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Research paper

Growth phenology of coast Douglas-fir seed sources planted in diverse environments

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The timing of periodic life cycle events in plants (phenology) is an important factor determining how species and populations will react to climate change. We evaluated annual patterns of basal-area and height growth of coast Douglas-fir (*Pseudotusga menziesii* var. *menziesii* (Mirb.) Franco) seedlings from four seed sources that were planted in four diverse environments as part of the Douglas-fir Seed-Source Movement Trial. Stem diameters and heights were measured periodically during the 2010 growing season on 16 open-pollinated families at each study installation. Stem diameters were measured on a subset of trees with electronic dendrometers during the 2010 and 2011 growing seasons. Trees from the four seed sources differed in phenology metrics that described the timing of basal-area and height-growth initiation, growth cessation and growth rates. Differences in the height-growth metrics were generally larger than differences in the basal-area growth metrics and differences among installations were larger than differences among seed sources, highlighting the importance of environmental signals on growth phenology. Variations in the height- and basal-area growth metrics were correlated with different aspects of the seed-source environments: precipitation in the case of height growth and minimum temperature in the case of basal-area growth. The detailed dendrometer measurements revealed differences in growth patterns between seed sources during distinct periods in the growing season. Our results indicate that multiple aspects of growth phenology should be considered along with other traits when evaluating adaptation of populations to future climates.

Keywords: adaptation, assisted migration, budburst, cambium, dormancy, genecology.

Introduction

Understanding how environmental signals affect the timing of periodic life cycle events in plants (phenology) is a key factor in predicting the effects of climate change. Shifts in plant phenology, such as the timing of budburst, present some of the most visible evidence of the impacts of climate change in recent decades (Walther et al. 2002, Menzel et al. 2006). Phenological events are closely tied to environmental signals such as seasonal changes in temperature (Menzel and Sparks 2006). Plants have evolved mechanisms to coordinate the timing of phenological events so that periodic growth and other events occur when environmental conditions are optimal with respect to resource availability and minimizing the likelihood of damage from cold, drought or other factors (Rehfeldt 1978, Howe et al. 2003, Chuine 2010, Wilczek et al. 2010). Adaptation to different environments has produced genetic variation in phenological traits within plant species. This variation is a valuable resource for adapting to climate change as it may provide opportunities to select populations that are well suited to future climates (Millar et al. 2007, St. Clair and Howe 2007, Hamann et al. 2011). Understanding genetic variation in a wide range of phenological traits, and the environmental signals that trigger phenological events, is critical to evaluating both climate change impacts and the value of assisted migration or other mitigation strategies (Wilczek et al. 2010).

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We use the term growth phenology to describe seasonal pattern of primary (apical) and secondary (cambial) growth in woody species. Primary growth is often measured in terms of height growth and secondary growth is often measured in terms of diameter or basal-area growth. Height growth begins with budburst and ends shortly after budset (i.e., after the last formed stem units elongate). Genetic variation in the timing of budburst and budset in coast Douglas-fir (*Pseudotusga menziesii* var. *menziesii* (Mirb.) Franco) has been documented in numerous studies (Campbell and Sorensen 1973, Campbell 1974, Campbell and Sugano 1975, Sorensen 1983, St. Clair et al. 2005). Other traits that describe growth phenology, such as the initiation and cessation of diameter growth, are less obvious and more difficult to measure than budburst. Consequently, there is relatively little information on genetic variation in these traits. The timing of diameter growth initiation and cessation has been found to differ among populations within several tree species (Daubenmire 1950, Dietrichson 1964, Emmingham 1977, Jayawickrama et al. 1998). Clinal variation in these traits has been reported with early initiation and early cessation of diameter growth among populations from colder environments (Dietrichson 1964, Worrall 1975, Jayawickrama et al. 1998). Cambial cells are susceptible to cold damage during active growth (e.g., Glock 1951), thus growth phenology has implications for cold hardiness (Mellerowicz et al. 1992, Repo et al. 2000). Dietrichson (1964) found populations of Scots pine (*Pinus sylvestris* L.) from southern latitudes generally had more frost damage to cambial cells than those from northern latitudes when grown in a common environment. Genetic variation in growth phenology is also related to wood properties. Vargas-Hernandez and Adams (1994) reported that families of coast Douglas-fir with later growth cessation had greater wood density than those with earlier cessation owing to a longer period of latewood growth.

Growth phenology is also strongly affected by environmental factors. The initiation of height growth (i.e., budburst) is largely controlled by air temperatures during the dormant period (Campbell and Sugano 1979, Harrington et al. 2010). Low heritabilities have been reported for traits related to diameter-growth phenology (Li and Adams 1994, Emhart et al. 2006), indicating that environmental variation has a relatively strong effect on the phenotypic expression of these traits. Interannual variation in the environment can substantially change the timing of diameter growth. Dimock (1964) reported a difference of 22 days in the date of diameter growth initiation of Douglas-fir in two successive years. Griffith (1960) and Reukema (1965), also working with Douglas-fir, each reported a range of 45 days within a 5-year period in the date when 50% of diameter growth was completed. Gonzalez-Benecke et al. (2010) demonstrated that the timing of growth cessation can be delayed substantially by maintaining high soil water content. Environmental stress resulting from competition with other trees can delay growth initiation and hasten growth cessation, possibly as a result of resource limitations and differences in auxin concentrations within stems (Kozlowski and Peterson 1962).

Coast Douglas-fir occurs in varied environments in western North America between latitudes of ~34°N to 54°N and elevations between sea level and 2300 m (Hermann and Lavender 1990). Populations of Douglas-fir are closely adapted to their local environments, and pronounced clines associated with environmental gradients have been found for many traits (Campbell and Sugano 1979, Sorensen 1983, Loopstra and Adams 1989, St. Clair et al. 2005). The effects of genetics and environment on growth phenology have been investigated in some past work, but there are few examples where diameter-growth phenology, in particular, has been compared among populations from a wide range of environments (e.g., Emmingham 1977). In addition to being difficult to measure, the period of cambial activity occurs over a relatively long period of time. Detailed measurements throughout the growing season are needed to evaluate differences among populations and among environments. In the present study, we measured the timing of budburst, budset, periodic height growth and periodic diameter growth on Douglas-fir seedlings from different seed sources that were planted into multiple test environments. We also measured stem diameter on a subset of trees every 0.5 h using electronic dendrometers. These data provided detailed information on cambial growth phenology that we used to test the hypothesis that seasonal patterns of diameter and height growth would differ among seed sources and test environments.

