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Will changes in phenology track climate change? A study of growth initiation timing in coast Douglas-fir

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Abstract

Under climate change, the reduction of frost risk, onset of warm temperatures and depletion of soil moisture are all likely to occur earlier in the year in many temperate regions. The resilience of tree species will depend on their ability to track these changes in climate with shifts in phenology that lead to earlier growth initiation in the spring. Exposure to warm temperatures ('forcing') typically triggers growth initiation, but many trees also require exposure to cool temperatures ('chilling') while dormant to readily initiate growth in the spring. If warming increases forcing and decreases chilling, climate change could maintain, advance or delay growth initiation phenology relative to the onset of favorable conditions. We modeled the timing of height- and diameter-growth initiation in coast Douglas-fir (an ecologically and economically vital tree in western North America) to determine whether changes in phenology are likely to track changes in climate using data from field-based and controlled-environment studies, which included conditions warmer than those currently experienced in the tree's range. For high latitude and elevation portions of the tree's range, our models predicted that warming will lead to earlier growth initiation and allow trees to track changes in the onset of the warm but still moist conditions that favor growth, generally without substantially greater exposure to frost. In contrast, toward lower latitude and elevation range limits, the models predicted that warming will lead to delayed growth initiation relative to changes in climate due to reduced chilling, with trees failing to capture favorable conditions in the earlier parts of the spring. This maladaptive response to climate change was more prevalent for diameter-growth initiation than height-growth initiation. The decoupling of growth initiation with the onset of favorable climatic conditions could reduce the resilience of coast Douglas-fir to climate change at the warm edges of its distribution.

Keywords: bud break, budburst, cambial reactivation, climate change, dormancy, flushing, leaf-out, parallel model, phenology, *Pseudotsuga menziesii* var. *menziesii*

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Introduction

The ability of organisms to match their phenology to the timing of seasonal changes in climate strongly influences individual fitness, species distributions, interspecific interactions, species invasions and ecosystem function (Chuine, 2010; Forrest & Miller-Rushing, 2010; Richardson *et al.*, 2013; Wolkovich & Cleland, 2014). Thus, the resilience of species and ecosystems to climate change will depend on the capacity of organisms to shift their phenology to track changes in climate. In many temperate forests, tree species will need to initiate growth earlier in the year to match their periods of growth with favorable climatic conditions (Saxe *et al.*, 2001; Hänninen & Kramer, 2007; Polgar & Primack, 2011), as the reduction of frost risk, onset of warm temperatures and depletion of soil moisture all occur earlier (IPCC, 2013). But how well trees will track these changes in climate remains an open question. Studies of responses to recent climate change have found that growth initiation is occurring earlier in the year on average, but there are many examples of species not responding or even initiating growth later (Parmesan, 2007; Cook *et al.*, 2012). Furthermore, phenological responses to the relatively small changes in climate over the past several decades might differ from responses to the larger changes expected for the future, due to nonlinear relationships between climate and phenology (Loustau *et al.*, 2007; Iler *et al.*, 2013; Pope *et al.*, 2013; Fu *et al.*, 2015b).

Predicting phenological responses to climate change is complicated by the contrasting effects of warming on the timing of growth initiation in trees and other

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plants. On one hand, warming could promote earlier initiation that allows trees to track climate change because it is exposure to warm temperatures ('forcing') that typically triggers the initiation of both height and diameter growth. However, these advances in growth initiation could have negative consequences if they cause growth to begin before the risk of frost has passed (i.e., advances in phenology outpace reductions in frost) (Cannell, 1985; Cannell & Smith, 1986). On the other hand, warming could delay growth initiation relative to the onset of suitably warm and moist conditions because many species require prolonged exposure to cool temperatures ('chilling') while dormant to readily initiate growth in the spring (Romberger, 1963; Vegis, 1964; Sarvas, 1974). This sensitivity to chilling allows trees to avoid initiating growth during brief warm periods midwinter by either blocking sensitivity to forcing until a chilling requirement has been met (according to 'sequential' models of growth initiation) or requiring a higher level of forcing for triggering growth initiation when the amount of chilling experienced is low (according to 'parallel' models). If warming reduces the amount of chilling trees experience, more forcing may be required for growth initiation to occur (Campbell & Sugano, 1975; Cannell & Smith, 1983; Chuine, 2000; Harrington *et al*., 2010; Fu *et al*., 2015a), potentially causing changes in the timing of growth initiation to lag behind climate change (Morin *et al*., 2009; Yu *et al*., 2010; Duputie *et al*., 2015). These lags would result in trees forgoing growth during periods of favorable conditions early in the spring, leading to lower productivity than what would be possible if growth began earlier in the year. Thus, trees could respond to warming with changes in growth initiation timing that match climate change or could initiate growth too early or too late, depending on the quantitative relationship growth initiation has with chilling and forcing. In some species, photoperiod cues and their interaction with temperature can also influence the timing of growth initiation (Laube *et al*., 2014).

Phenological responses to climate change are also likely to differ across a species' range. The effect of reduced chilling on phenology is often nonlinear, with the forcing required for growth initiation increasing more rapidly with loss of chilling in warm environments where chilling is already low (Harrington *et al*., 2010). Thus, climate change may lead to earlier growth initiation in cooler parts of the range, but delayed initiation in warmer parts (Murray *et al*., 1989). Therefore, trees in warm, low-chilling locations (such as lower latitudes and elevations) might be most likely to experience a decoupling of growth initiation with the onset of favorable conditions, which could contribute to reductions in resilience to climate change in these portions of the range (Morin *et al*., 2008; Amano *et al*., 2014).

