping the cell cycle in this way for multiple days may induce a form of dormancy similar to heat-induced dormancy in seeds, which requires prolonged exposure to chilling temperatures to break (Vegis, 1964). In addition, some aspects of the phytochrome system might be involved in controlling hormone production or transport to the cambium and be affected by high temperatures (Jung et al., 2016; Legris et al., 2016; Leivar & Quail, 2011; Rockwell, Su, & Lagarias, 2006).

These analyses of growth cessation in summer are based on limited data, so caution should be used in interpreting the results. However, ignoring the events entirely would also be unwise. These types of anomalously hot years produce valuable natural experiments that enable researchers to observe organisms under conditions that are currently rare but could become prevalent with climate change, and to better anticipate potential ecological surprises (Lindenmayer, Likens, Krebs, & Hobbs, 2010; Parmesan & Hanley, 2015). We hope this result will spur new research on the possibility of summer growth cessation that leads to more robust predictions of the occurrence of this potential phenological response to climate change. By closely examining the diameter-growth-cessation process under both normal and abnormal conditions, we have identified some possible surprises that may result from photoperiod cues, patterns in genetic variation, and (potentially) summer heat waves limiting the ability of coast Douglas-fir to phenologically track climate change in the warmer parts of its range.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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