Methods

Data were collected during the 2010 and 2011 growing seasons at four installations of the Douglas-fir Seed-Source Movement Trial (Figure 1). The trial is a set of common gardens established before the beginning of the 2009 growing season at nine sites in Oregon and Washington. The trial includes 120 open-pollinated families of coast Douglas-fir that were grown from seed collected from populations in western Washington and Oregon and northern California. Seed were collected from a sample of dominant and codominant trees in wild stands without considering phenotype (i.e., no 'plus-tree' selection). Seedlings were grown in 700 ml foam blocks for one growing season and then transplanted into 2800 ml pots for a second growing season before being outplanted. Eight seedlings of each family were planted at each installation in most cases. Fewer seedlings were planted in some cases owing to poor survival prior to planting and additional seedlings of other families were planted in their places. Seedlings were planted at a 3.6-m spacing in 20-tree plots composed of families from the

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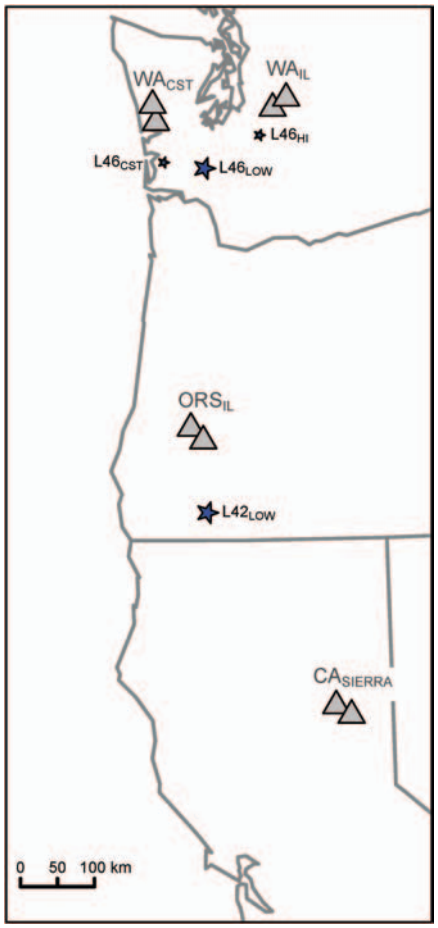

Figure 1. Locations of the study installations (stars) and seed sources (triangles). Dendrometer measurements were made at the L46$_{LOW}$ and L42$_{LOW}$ installations (large stars).

same seed source in a replicated-block design (four blocks each containing all of the seed sources). The installations are located within three latitudinal bands (42, 44 and 46°N) and within three physiographic regions (coast, inland-low elevation and inland-high elevation). We selected four installations for this study that represent a wide range of environmental conditions: the coast, inland-low and inland-high elevation installations within the 46°N band (L46$_{CST}$, L46$_{LOW}$, L46$_{HI}$, respectively), and the inland-low elevation installation within the 42°N band (L42$_{LOW}$). The L46$_{CST}$, L46$_{LOW}$ and L46$_{HI}$ installations were established following commercial clear cuts of stands composed primarily of Douglas-fir. Competing vegetation was manually removed periodically around the study trees to prevent overtopping, but the development of vegetation at these sites has generally been typical of young stands in the Pacific Northwest. The L42$_{LOW}$ installation was established at a tree nursery where competing vegetation was periodically eliminated. Each installation was fenced to prevent browsing.

A set of 16 families was selected for measurements of growth phenology (Figure 1). The families represent four regions from the natural range of coast Douglas-fir: (i) Washington coast (WA$_{CST}$), (ii) Washington inland, low-elevation (WA$_{IL}$), (iii) Oregon southern inland, low-elevation (ORS$_{IL}$), and (iv) the California Sierra Range (CA$_{SIERRA}$). Four families were selected from each region. We refer to the group of families from the same region as a seed source. The seed sources were selected based on previous measurements of budburst (Gould et al. 2011) to include families that burst bud early (CA$_{SIERRA}$ followed by ORS$_{IL}$) and families that burst bud late (WA$_{CST}$ followed by WA$_{IL}$). It was not known at the time the families were selected how other aspects of growth phenology might differ among seed sources.

We measured stem diameters (to the nearest 0.1 mm, using calipers) and heights (to the nearest 1 mm, using rulers) periodically during the 2010 growing season on all four families from each seed source. The first measurement occurred between 10 February and 22 March on all installations other than L46$_{HI}$ where snow prevented measurement until 22 April. At the time of the first measurement, each tree was marked ~5 mm from its base with a paint marker. A cross was marked on both sides of the measurement diameter to align the calipers for subsequent measurements. Trees were remeasured on a weekly or bi-weekly basis. The final measurement occurred between 2 November and 11 November. A total of 526 trees were measured.

Stem diameter on a subset of trees was monitored continuously using electronic dendrometers. Beginning in 2010, dendrometers were installed on four trees from two of the CA$_{SIERRA}$ families and four trees from two of the WA$_{CST}$ families at the L42$_{LOW}$ and L46$_{LOW}$ installations (16 trees at each installation, 32 trees total). Dendrometers were installed on 12 February at L42$_{LOW}$ and 6 March at L46$_{LOW}$. An additional eight dendrometers were added on 19 February 2011 at L42$_{LOW}$ to monitor four trees from each of two families from the ORS$_{IL}$ seed source. Dendrometers were added at L46$_{LOW}$ to eight trees from the same ORS$_{IL}$ families on 3 March 2011. Dendrometer data were collected beyond the end of the 2011 growing season (until 15 December). Dendrometers were placed ~5 mm above the base of each tree. The dendrometers used were DEX70s and DEX100s from Dynamax (Houston, TX, USA) and Model DRs from Ecomatik (Munich, Germany). The precision of the dendrometers was <0.01 mm. Diameter measurements were recorded every 30 min by either a Campbell CR10X or CR1000 datalogger (Campbell Scientific, Logan, UT, USA).

Environmental data including air temperature, relative humidity, precipitation and volumetric soil water content were collected using automated weather stations located at each installation (model U30, Onset Computer Corporation, Pocasset, MA, USA). Soil water content was measured by the weather stations using dielectric sensors (model EC-20, Decagon Devices, Pullman, WA, USA). Variables describing the climates of the seed sources were derived from Rehfeldt's (2006) thin-plate splines of climate normals for the period

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1961–1990 at the seed-collection locations (Crookston 2008). Trees were examined at least weekly during each spring to record the timing of terminal budburst (when green needles were first visible) and weekly or bi-weekly in the summer to record final budset (defined as the appearance of a new terminal bud that did not burst later in the growing season).

A set of phenology metrics was calculated for each tree to summarize basal-area and height-growth phenology. Diameter-growth metrics were based on basal area (area of the stem cross-section) rather than diameter. Because of the relatively low precision of the caliper dataset, the approximate timing of growth initiation and cessation was calculated as the day when 10% of growth was completed (BA_{10}) and the day when 90% of growth was completed (BA_{90}). The approximation approach has been used in other studies that relied on periodic measurements with relatively low frequency and potentially high measurement error (Emmingham 1977, Li and Adams 1994). The day when basal-area growth was 50% complete (BA_{50}) and the percentage of growth completed by 1 August (BA_{AUG1}) were also calculated. Height-growth metrics (HT_{10}, HT_{50}, HT_{90} and HT_{AUG1}) were similarly calculated. The timing of growth initiation and cessation was calculated in the dendrometer dataset by calculating daily growth rates (the differences between daily median values of basal area) and identifying the point when sustained growth began in the spring and terminated in the fall. Growth initiation was defined as the beginning of a period of five or more consecutive days of increasing basal area. Exceptions were made in three cases where the beginning of the growth pattern was clear but there were interruptions in the five consecutive days of growth. Growth cessation was defined as the beginning of a period of five or more days without basal-area growth. BA_{50} and BA_{AUG1} were also calculated from the dendrometer measurements.