Despite being the focus of numerous studies, projections of the effects of climate change on the phenology of trees and other plants remain uncertain (Wolkovich *et al*., 2012; Settele *et al*., 2014), and important unanswered questions remain such as:

1 How will phenological responses to climate change affect the conditions plants experience while growing, and how will these effects vary across a species' range? Many studies project changes in the dates of phenological events, but do not go on to assess how these changes correspond with the new climatic regimes. Other studies have examined the impacts of climate change and phenological shifts on growing conditions (particularly exposure to frost following budburst), but typically only at a few locations (Cannell, 1985; Cannell & Smith, 1986; Hänninen, 2006; Kramer, 1994; Leinonen, 1996; Murray *et al*., 1989, 1994; but see Morin & Chuine, 2014). Thus, region-wide assessments are needed to identify the parts of a species' range where climate change is most likely to lead to a decoupling of growth initiation with favorable growing conditions.
2 Are there differences between the responses of height- and diameter-growth initiation (terminal budburst and stem cambial reactivation, respectively) to climate change? Height-growth initiation and other forms of budburst are relatively well understood (reviewed by Polgar & Primack, 2011), and process-based models that predict the timing of height-growth initiation according to mathematical functions for chilling and forcing have been developed for a number of species (Hänninen & Kramer, 2007). Diameter-growth initiation is much less understood, and while both chilling and forcing are known to impact the timing of this event, quantitative models are lacking (Begum *et al*., 2013). Even less understood is how the effects of climate change on growth initiation will differ for height and diameter growth. However, both phenological events are critical to tree performance, and differences in their responses to climate change could impact tree form and function.

We address these questions by modeling the relationship between climate and growth phenology using a unique and extensive dataset for coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco), a foundation species vital to ecosystems throughout the Pacific Northwest region of North America and to timber economies around the world (Franklin & Dyrness, 1988). We used data from two experimental studies: (i) a multiyear, field-based study in which we planted trees from 60 seed sources at each of nine sites

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encompassing much of the climate coast Douglas-fir currently experiences; and (ii) a controlled-environment study in which we exposed trees from the same 60 seed sources to warmer conditions not currently experienced in the tree's range. The studies are complementary. While field-based studies avoid the potentially confounding artifacts of manipulated environments, controlled-environment studies can simulate the conditions trees will experience with climate change.

Our approach is rare and valuable because it allowed us to capture a wide variety of climatic conditions and control for genetic variation in fitting our models, and thus make realistic and robust predictions of phenological responses to climate change (Hänninen, 1995; Clark *et al.*, 2014a,b). We used these models to examine how changes in climate and phenology jointly affect the growing conditions trees experience (question 1) and differences in the responses of height- and diameter-growth initiation to climate change (question 2).

Materials and methods

Study descriptions

The coast Douglas-fir seedlings used in these studies (both field-based and controlled-environment) were grown from seed collected from 60 locations throughout the tree's range in Washington, Oregon and California, with two parent trees per location (Fig. 1). The parent trees were randomly selected dominant or codominant individuals in wild stands.

In the field-based study, we planted coast Douglas-fir seedlings from each parent tree in a climatically diverse set of locations and monitored growth initiation. The study included nine sites separated into three latitudinal bands, with sites in each band in three physiographic locations (coast, inland low elevation and inland high elevation) (Fig. 1). Seeds were germinated in spring 2007 and transplanted to the sites after two growing seasons. We monitored trees for height-growth initiation from 2009 to 2012 and in 2014, and for diameter-growth initiation on a subset of trees at three sites from 2010 to 2014. 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 (Table S1).

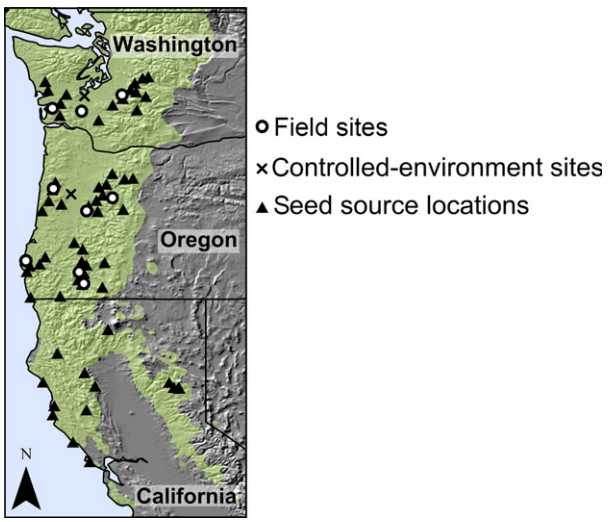

Fig. 1 Study site and seed source locations, and the range of coast Douglas-fir (Little, 1971).

In the controlled-environment study, we exposed coast Douglas-fir seedlings from each of the seed sources to a range of conditions in controlled settings and monitored growth initiation. We conducted these experiments in Olympia, Washington and Corvallis, Oregon, USA from 2010 to 2014 (Fig. 1). We planted seedlings (1–3 years old) into pots or large styroblocks and divided them into treatment groups that differed in the temperature experienced prior to growth initiation. To impose these treatments, we kept some groups in greenhouses (enclosed and heated structures) to experience warm conditions and others in a lathhouse (partially open and unheated structure) or outside to experience cool conditions, with other groups moved in between the warm and cool environments at weekly intervals to experience intermediate conditions. These intermediate groups spent either 2, 3 or 5 days per week in a greenhouse. The treatments produced 17 unique sets of temperature conditions. We monitored height-growth initiation for all 17 treatments and diameter-growth initiation for four treatments and recorded hourly air temperature for each treatment using Onset H08 data loggers (Table S2).