Differences among seed sources and installations in the metrics were tested with analysis of variance (Neter et al. 1996) using the following model:

$$M_{ijk} = \mu + S_j + I_k + S_j \cdot I_k + \varepsilon_{ijk}$$

where M_{ijk} is the value of a given metric for tree i from seed source j and installation k, μ is the grand mean, S_j is the main effect of seed source, I_k is the main effect of installation, $S_j \cdot I_k$ is the interaction between seed source and installation and ε_{ijk} is the error term. Model parameters were estimated using the lm package in R (R Development Core Team 2006). Parameters were considered statistically significant at $\alpha < 0.05$. Means were separated using the Bonferroni method to control the family-wise error rate (Neter et al. 1996).

We evaluated evidence that variation in growth phenology among populations is adaptive by calculating Pearson correlation coefficients (Ott 1993) between the phenology metrics measured on all 16 families and variables that describe the climates of the seed-collection locations (e.g., mean annual temperature, growing-season precipitation). Relationships between growth metrics and climatic variables were evaluated at the family level. Correlations were calculated separately for each installation to help understand how the families performed at each installation and how the installations differed. Correlations between the growth metrics and the median date of terminal budburst and budset of each family were also examined. P values were calculated for the correlation coefficients to assess the strength of the correlations; however, both the phenological traits and climate variables are spatially autocorrelated to some degree which increases the probability of a type I error. Thus, the P values should be interpreted with caution (Dutilleul 1993, Legendre et al. 2002).

Basal-area growth patterns during the 2010 and 2011 growing seasons were examined in detail using the dendrometer measurements. We calculated the 5-day running mean of daily growth to reduce the short-term variability in growth rates so that seasonal patterns would be easier to recognize. Differences in growth rates among seed sources were evaluated by calculating a t-statistic for each day of the 2010 growing season (to compare two seed sources) and an F-statistic for each day of the 2011 growing season (to compare three seed sources) (Ott 1993). To compare growth rates between installations, we first normalized the time series by dividing each measurement by the tree's total annual growth to yield proportional values as absolute growth was much greater at $L42_{LOW}$ than at $L46_{LOW}$. Differences in growth rates between installations were evaluated by calculating a t-statistic for each day of the 2010 and 2011 growing season. Critical values ($\alpha < 0.05$) for the t- and F-statistics were calculated to serve as a benchmark to evaluate how extreme the differences were among seed sources and installations. The critical values were not intended to formally test the null hypothesis of no differences as the probability of a type I error would be inflated owing to multiple comparisons (Neter et al. 1996).

To evaluate potential trade-offs between basal-area and height growth, Pearson correlation coefficients were calculated between basal-area and height-growth increments during the 2010 growing season. Height-growth increments were calculated from periodic measurements and basal-area growth increments were calculated for the same periods using the dendrometer data. Both basal-area and height-growth increments were normalized (scaled to the total growth of each tree) so that the correlations would reflect the relative growth rate of each tree during the growing season (i.e., the correlation would not be affected if the trees that had the greatest total height growth also had the greatest total basal-area growth).

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Results

Environments at the seed-source locations and test installations

The climate normals at the seed-source locations and the weather data collected at the installations illustrate differences among the seed-source and test environments (Table 1). The seed-source environments ranged from an interior-montane environment (CA_{SIERRA}) to a temperate-coast environment (WA_{CST}). The CA_{SIERRA} environment is characterized by high daily maximum temperatures, low daily minimum temperatures and little precipitation during the growing season, while the WA_{CST} environment has relatively high minimum temperatures, low maximum temperatures and much greater precipitation during the growing season.

Based on weather data, the $L42_{LOW}$ installation was similar to the CA_{SIERRA} and ORS_{IL} seed-source environments with high temperatures during the growing season and relatively low precipitation. The $L46_{CST}$, $L46_{HI}$ and $L46_{LOW}$ installations were fairly similar to the WA_{IL} and WA_{CST} environments.

Phenology metrics

The main effects of seed source and installation were statistically significant for all of the phenology metrics calculated from the caliper and height measurements, but the seed source × installation interaction was significant only for HT_{50} (Table 2). Among the phenology metrics calculated from the dendrometer measurements, the main effect of seed source was significant in both years (or nearly so) for growth intiation, BA_{50} and BA_{AUG1}. The main effect of installation was significant for growth initiation and cessation in both years and for BA_{50} in 2010. The interaction term was not significant for any of the metrics calculated from the dendrometer data.

The seed sources had different patterns of seasonal growth based on the caliper and height measurements (Table 3). The CA_{SIERRA} seed source generally reached each phenological stage earlier than the other seed sources, while the WA_{CST} seed source was generally the last to reach each stage. The ORS_{IL} trees could not be characterized as either 'early' or 'late'; basal-area growth began and ended relatively late, but height growth began early and ended late. Growth of the WA_{IL} trees began later than the CA_{SIERRA} trees and ended earlier than the WA_{CST} trees. Differences among seed sources were much greater for the height-growth metrics (up to 21.7 days) than for the basal-area growth metrics (up to 8.3 days). Differences among installations were generally greater than differences among seed sources. Differences among installations were also of similar magnitudes for both the basal-area and height-growth metrics. Height growth began (as measured by HT_{10}) at around the same time at all of the installations other than the coldest installation ($L46_{HI}$) where it began considerably later. Basal-area growth also started last, but ended first, at $L46_{HI}$. Height growth ended first at the warmest installation ($L42_{LOW}$); however, basal-area growth ended later at that installation than at any of the others.

The phenology metrics calculated from the dendrometer measurements indicated that differences among seed sources and installations were greater in some cases than those calculated from the caliper measurements (Table 4). Growth initiation (measured with dendrometers) differed significantly between seed sources in 2010 (4.2 days) but BA_{10} (measured with calipers) was nearly equal. Growth initiation occurred 15.1 days later at $L46_{LOW}$ than at $L42_{LOW}$ but BA_{10} differed by only

Table 1. Variables[1] describing the seed-source environments based on 1961–90 climate means and weather variables at the study installations based on measurements from on-site weather stations in 2010 and 2011.

Seed source/ installation	Elevation (m)	T_{ANN} (°C)	T_{GSmin} (°C)	T_{GSmax} (°C)	FFP (days)	PPT_{ANN} (mm)	PPT_{GS} (mm)
Seed sources							
CA_{SIERRA}	1410	8.6	3.8	23.9	93	969	165
ORS_{IL}	427	10.9	7.3	23.1	166	1202	265
WA_{IL}	550	7.8	6.1	18.4	137	2151	612
WA_{CST}	102	9.7	7.7	18.9	180	2705	626
Installations							
2010							
$L42_{LOW}$	415	11.7	8.8	24.9	174	538	184
$L46_{CST}$	177	9.8	8.9	17.8	248	1989	568
$L46_{HI}$	860	7.8	6.9	16.1	196	1305[2]	671
$L46_{LOW}$	241	9.6	8.5	18.7	233	1454	420
2011							
$L42_{LOW}$	415	10.7	5.7	20.6	179	417	143
$L46_{LOW}$	241	8.8	6.5	15.8	198	1212	301

[1]T_{ANN}, annual temperature, T_{GSmin}, minimum temperature during the growing season (1 April to 31 September), T_{GSmax}, maximum temperature during the growing season, FFP, frost-free period, PPT_{ANN}, annual precipitation, PPT_{GS}, precipitation during the growing season.
[2]The rain gauge may have under-measured snow precipitation.

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Table 2. Results of analyses of variance of phenology metrics describing basal-area and height growth.