Data collection

To observe height-growth initiation (terminal budburst), we checked the terminal buds of study trees at least once per week from February until all trees burst bud or until mid-August (whichever came first). We defined budburst as occurring when the bud scales had parted enough to observe leaf tissue. In the field-based study, we observed 29 990 instances of budburst from 8312 unique trees, while in the controlled-environment study we observed 9142 instances of budburst, each from a unique tree (Table S3, S4).

To observe diameter-growth initiation, we equipped a subset of the trees with electronic dendrometers that measured and recorded stem diameter at the base of the tree every 30 min to determine when annual diameter growth began. We used DEX dendrometers from Dynamax (Houston, TX, USA) and DR dendrometers from Ecomatik (Munich, Germany) and recorded measurements on a Campbell CR10X or CR1000 data logger (Campbell Scientific, Logan, UT, USA). In the field-based study, we observed 252 instances of diameter-growth initiation from 99 unique trees, while in the controlled-environment study we observed 27 instances of diameter-growth initiation, each from a unique tree (Table S3, S4).

Chilling and forcing functions

We modeled the timing of growth initiation using functions that characterize how different values of hourly temperature

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contribute to the accumulation of chilling and forcing as sensed by trees throughout the dormant season (assumed to be November 1 through the date of growth initiation) (Fig. 2). Our models allowed trees to accumulate chilling and forcing units simultaneously. In previous studies with coast Douglas-fir, this type of 'parallel' model of chilling and forcing accumulation successfully predicted the timing of height-growth initiation and led to better predictions than other approaches (e.g., 'sequential' models or parallel models with different dormant season starting dates) (Harrington *et al.*, 2010; Gould *et al.*, 2011). However, the effectiveness of these functions for predicting other phenological events, particularly diameter-growth initiation, has remained an open question which we sought to address in this study.

Model fitting

We fit models of the growth initiation processes using a hierarchical Bayesian approach and Markov chain Monte Carlo (MCMC) simulations. We assigned noninformative prior distributions to all parameters, allowing the data and likelihood to predominate in parameter estimation. We ran the models with three MCMC chains, confirmed the chains had converged using the Gelman–Rubin statistic and visual inspection of the chains and posterior parameter distributions, and checked for autocorrelation in the chains. For each analysis, we calculated the deviance information criterion (DIC) for models with and without the parameters related to chilling to assess whether and how much incorporating chilling improved model fit. Models were implemented in JAGS using the rjags package (Plummer, 2014) in R version 3.1.2 (R Core Team, 2014).

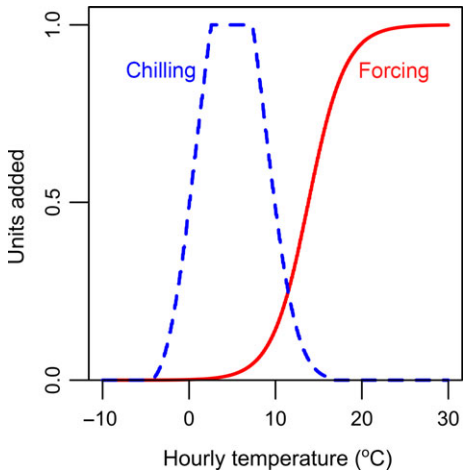

Fig. 2 The functions that depict how trees sense chilling and forcing (i.e., accumulate chilling/forcing units), based on hourly temperature from November 1 through growth initiation. See Harrington *et al.* (2010) for a description of function development.

Determining minimum chilling requirements for growth initiation

Using data from the controlled-environment study, which had some very low-chilling treatments (i.e., very warm winters), we estimated the minimum amount of chilling required for most trees to initiate growth. To do this, we fit a binomial model of the probability of a tree initiating growth as a function of chilling using data on the proportion of trees within a family (individuals grown from seed collected from the same parent tree) that successfully initiated growth:

$$p = \frac{C^b}{c^{*b} + C^b} \quad (1)$$

where p is the probability of growth initiation, C is the amount of chilling received, c^* is a parameter indicating the number of chilling units at which p equals 0.5 and b is a parameter that affects the shape of the relationship between p and C. We included random effects for each unique treatment environment (to account for any phenologically relevant variability in the treatments not related to chilling and/or any variability in measurements across treatments) and for family (to account for genetic variability) by allowing c^* to vary with these variables.

Modeling growth initiation dates

To predict dates of growth initiation based on the temperatures that trees experienced, we modeled the number of accumulated forcing units required for initiation to occur based on the number of chilling units accumulated at any point in time. We focused on temperature cues and not photoperiod because previous studies have shown no evidence of photoperiod effects on budburst in Douglas-fir, although strong support for temperature effects (Laube *et al.*, 2014; Appendix S1).

For the height-growth initiation model, we used the number of chilling and forcing units accumulated on the date when 50% of the trees within a family experiencing the same preinitiation environment burst terminal bud. These preinitiation environments represented a unique series of hourly temperatures and were either a particular year at a particular site for the field-based study, or a unique treatment for the controlled-environment study. We used the date of 50% budburst to provide a central response of closely related individuals to a particular set of environmental conditions. We then fit a Gaussian regression model in which the natural logarithm of forcing was a linear function of the natural logarithm of chilling. Thus, on the non-log-transformed scale, required forcing and its variance change nonlinearly with chilling. This model defines the 'possibility line' (sensu Harrington *et al.*, 2010) that characterizes the different combinations of chilling and forcing at which growth initiation is able to occur:

$$F = e^{a - b\log(C)} \quad (2)$$

where F is the forcing required for height-growth initiation, C is amount of chilling experienced and a and b are parameters. We included random effects for unique pre-initiation environment (to account for any phenologically relevant variability in

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the environment not related to chilling or forcing, and/or any variability in measurements across site, year or treatment) and for family (to account for genetic variability).

For the diameter-growth initiation model, we used the number of chilling and forcing units accumulated at the time of growth initiation for each tree. We modeled diameter-growth initiation at the individual instead of family level because we had fewer observations compared to height-growth initiation. However, the more frequent measurements used for observing diameter-growth initiation (stem diameter measurements once every 30 min, compared to the ~weekly observations for height) were likely to compensate to some degree for the smaller sample size in terms of accurately describing the relationship between required forcing and chilling. We modeled the relationship between required forcing and chilling using a Gaussian spline regression model with one knot that allowed the expected amount and variability of required forcing to vary nonlinearly with chilling:

$$w = \frac{C^{\gamma}}{\beta^{\gamma} + C^{\gamma}}$$

$$F = (a_1 - b_1 C)(1 - w) + (a_2 - b_2 C)w \quad (3)$$

$$\sigma = \sigma_1(1 - w) + \sigma_2 w$$

where F is the forcing required for diameter-growth initiation, σ is the standard deviation in F, C is the amount of chilling experienced and the rest of the letters are parameters. The function w allows the functions for F and σ to transition smoothly from one linear equation for F (defined by a_1 and b_1) and one value of σ (σ_1) to a second linear equation for F (defined by a_2 and b_2) and value of σ (σ_2) between low and high values of C. We also included random effects for unique pre-initiation environment and individual (to account for genetic variability). We fit other models, such as a log-transformed linear model (used for height-growth initiation) and a negative exponential model (used in other budburst studies), but did not use these because they did not accurately describe the relationship across the range of chilling values observed in this study.

Projecting changes in growth initiation phenology with climate change

We used the fitted models of height- and diameter-growth initiation to project how climate change might alter the timing of these phenological events across the region. We first estimated hourly temperatures in each cell of a gridded map of coast Douglas-fir's horizontal distribution in the region (1 arc-minute resolution) under current conditions (1981–2010). To do this, we compiled hourly temperature recordings from 420 weather stations in the region with data from 1981 to 2010. For each grid cell, we then estimated hourly temperature based on the records from the four nearest stations and the monthly mean differences in temperature between the cell and each station, which we calculated using ClimateWNA (Wang *et al*., 2012). Then, we calculated accumulated chilling and forcing for each hour of those temperature time series and used the growth initiation models to calculate the expected dates of height- and diameter-growth initiation for each year of station data, and calculated the median initiation date across those years for each station-grid cell pairing. To account for geographic patterns in genetic variation related to growth initiation timing (Aitken & Hannerz, 2001; St. Clair *et al*., 2005; Gould *et al*., 2011, 2012), we used the inverse-distance-weighted mean effect of genetic source for the eight nearest seed sources in estimating growth initiation date at each grid cell. Next, for each grid cell, we calculated the inverse-distance-weighted mean initiation date based on the four nearest stations to produce our final estimates of growth initiation dates under the current climate. Because we modeled growth initiation across all locations in the tree's horizontal range, some of these grid cells are outside of its elevational range. However, information on elevational distribution is less reliable and we wanted to ensure that we did not exclude locations at marginal elevations that might support coast Douglas-fir, although we did drop grid cells with projected initiation dates of August 15 or later from the analyses.

To produce estimates of growth initiation dates in the future, we calculated monthly mean temperatures for each weather station under current (1981–2010) and future (2071–2100) climates (using ClimateWNA), applied the difference in these values to the temperature records from the stations and then repeated the process described above. We based future temperature estimates on the model ensemble projections used in the Intergovernmental Panel on Climate Change Fifth Assessment Report (IPCC, 2013) with the RCP8.5 climate change scenario, a high-warming scenario that we selected to cover a large range of potential temperatures.

Projecting changes in growing season conditions due to changes in climate and phenology

In these analyses, we assessed how the direct impacts of climate change and phenological responses to climate change might together alter the growing conditions trees experience across the region, specifically assessing changes in the exposure of trees to frost and to suitably warm and moist conditions while growing. To quantify changes in frost exposure, we calculated the number of hours with temperatures ≤ -2 °C (hard frost events that could be damaging – Bigras *et al*., 2001) in the spring or summer (up to September 1) following growth initiation under current and future climates using the mapped hourly temperature and growth initiation estimates described above.

We used actual evapotranspiration (AET) as our metric of suitably warm and moist growing conditions. AET is a well-established, integrative and physiologically meaningful indicator of the simultaneous availability of energy and water for plant growth; in other words, it is a representation of the climatic favorability of an environment for growth (Stephenson, 1990, 1998). More specifically, AET is a standardized estimate of the expected amount of evapotranspiration at a point in the landscape given the amounts of energy and water available and integrates information on the values and seasonal dynamics of temperature, precipitation, insolation (itself a function of latitude, day length, slope and aspect), snowpack and soil

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moisture. To calculate AET across the region, we used a Thornthwaite-type water balance model following Lutz *et al.* (2010), an approach considered most appropriate when reliable measures of humidity and wind speed are not available (Dingman, 2002), as with this study. The climatic data 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). For both current and future time periods, we estimated the annual amount of AET and the amount of AET during the growing season (time between growth initiation and November 1) and then calculated the proportion of AET experienced during the growing season as a metric of the proportion of favorable conditions trees experience while actually growing.