Model term	df	*P* values for phenology metrics[1]			
Basal-area growth (caliper measurements)					
		BA_{10}	BA_{50}	BA_{90}	BA_{AUG1}
S (seed source)	3	<0.001	<0.001	<0.001	<0.001
I (installation)	3	<0.001	<0.001	<0.001	<0.001
S × I	9	0.224	0.547	0.338	0.463
Residual	510				
Basal-area growth (dendrometer measurements)					
		Initiation	BA_{50}	Cessation	BA_{AUG1}
		2010 growing season			
S (seed source)	1	0.005	<0.001	0.421	0.002
I (installation)	1	<0.001	0.223	<0.001	0.091
S × I	1	0.372	0.690	0.597	0.785
Residual	28				
		2011 growing season			
S (seed source)	2	0.070	0.015	0.215	<0.001
I (installation)	1	<0.001	0.010	<0.001	0.558
S × I	2	0.069	0.897	0.892	0.498
Residual	40				
Height growth					
		HT_{10}	HT_{50}	HT_{90}	HT_{AUG1}
S (seed source)	3	<0.001	<0.001	<0.001	<0.001
I (installation)	3	<0.001	<0.001	<0.001	<0.001
S × I	9	0.434	0.025	0.637	0.063
Residual	510				

[1]BA_{10}, BA_{50}, BA_{90}, day when 10, 50 or 90% of basal-area growth was completed; BA_{AUG1}, proportion of basal-area growth completed on 1 August; HT_{10}, HT_{50}, HT_{90}, day when 10, 50 or 90% of height growth was completed; HT_{AUG1}, proportion of height growth completed on 1 August.

6.1 days and was earliest at $L46_{LOW}$. Similarly, the difference between installations in the date of growth cessation was ~21 days, but the difference in BA_{90} was only ~12 days. Differences among seed sources and installations were fairly consistent between 2010 and 2011. An exception was BA_{50}, which occurred first at $L42_{LOW}$ in 2010 (4 days earlier than at $L46_{LOW}$), but first at $L46_{LOW}$ in 2011 (9.5 days earlier that at $L42_{LOW}$).

To add context to the phenology metrics, total basal-area and height growth in 2010 were summarized for each seed source at each installation (Table 5). Differences among installation in basal-area and height growth were generally greater than differences among seed sources. Basal-area and height growth were much greater at the warm, dry $L42_{LOW}$ installation than at the other installations. Growth was lowest at the cool, moist $L46_{HI}$ installation and it was similar at the $L46_{CST}$ and $L46_{LOW}$ installations. The ORS_{IL} trees had the greatest basal-area growth at each of the installations and had particularly high growth at the $L42_{LOW}$. Seed-source ranks for basal-area growth at each of the installations were generally $ORS_{IL} > WA_{CST} > WA_{IL} > CA_{SIERRA}$. The ORS_{IL} trees also had the greatest height growth among the four seed sources at the $L42_{LOW}$ installation, but the WA_{CST} trees had the greatest height growth at the other three installations. The CA_{SIERRA} trees had the least height growth at all four installations.

Basal-area growth patterns: comparisons among seed sources

The WA_{CST} and CA_{SIERRA} seed sources had different rates of basal-area growth during distinct periods of the 2010 growing season (Figure 2). The first period was linked to the timing of terminal budburst, which occurred first in the CA_{SIERRA} trees at both installations. Basal-area growth rates decreased in both seed sources during the period immediately after budburst. As a result of differences in the timing of budburst, growth was greater in the WA_{CST} trees than in the CA_{SIERRA} trees from late April through early May at the $L42_{LOW}$ installation and in the first half of May at the $L46_{LOW}$ installation. Growth rates of both seed sources increased rapidly after the period of slow growth ended. The CA_{SIERRA} trees entered the period of rapid growth sooner than the WA_{CST} trees, which were still in the period of slow growth following budburst. Consequently, the seed sources shifted ranks in late May or early June so that the CA_{SIERRA} trees had a greater average growth rate for a short period of time. The WA_{CST} trees began their period of rapid growth in mid to late June, and their growth exceed that of the CA_{SIERRA} trees for most of the growing season after 1 July at both installations. The magnitude of the difference in growth rates tended to increase over the remainder of the growing season. There were no distinct changes in growth rates following budset, but growth began to slow down at around the

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Table 3. Differences in treatment means for the phenology metrics describing basal-area growth (from caliper measurements) and height growth. For each metric, the lowest value within the set of seed sources or installations is set to zero and other values are the difference from the lowest value. The original lowest value is given in parentheses. For example, BA_{10} occurred first at the $L46_{LOW}$ installation (4 May) and in the WA_{CST} trees. It occurred 3.8 days later in the WA_{CSL} trees. Means that do not share the same superscript letter within each set of seed sources or installations are significantly different at $\alpha < 0.05$.

Seed source/ installation	Phenology metric[1]			
	Basal-area growth (caliper measurements)			
Seed source	BA_{10}	BA_{50}	BA_{90}	BA_{AUG1}
CA_{SIERRA}	0.7^{b}	0.0^{b}	0.0^{b}	0.08^{a}
ORS_{IL}	8.0^{a}	8.3^{a}	4.7^{a}	0.02^{b}
WA_{IL}	3.8^{ab}	5.5^{a}	1.6^{ab}	0.04^{b}
WA_{CST}	0.0^{b}	10.4^{a}	5.1^{a}	0.00^{b}
Installation				
$L42_{LOW}$	6.1^{c}	9.1^{b}	13.8^{b}	0.07^{b}
$L46_{CST}$	20.5^{b}	18.2^{a}	8.4^{b}	0.00^{c} (0.45)
$L46_{HI}$	37.7^{a}	15.7^{a}	0.0^{a} (21 Sept)	0.02^{c}
$L46_{LOW}$	0.0^{d} (4 May)	0^{c} (20 July)	1.4^{a}	0.13^{a}
	Height growth			
Seed source	HT_{10}	HT_{50}	HT_{90}	HT_{AUG1}
CA_{SIERRA}	0.0^{c}	0.0^{d}	0.0^{b}	0.04^{a}
ORS_{IL}	0.6^{c}	6.8^{c}	7.9^{a}	0.00^{b}
WA_{IL}	15.3^{b}	15.1^{b}	3.3^{ab}	0.04^{a}
WA_{CST}	21.3^{a}	21.7^{a}	7.8^{a}	0.01^{ab}
Installation				
$L42_{LOW}$	0.0^{b} (9 May)	0.0^{c} (13 June)	0.0^{c} (19 July)	0.15^{a}
$L46_{CST}$	3.3^{b}	9.8^{b}	24.3^{a}	0.00^{c} (0.83)
$L46_{HI}$	25.8^{a}	19.0^{a}	26.8^{a}	0.02^{c}
$L46_{LOW}$	1.6^{b}	0.1^{c}	16.9^{b}	0.06^{b}

[1]BA_{10}, BA_{50}, BA_{90}, day when 10, 50 or 90% of basal-area growth was completed; BA_{AUG1}, proportion of basal-area growth completed on 1 August; HT_{10}, HT_{50}, HT_{90}, day when 10, 50 or 90% of height growth was completed; HT_{AUG1}, proportion of height growth completed on 1 August. The unit of measurement for BA_{10-90} and HT_{10-90} is number of days after the date given in parentheses in each column.