Results

Our results suggest that coast Douglas-fir has an obligate chilling requirement for height- but not diameter-growth initiation. At reduced levels of chilling, the proportion of trees with successful height-growth initiation declined sharply (Fig. 3), suggesting that some minimal amount of chilling is required for terminal budburst to occur in most trees. The chilling threshold below which 50% or less of trees were expected to initiate height growth was 327 chilling units (95% credible interval of 162–497) (Table S5). Incorporating chilling improved model fit substantially, reducing DIC by 98 (reductions >10 are considered substantial, such that the poorer-fitting model is unlikely to be useful in making predictions – Bolker, 2008). In contrast, all monitored trees initiated diameter growth under all levels of chilling.

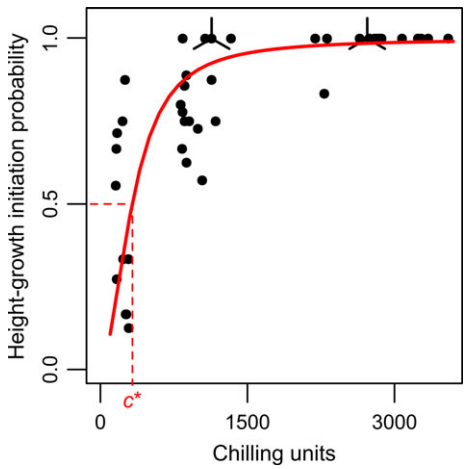

Fig. 3 The probability of trees initiating height growth declined sharply as chilling reached low levels. In contrast, all monitored trees initiated diameter growth across all values of chilling (data not shown). Data points show the proportion of trees in a family initiating height growth versus the number of chilling units accumulated. Lines arising from some of the dots indicate the number of data points that share the same values (sunflower plot). The curve shows modeled probability of height-growth initiation. The value of c^* (327) indicates the number of chilling units at which the probability of height-growth initiation equals 0.5.

For both height- and diameter-growth initiation, we found that reductions in chilling resulted in an accelerating increase in the amount of forcing required for growth initiation (Fig. 4, Table S5). The variability in required forcing also increased with reduced chilling, as evidenced by the widening prediction intervals for required forcing at lower chilling. Incorporating chilling improved model fit substantially, reducing DIC by 6204 and 1291 for height- and diameter-growth initiation, respectively. Although height- and diameter-growth initiation showed the same general relationship between required forcing and chilling, there were some notable distinctions. One was that for any given amount of chilling, more forcing was required for height- than diameter-growth initiation, consistent with our observation that height-growth initiation tended to occur later in the year (by an average of 48 days). A second was that at low values of chilling, the increase in required forcing with reduced chilling was greater for height- than diameter-growth initiation.

Model predictions of growth initiation processes explained a relatively high proportion of the variation in the observed values (Table 1). While information on genetic source improved model predictions substantially for the probability of height-growth initiation, it had little effect on predictions of the forcing required for height- or diameter-growth initiation across the wide range of chilling we examined (Table 1). For our field sites, the root-mean-square error for growth initiation date predictions across all years was 9.7 and 5.7 days for height- and diameter-growth initiation, respectively.

The modeled impacts of climate change on the dates of height- and diameter-growth initiation differed across the region (Fig. 5). At higher latitudes and elevations, growth initiation dates tended to advance strongly with warming (occurring much earlier in the year). This advance was weaker toward lower latitudes and elevations, and switched to a delay (initiation occurring later in the year) near the lower latitude and elevation edges of the coast Douglas-fir range. Because growth initiation generally occurs later in the year at higher latitudes and elevations under current conditions, the predicted changes in initiation timing result in a more homogenous regional pattern of initiation dates in the future.

The joint effects of changes in climate and phenology on predicted growing season conditions also differed across the region. Our models suggest that under climate change, trees in most locations will generally be

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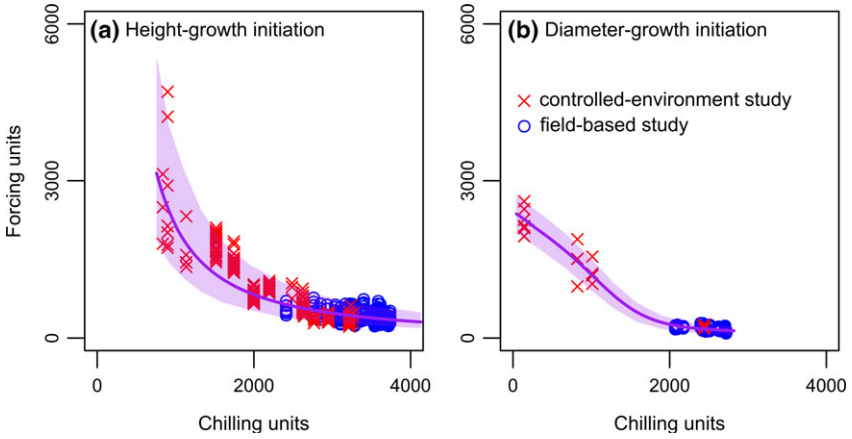

Fig. 4 With reductions in chilling, the forcing required for growth initiation increased at an accelerating rate and became more variable. (a) Height-growth initiation. Points show the number of chilling and forcing units accumulated when 50% of individuals within a family initiated height growth. Data not shown for conditions that resulted in less than 50% of individuals initiating height growth. (b) Diameter-growth initiation. Points show the number of chilling and forcing units accumulated when diameter-growth initiation occurred for an individual. Curves show the expected amount of forcing required for growth initiation to occur given the amount of chilling experienced. Shading shows 95% prediction intervals.