Table 4. Differences in treatment means for the phenology metrics calculated from the dendrometer measurements. Treatment means are presented as in Table 3.

Seed source/ installation	Phenology metric[1]			
	Initiation	BA_{50}	Cessation	BA_{AUG1}
	2010 growing season			
Seed source				
CA_{SIERRA}	0.0^{b}	0^{b}	0.0	0.09^{a}
WA_{CST}	4.2^{a}	14.4^{a}	3.6	0.00^{b}
Installation				
$L42_{LOW}$	0.0^{b} (24 Feb)	4.4	20.9^{a}	0 (0.63)
$L46_{LOW}$	15.1^{a}	0 (21 July)	0.0^{b} (11 Oct)	0.04
	2011 growing season			
Seed source				
CA_{SIERRA}	0.0	0^{b}	0.0	0.11^{a}
ORS_{IL}	6.1	12.6^{a}	11.2	0^{b}
WA_{CST}	6.5	11.8^{a}	6.4	0.02^{b}
Installation				
$L42_{LOW}$	0.0^{b} (12 Mar)	0^{b} (12 July)	17.8^{a}	0.02
$L46_{LOW}$	11.5^{a}	9.5^{a}	0.0^{b} (8 Oct)	0 (0.70)

[1]Initiation, day when basal-area growth began; BA_{50}, day when 50% of basal-area growth was completed; Cessation, day when basal-area growth ended; BA_{AUG1}, proportion of basal-area growth completed on 1 August. The unit of measurement for Initiation, BA_{50} and Cessation is number of days after the date given in parentheses in each column.

Table 5. Basal-area and height growth of Douglas-fir from four seed sources at four test installations during the 2010 growing season.

Seed sources	Installation			
	$L42_{LOW}$	$L46_{CST}$	$L46_{HI}$	$L46_{LOW}$
	Basal-area growth (mm^2) [diameter growth (mm)]			
CA_{SIERRA}	934 [19.7]	357 [12.4]	198 [8.0]	345 [12.2]
ORS_{IL}	1519 [25.1]	462 [14.6]	318 [11.2]	463 [14.7]
WA_{IL}	986 [19.4]	327 [11.8]	236 [8.9]	379 [13.0]
WA_{CST}	1049 [20.4]	361 [12.4]	264 [9.9]	440 [14.1]
All sources	1133 [21.3]	379 [12.8]	256 [9.5]	410 [13.6]
	Height growth (mm)			
CA_{SIERRA}	455	266	171	249
ORS_{IL}	702	351	213	315
WA_{IL}	570	360	223	375
WA_{CST}	633	434	260	431
All sources	592	354	216	343

same time that budset occurred. Growth rates were closely coupled during the latter part of the growing season, suggesting that the two seed sources responded similarly to daily variation in environmental conditions.

Basal-area growth increments of trees measured with dendrometers during the 2010 growing season were strongly correlated with height-growth increments only shortly after budburst (Figure 3). The patterns of height growth were similar to the patterns of basal-area growth in that the CA_{SIERRA} seed source had a greater proportion of its growth early in the growing season, but growth of the WA_{CST} seed source was greater later in the growing season and its total growth exceeded that of the CA_{SIERRA} seed source. Although the correlations between basal-area and height growth were weak after budburst, they tended to be positive or negative at both installations during the same parts of the growing season.

Trees from the ORS_{IL} seed source were measured with dendrometers in 2011 in addition to the CA_{SIERRA} and WA_{CST} trees (Figure 4). The growth pattern of the ORS_{IL} trees combined some aspects of the patterns of both the CA_{SIERRA} and WA_{CST} trees. Budburst occurred first in the ORS_{IL} and CA_{SIERRA} trees

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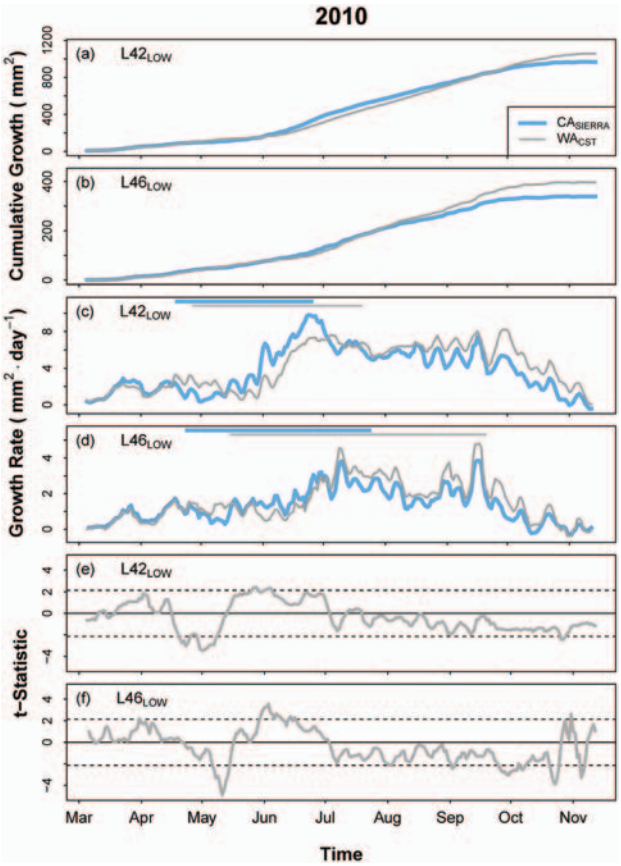

Figure 2. Basal-area growth patterns of Douglas-fir from two seed sources (CA_{SIERRA} and WA_{CST}) at two planting installations ($L42_{LOW}$ and $L46_{LOW}$) during the 2010 growing season. Shown are cumulative basal-area growth (a and b), daily growth rates (c and d) and the *t*-statistics to gauge differences between seed sources in daily growth rate (e and f). The dotted lines in panels e and f show where the null hypothesis of no difference between seed sources would be rejected. The horizontal lines in panels c and d show the period between budburst and budset for each seed source.

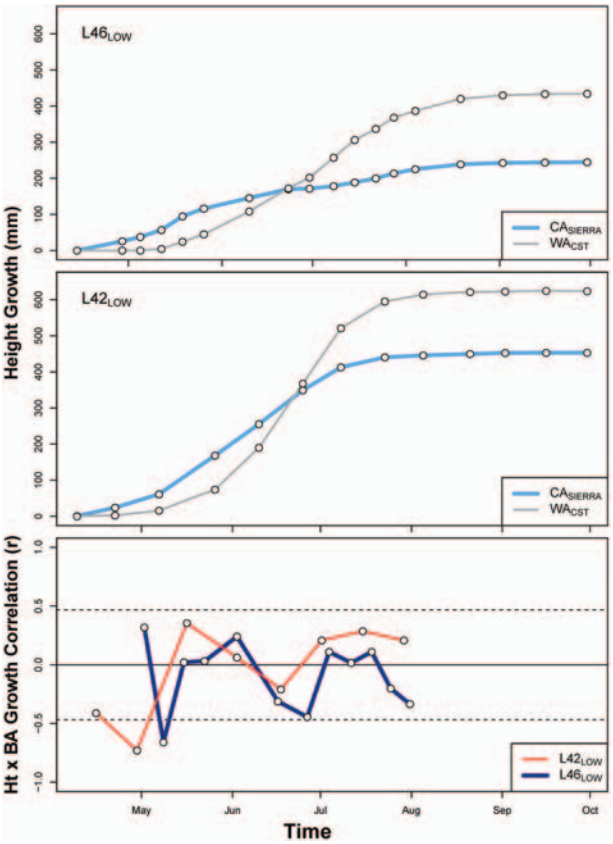

Figure 3. Height growth during the 2010 growing season of trees measured with dendrometers at two installations (upper two panels) and the correlation between periodic height- and basal-area growth increments (lower panel). Dotted lines show critical values for rejecting the null hypothesis of zero correlation between basal-area and height increments at $\alpha = 0.05$.