Table 1 The r^2 values for comparisons between predicted and observed values for the growth initiation models

Explanatory variables used to make predictions	Probability of height-growth initiation	Forcing required for height-growth initiation	Forcing required for diameter-growth initiation
Chilling only	0.563	0.795	0.974
Chilling plus genetic random effect	0.715	0.805	0.975

exposed to a similar or smaller number of frost events in the spring or summer following growth initiation for both height and diameter growth, although trees in some locations could experience substantial increases in spring/summer frost exposure while growing, especially in terms of diameter growth (Fig. 6a). For all modeled grid cells, 9.0 and 23.4% showed predicted increases in frost exposure for height and diameter growth, respectively. Also, 0.068 and 7.9% of all grid cells showed relatively large predicted increases in frost exposure (greater than 10 hours), for height and diameter growth, respectively. Locations with predicted increases in frost exposure during the spring/summer growth period were mostly at high elevations, and the increases tended to be greater and more widespread for diameter- compared to height-growth initiation. For both height and diameter growth, trees at higher latitudes and elevations were predicted to experience a similar or greater proportion of the year's favorable growing conditions (as measured by AET) while actually growing, implying that shifts in the timing of growth initiation will generally track shifts in the onset of suitably warm and moist conditions (Fig. 6b). In contrast, trees at lower latitudes and elevations are predicted to experience a smaller proportion of the year's favorable conditions while growing, implying that shifts in growth initiation will lag behind shifts in the onset of favorable conditions. Locations where growth initiation lags behind climate change are expected to be more widespread for diameter growth than height growth.

Discussion

By projecting shifts in both climate and the timing of growth initiation, we were able to assess the ability of trees to track climate change with changes in phenology. Our results suggest that the phenological responses of coast Douglas-fir to climate change will differ substantially across its geographic range for both height- and diameter-growth initiation. At high latitudes and elevations, our models predict that growth initiation will occur earlier in the year and allow trees to track the onset of favorable growing conditions (Fig. 6b), generally without exposing trees to substantially greater frost risk (although some locations may experience large increases in frost risk following diameter-growth initiation) (Fig. 6a). In contrast, toward

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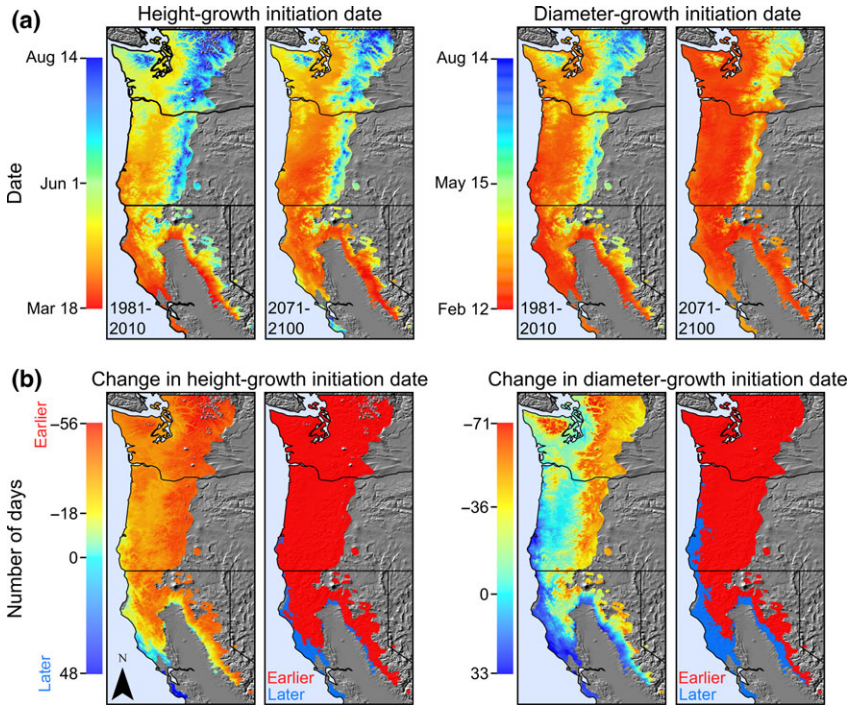

Fig. 5 Climate change affects the timing of growth initiation differently across the region for both height- and diameter-growth initiation. Under climate change, growth initiation is expected to occur earlier in the year in the higher latitude and elevation portions of the region, but remain unchanged or even occur later toward the lower latitude and elevation limits of coast Douglas-fir. (a) Expected dates of growth initiation under the current climate (1981–2010) and a future climate scenario (RCP8.5, 2071–2100) for height- and diameter-growth initiation. (b) Expected change in growth initiation dates between the current and future time periods shown in 'a'. Negative values (red) indicate that growth initiation is expected to occur earlier in the year; positive values (blue) indicate that it is expected to occur later.

lower latitude and elevation range limits, the models predict that advances in growth initiation will lag behind shifts in climate due to reduced chilling (Fig. 6b), with growth initiation even occurring later in the year in some locations (Fig. 5). Our models also predict that growth initiation will lag behind climate change over a greater area for diameter growth than height growth, suggesting that diameter-growth phenology may be less likely to track advances in favorable growing conditions with advances in growth initiation (Fig. 6b). These maladaptive phenological responses could reduce the resilience of coast Douglas-fir to climate change in the warmer portions of the tree's range.

Joint effects of changes in climate and phenology on growing conditions

Under future climates, the conditions trees experience while growing will be determined by both changes in climate and phenological responses to those changes (i.e., advances or delays in growth initiation timing). In terms of frost exposure, warming will generally lead to fewer frost events at any particular time of year for most of the world (IPCC, 2013), including the Pacific Northwest region of the United States (Mote *et al.*, 2013). But if warming also leads to earlier growth initiation, plants could be exposed to more frost events while growing if changes in phenology outpace changes in frost risk (Cannell, 1985; Cannell & Smith, 1986). Our models predict that the number of spring/summer frost events following height- and especially diameter-growth initiation will increase for some locations, which could represent an important threat to tree performance in these areas (Saxe *et al.*, 2001). Nevertheless, the models predict that for most of the region, height- and diameter-growth initiation will track changes in climate and not lead to greater frost risk (Fig. 6a) (also see Morin & Chuine, 2014). However, changes in temperature variability are poorly constrained in climate projections and could alter the risk of frost following growth initiation, and late-spring frosts can still occur even in a warmer climate, so the threat of frost is unlikely to disappear even in locations where it might be reduced (IPCC, 2013).

In addition to changes in frost risk, the onset of favorable growing conditions (i.e., periods with warm

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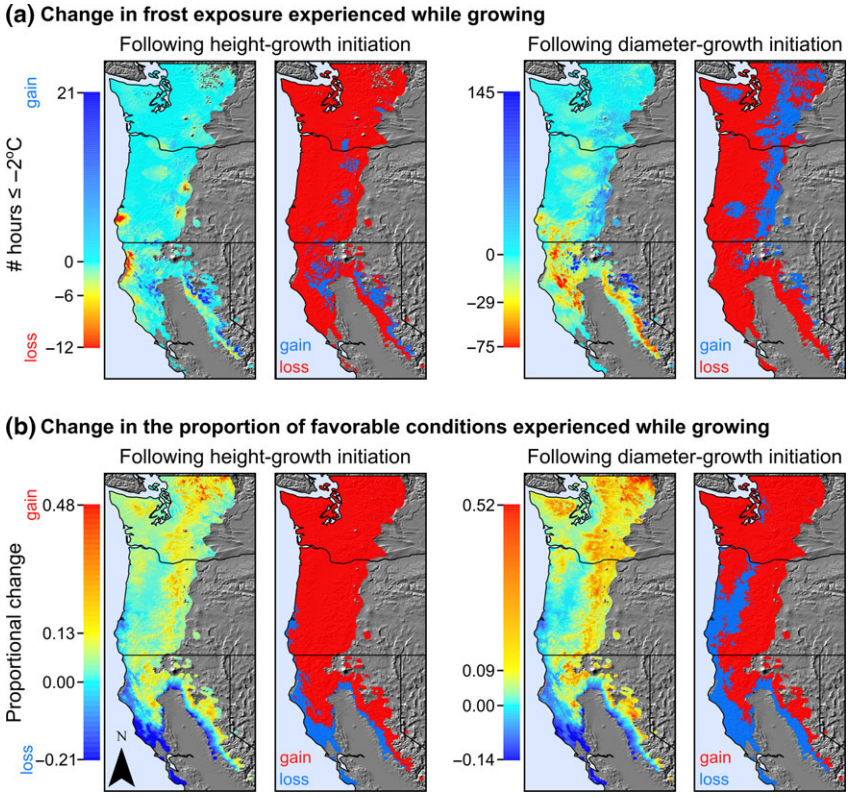

Fig. 6 The joint effects of changes in climate and phenology on the conditions trees experience while growing. (a) Frost exposure. Maps show the expected change in the number of hours with temperatures ≤−2°C (hard frost events) trees experience between growth initiation and September 1. Positive values (blue) indicate trees are likely to experience a gain in frost exposure, suggesting that phenological shifts will outpace reductions in frost, while negative values (red) indicate a loss. (b) Favorable growing conditions. Maps show the expected change in the proportion of favorable growing conditions (based on actual evapotranspiration) experienced while growing. Positive values (red) indicate a gain in this proportion, suggesting phenological shifts will track climate, while negative values (blue) indicate a loss, suggesting that phenological shifts will lag behind climate shifts.

temperatures and high soil moisture) will also occur earlier in the year with climate change. Our models indicate that coast Douglas-fir growth initiation will likely track these changes in favorable climatic conditions at high latitudes and elevations, but lag behind these shifts at lower latitudes and elevations, particularly along the coast (Fig. 6b). These results highlight the importance of considering the joint effects of shifts in phenology *and* climate on the growing conditions plants experience, and not simply changes in phenology alone. For example, advances in diameter-growth initiation are expected to lag behind climate shifts in large sections of Oregon (Fig. 6b) despite exhibiting advances in initiation date (Fig. 5b). However, genotypic differences in certain plant traits (e.g., drought or cold resistance) could affect how vulnerable trees will be to this misalignment of phenology and climate (Bansal *et al.*, 2015a,b). In addition, temperatures in the previous spring can impact phenological events, so changes in interannual temperature variability could be important for phenological shifts (Fu *et al.*, 2014). Shifts in the timing of growth cessation events in the autumn will also impact how well trees track climate change, but these shifts can be complex (Keenan & Richardson, 2015) and are much less understood than changes in spring events (Gallinat *et al.*, 2015), and thus warrant further research.