and was followed by a period of slow growth. Growth of the WA_{CST} trees exceeded that of the other seed sources during this period. Growth of the CA_{SIERRA} trees began to decrease following budset at both installations, while the ORS_{IL} trees had later budset and maintained a higher growth rate during the latter part of the growing season. The ORS_{IL} and WA_{CST} trees had similar cumulative basal-area growth at $L42_{LOW}$ and the WA_{CST} trees had slightly greater growth at $L46_{LOW}$ than the ORS_{IL} trees. Cumulative growth of both the WA_{CST} and ORS_{IL} trees exceeded that of the CA_{SIERRA} trees.

Basal-area growth patterns: comparisons between installations

Differences in relative growth rates were found between installations during distinct periods of the 2010 and 2011 growing seasons (Figure 5). During both growing seasons, the period of slow growth following budburst occurred first at $L42_{LOW}$ as did the transition to the period of rapid growth. Consequently, the relative growth rate at $L46_{LOW}$ was greater than that at $L42_{LOW}$ from mid-April to late May of both years and then the installations switched ranks. The installations switched ranks again with more growth occurring in early July through early August of each year at $L46_{LOW}$. The $L46_{LOW}$ installation had slightly greater cumulative growth than the $L42_{LOW}$ installation during much of the 2010 growing season, but the $L42_{LOW}$ installation had considerably greater cumulative growth from April through August of the 2011 growing season. The cumulative growth patterns were similar at $L46_{LOW}$ during both years, but the $L42_{LOW}$ installation had less growth early in the growing season in 2010 than in 2011 (growth completed by 1 August = 55% in 2010 and 65% in 2011). Growth rates were more variable at $L46_{LOW}$ than at $L42_{LOW}$. There was a distinct increase in the growth rate at $L46_{LOW}$ in mid-September 2010 that corresponded to a recovery of soil water content following late summer precipitation (measured by the on-site soil moisture sensors). Soil water content did not decline as much during the 2010 growing season at $L42_{LOW}$ as at $L46_{LOW}$, but it did not begin to recover until around 1 November at $L42_{LOW}$. Soil water content declined more at both installations during the 2011 growing season and did not recover

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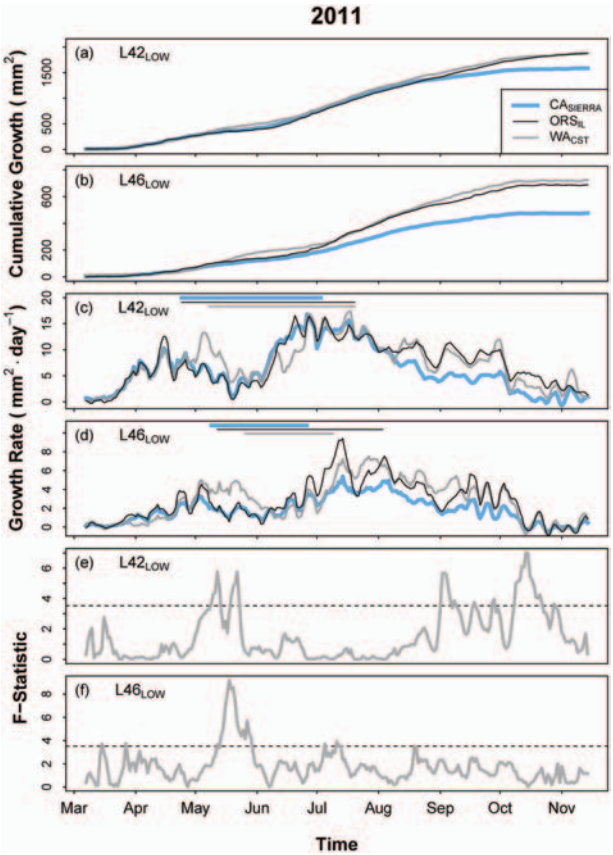

Figure 4. Basal-area growth patterns of Douglas-fir from three seed sources (CA_{SIERRA}, ORS_{IL} and WA_{CST}) at two planting installations ($L42_{LOW}$ and $L46_{LOW}$) during the 2011 growing season. Shown are cumulative basal-area growth (a and b), daily growth rates (c and d), and the *F*-statistics to gauge differences among seed sources in daily growth rate (e and f). The dotted lines in panels e and f show where the null hypothesis of no difference between seed sources would be rejected. The horizontal lines in panels c and d show the period between budburst and budset for each seed source.

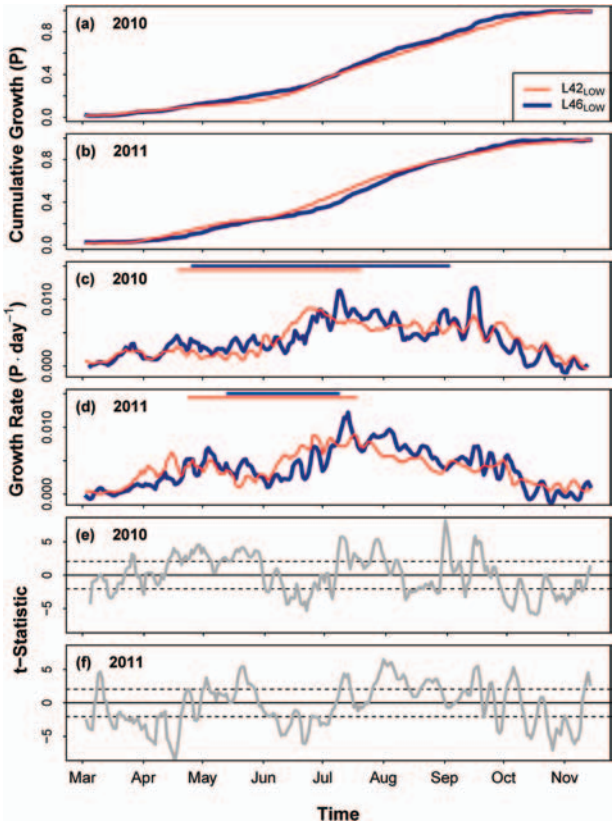

Figure 5. Basal-area growth patterns of Douglas-fir at two planting installations ($L42_{LOW}$ and $L46_{LOW}$) during the 2010 and 2011 growing seasons. Shown are cumulative basal-area growth (a and b), daily growth rates (c and d) and the *t*-statistics to gauge differences between installations in daily growth rate (e and f). Growth was standardized to eliminate differences in total growth between installations. The dotted lines in panels e and f show where the null hypothesis of no difference between installations would be rejected. The horizontal lines in panels c and d show the period between budburst and budset at each installation.

until mid-November at $L46_{LOW}$ and late-December at $L42_{LOW}$. Soil water recovery likely occurred too late to benefit basal-area growth in the latter part of the growing season.