Comparison of height- and diameter-growth initiation relationships with climate

Our chilling and forcing functions led to similar predictions for height- and diameter-growth initiation timing (Figs 4 and 5), suggesting that these two phenological events share similar relationships between exposure to chilling and the amount of forcing required for growth initiation. Thus, well-established methods for modeling budburst based on chilling and forcing functions can be extended to diameter-growth initiation for coast Douglas-fir and could represent a promising approach for modeling a variety of phenological events.

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Even though we found the relationships of height- and diameter-growth initiation with climate to be broadly similar, there were some important distinctions. Many plant species, including coast Douglas-fir, require some chilling for budburst to occur (Irgen-Moller, 1958; Wommack, 1960; Romberger, 1963; Vegis, 1964), but it has remained unclear whether diameter-growth initiation has a similar obligate chilling requirement. We found strong evidence for a minimum chilling requirement for height-growth initiation (Fig. 3), consistent with previous results, but found no evidence for a minimum chilling requirement for diameter-growth initiation. Thus, at extremely low-chilling, diameter-growth initiation will still likely occur for coast Douglas-fir, even though height-growth initiation might not.

Although diameter-growth initiation did not appear to have an obligate chilling requirement, our models suggest that warming (and the associated loss of chilling) could cause shifts in diameter-growth initiation to lag behind climate change across a greater geographic area compared to height-growth initiation for coast Douglas-fir (Fig. 6b), which could have important consequences for the tree's ability to cope with climate change. This possibility is worrying because while diameter-growth initiation is a critical component of tree function and development, it is much less understood than height-growth initiation due to the greater difficulty of observation. Trees in locations where height- and diameter-growth initiation respond differently to warming might experience changes in tree form (particularly stem taper) and carbon balance (due to potential changes in the ratio of photosynthetic to nonphotosynthetic tissues). Additional changes in tree form could result from differences in the relationships between growth initiation and climate for terminal budburst (which leads to elongation of the stem and height-growth initiation) and lateral budburst (which leads to elongation of branches). Thus, it is important to analyze multiple growth initiation events when studying the relationship between tree growth phenology and climate.

There are some important uncertainties in the type of process-based phenological models used in this study that should be considered when interpreting growth initiation projections. Currently, we have a poor understanding of the biochemical mechanisms that control the timing of growth initiation in trees (Hänninen & Kramer, 2007; Hänninen, 2016), and simulation studies have shown that mathematical models based on different biological assumptions can produce very similar phenological predictions for the current climate, but potentially very different predictions for future conditions (Hunter & Lechowicz, 1992). Thus, better understanding of the biochemical mechanisms underlying growth initiation is an important goal for future research. But in the absence of this understanding, process-based models that use metrics of chilling and forcing remain one of the best tools available for predicting the impacts of climate change on tree phenology (Hänninen & Kramer, 2007). The uncertainty in biochemical mechanism also highlights the importance of fitting phenological models to data collected from a wide range of climatic conditions, including those warmer than what is currently experienced in a species' range but likely to occur in the future, as we did in this study. By doing so, predictions of future growth initiation events are not extrapolations beyond the range of temperatures used to fit the models.

Implications of phenological responses to climate change

The geographic patterns in predicted phenological responses to climate change could lead to differences in the resilience of coast Douglas-fir to climate change across its range. Our models suggest that near the lower latitude and elevation edges of the range, where changes in growth initiation timing are predicted to lag behind shifts in climate, trees will capture a smaller portion of the year's favorable growing conditions (Fig. 6b), resulting in lower productivity than what would be possible. If other species in these locations (either current residents or new migrants) are better able to track climate change, they could experience gains in productivity relative to coast Douglas-fir, which might give these species a competitive advantage (Cleland *et al.*, 2012; Harrington & Gould, 2015). This potential loss of competitive ability could be one factor that contributes to possible range contractions along the warm edges of coast Douglas-fir's distribution (also see Morin *et al.*, 2008; Chuine, 2010; Amano *et al.*, 2014). In addition, the variance in growth initiation timing was greater at low levels of chilling (Fig. 4), which would likely make predicting the exact timing of these phenological events increasingly difficult with warming.

In contrast, phenological responses in the higher latitude and elevation portions of the range appear to generally promote resilience to climate change by allowing coast Douglas-fir to initiate growth earlier in the year and track the onset of favorable growing conditions (Fig. 6b). These adaptive phenological responses could facilitate migration to higher latitudes and elevations, depending on changes in other range determinants. However, in some higher elevation locations, coast Douglas-fir might experience more frost damage because advances in growth initiation outpace reductions in frost risk (Fig. 6a), which could slow local range expansions. Thus, phenology could play an

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important role in mediating the impacts of climate change on coast Douglas-fir across its range.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Testing for photoperiod effects.
Table S1. Mean temperatures at the sites in the field-based study from November through April (period when plants receive most of their chilling).
Table S2. Mean temperatures in the controlled-environment study from November through April (period when plants receive most of their chilling).
Table S3. The number of growth initiation observations for each seed source.
Table S4. Range of annual mean growth initiation dates at each site in the field-based study.
Table S5. The parameter estimates (posterior means) for each of the growth initiation models.

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