Relationships between phenology metrics and seed-source environments

Several of the phenology metrics were strongly correlated with variables describing the seed-source environments (Table 6). Among the basal-area growth metrics, the strongest correlations were between BA_{50} and BA_{AUG1} and variables related to minimum temperature at the seed source locations. The correlations indicated that seed sources from environments that are relatively warm during the growing season and have long frost-free periods had more growth later in the growing season than those from colder environments. Correlations were generally poor between the environmental variables and variables describing the beginning and end of the growth period. The height-growth metrics were strongly correlated with variables related to both minimum temperature and precipitation. The correlations indicate that seed sources from wetter environments began height growth later and took more time to complete 50% of height growth than those from drier environments. None of the basal-area growth metrics were strongly correlated with the timing of budburst or budset. HT_{10} and HT_{50} were correlated with the timing of budburst, which was expected as height growth begins after budburst. The strongest correlation between a basal-area and height-growth metric was the correlation between HT_{50} and BA_{50}, which were significantly and positively correlated at all four installations ($r = 0.57$).

The relationship between BA_{50} and the length of the frost-free period (FFP) at the seed-source locations was selected as an example of a strong environmental correlation to evaluate in more detail (Figure 6). The relationship between FFP and BA_{50} was fairly strong at each of the installations ($r = 0.60–0.80$). It was weakest at $L46_{HI}$ where BA_{50} occurred relatively late in the year and differences among seed sources were relatively small.

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Table 6. Correlations between phenology metrics and variables describing the seed-source environments and the timing of budburst and budset. Values shown are averages of the correlations at each of the four installations. The number of installations where the correlation was statistically significant ($\alpha < 0.05$) is given in parentheses. Correlations that were significant at all four installations appear in bold.

Variable[2]	Phenology metric[1]							
	BA_{10}	BA_{50}	BA_{90}	BA_{AUG1}	HT_{10}	HT_{50}	HT_{90}	HT_{AUG1}
T_{ANN}	0.28 (1)	0.46 (2)	0.44 (1)	−0.46 (2)	−0.26 (0)	0.01 (0)	0.32 (1)	−0.28 (0)
T_{GSmin}	0.23 (0)	**0.73 (4)**	0.45 (3)	**−0.72 (4)**	0.42 (1)	**0.63 (4)**	0.47 (1)	−0.32 (0)
T_{GSmax}	0.18 (0)	−0.23 (0)	0.04 (0)	0.22 (0)	−0.81 (1)	−0.70 (3)	−0.11 (0)	−0.01 (0)
FFP	0.16 (0)	**0.73 (4)**	0.45 (2)	**−0.71 (4)**	0.45 (1)	**0.65 (4)**	0.47 (1)	−0.33 (0)
PPT_{ANN}	−0.14 (0)	0.44 (1)	0.13 (0)	−0.43 (1)	**0.86 (4)**	**0.84 (4)**	0.27 (0)	−0.07 (0)
PPT_{GS}	−0.07 (0)	0.41 (0)	0.08 (0)	−0.39 (0)	**0.86 (4)**	**0.82 (4)**	0.23 (0)	−0.05 (0)
Budburst	−0.14 (0)	0.39 (1)	−0.07 (0)	−0.36 (1)	**0.94 (4)**	**0.82 (4)**	0.16 (0)	0.02 (0)
Budset	−0.02 (0)	−0.10 (0)	−0.2 (0)	0.10 (0)	−0.15 (0)	−0.02 (0)	0.31 (2)	−0.41 (1)

[1]BA_{10}, BA_{50}, BA_{90}, day when 10, 50 or 90% of basal-area growth was completed; BA_{AUG1}, proportion of basal-area growth completed on 1 August; HT_{10}, HT_{50}, HT_{90}, day when 10, 50 or 90% of height growth was completed; HT_{AUG1}, proportion of height growth completed on 1 August.
[2]T_{ANN} , mean annual temperature; T_{GSmin}, mean daily minimum temperature during the growing season (1 April 1–30 September); T_{GSmax}, mean daily maximum temperature during the growing season; FFP, frost-free period; PPT_{ANN}, mean annual precipitation; PPT_{GS}, mean precipitation during the growing season; Budburst, day of terminal budburst; Budset, day of terminal budset.

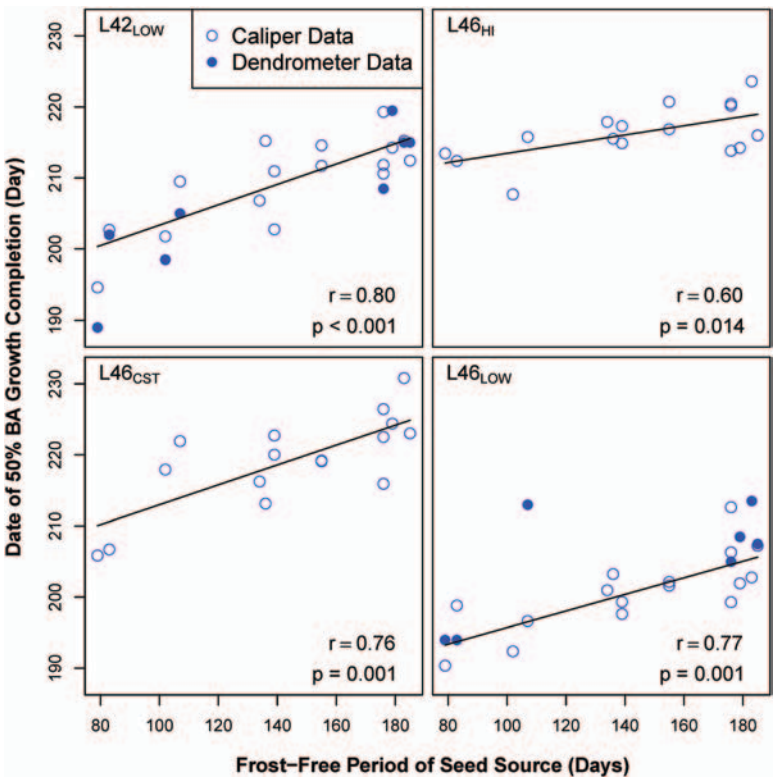

Figure 6. Relationship between the frost-free period at the local environments of 16 Douglas-fir families and the date when 50% of basal area growth was completed in 2010 (BA_{50}) at four planting installations. Linear regression models were fitted using the caliper measurements (open points); results from the dendrometer measurements are shown for comparison (closed points).

Discussion

Variation in phenology among seed sources

The seed-source locations selected for this study represent different ends of the range of environments where coast Douglas-fir occurs in terms of temperature and precipitation. Given the wide range of seed-source environments, the differences in phenology were surprisingly small in some cases. The CA_{SIERRA} and WA_{CST} seed sources were selected because they had the earliest and latest budburst in previous studies. In the present study, HT_{10} and HT_{50} were closely tied to the timing of budburst and large differences were found between seed sources as was expected (e.g., up to 21 days). Differences in the basal-area growth metrics were small

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relative to the height-growth metrics. For example, seed sources differed by up to 8 days in BA_{10} and up to 5 days in BA_{90}. Differences in the basal-area growth metrics were also small relative to the length of the period of basal-area growth. The differences in BA_{10} were equal to ~6% of the average basal-area growth period of 129 days. In contrast, the differences in HT_{10} were ~26% of the average height-growth period of 80 days. Even with the high-precision dendrometer measurements, the maximum difference among seed sources for basal-area growth initiation or cessation in either year was 11 days and the length of the basal-area growth period differed among seed sources by a maximum of 5 days. The significance of the differences among seed sources in each aspect of growth phenology is not clear; we cannot say that some differences are not important just because they are relatively small. However, it appears that the well-documented differences among genotypes in budburst are a poor analog for other phenological traits.

We did not find general patterns in the phenology metrics to suggest a simple classification of seed sources based on the suite of phenological traits. For example, the CA_{SIERRA} seed source was almost always the first to reach each phenological stage, but the ORS_{IL} seed source started height growth relatively early, started basal-area growth relatively late and ended both basal-area and height growth relatively late. Budburst (another measure of height-growth initiation) was poorly correlated with HT_{90} and all of the basal-area metrics. Budburst is relatively easy to measure and it would be convenient to use it as a phenological index for the purpose of evaluating the effects of climate change or seed transfer (Campbell 1974); however, it does not adequately represent other aspects of growth phenology. The poor correlation between budburst and several of the phenology metrics also indicates that the assumption on which we based the selection of seed sources—that differences in budburst correspond with difference in other aspects of phenology—was not well founded. It is possible that larger differences in the basal-area growth metrics could be found with a different sample of seed sources.

The small differences in the length of the basal-area growth period did not correspond to small differences in total growth. Seed sources differed by up to 39% in total basal-area growth during the 2010 growing season. Similarly, a longer period of height growth did not correspond with more growth. For example, the WA_{CST} seed source had the shortest growth period, but the greatest total growth in 2010 at three of the four installations. These results are in agreement with previous studies of Douglas-fir that found growth rates during the growing season were more important to total growth than differences in the growth period (Emmingham 1977, Li and Adams 1994).

The dendrometer measurements allowed for a detailed comparison of basal-area growth among seed sources. Although the timing of budburst was poorly correlated with the basal-area growth metrics, it clearly affected growth patterns in the first half of the growing season. Differences among seed sources in the timing of budburst created differences in basal-area growth patterns, specifically the timing of the growth pause around the time of budburst and the timing of the growth acceleration afterwards. The adaptive significance of the timing of budburst has often been evaluated in the context of environmental constraints on height growth (Campbell 1974, St. Clair et al. 2005, Gould et al. 2011), but it is important to recognize that the timing of budburst also affects other aspects of plant growth and physiology. The whole-tree production of photosynthate can be reduced during stem elongation and leaf expansion as some nutrients required for photosynthesis are translocated from older foliage to new foliage (Gordon and Larson 1968, Camm 1993). The new foliage initially exports little photosynthate until needles are completely expanded (Gordon and Larson 1968, Webb 1977). Thus, budburst creates a period when production can diminish while demand for photosynthate is high. The secondary effects of budburst, such as reduced basal-area growth, should be considered in addition to constraints on height growth when evaluating how well a population is adapted to a particular environment. Additionally, climatic conditions outside of the growing season need to be considered when characterizing a particular environment. Previous work has shown that temperatures throughout the winter affect the timing of budburst (Campbell and Sugano 1979, Harrington et al. 2010). In the present study, the dendrometer measurements indicated that the period of basal-area growth can be considerably longer (24 February 24–4 November in 2010 for the WA_{CST} trees at $L42_{LOW}$) than what is often defined as the growing season (e.g., 1 April 1–30 September); thus, basal-area growth is likely affected by environmental conditions throughout most of the calendar year.

Variation in phenology among test environments

Differences in the phenology metrics among installations were generally greater than the differences among the seed sources and, unlike the comparisons among seed sources, differences among installations were of similar magnitude for the basal-area and height-growth metrics. These results illustrate the major role that environment plays in growth phenology (Emmingham 1977, Li and Adams 1994, Emhart et al. 2006, Gonzalez-Benecke et al. 2010). Understanding the environment factors that affect different aspects of growth phenology is important to our ability to predict how environmental change will affect growth. The role of temperature in height-growth initiation is well established (Campbell and Sugano 1979, Harrington et al. 2010), but it also appeared to affect basal-area growth initiation. By most measures, basal-area growth began first at the relatively warm $L42_{LOW}$ installation. The period when most of the basal-area growth was completed (between BA_{10} and BA_{90}) began last and ended first at the relatively cold

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$L46_{HI}$ installation. Differences in the timing of basal-area growth initiation between the 2010 and 2011 growing seasons also appeared to be affected by temperature. Growth initiation (as measured with dendrometers) occurred 16 days earlier in 2010 when the average air temperature in February was ~3° warmer at $L42_{LOW}$ and 4° warmer at $L46_{LOW}$ than in 2011. Temperature alone cannot explain why BA_{10} and BA_{50} occurred considerably later in 2010 at the $L46_{CST}$ installation than at the $L46_{LOW}$. Spring air temperatures were similar at both installations and growth was evident at both installations at the end of March. The soils in some parts of $L46_{CST}$ are poorly drained and the installation received considerably more precipitation than $L46_{LOW}$. The wet soils may have taken longer to warm so that root growth was delayed. Excessive soil moisture could also have slowed down diameter growth in the spring (Khan et al. 1996). Growth accelerated later at $L46_{CST}$ and total basal-area growth was only slightly lower than at $L46_{LOW}$.

Temperature appeared to affect the timing of basal-area growth initiation but it is unclear as to whether cambial cells experience dormancy in the same respect as meristimatic cells in buds. Worrall (1971) and Bhella and Roberts (1975) argued that Douglas-fir cambial cells do not experience winter dormancy based on their findings that a period of chilling is not required for cambial reactivation. Air temperature has been suggested as the key environmental factor affecting cambial reactivation (Begum et al. 2008, Deslauriers et al. 2008). The importance of temperature has been demonstrated by artificial heat treatments that locally reactivate cambial cells and initiate the process of cell division and differentiation (Barnett and Miller 1994, Oribe and Kubo 1997, Begum et al. 2007). However, temperature is not likely to be the only factor limiting cambial reactivation (Seo et al. 2008). Heating has not been effective on some species or on some parts of the stem (Oribe and Kubo 1997), and cambial cells have also been found to respond more readily to heat when applied in late winter or spring compared with early winter treatments (Barnett and Miller 1994, Oribe and Kubo 1997). These results suggest that the activity of cambial cells is inhibited during winter and not just limited by temperature. Worrall (1971) suggested that cambial reactivation in Douglas-fir depends on chemical signals from the terminal bud or foliage as a response to photoperiod. In the present study, the timing of budburst was not strongly correlated with any of the metrics describing basal-area growth, suggesting that the timing of cambial growth initiation is not closely coupled with the timing of budburst. A better understanding of how cambial cells respond to the environment and interact with other plant organs is needed. Although the dendrometers provided precise measurements of stem expansion, anatomical or physiological studies would allow for a more detailed evaluation of the early stages of cambial reactivation.

The dendrometer measurements allowed for a detailed comparison of basal-area growth patterns throughout the growing season at the $L42_{LOW}$ and $L46_{LOW}$ installations. The differences between installations paralleled the differences between seed sources in the sense that relative basal-area growth was initially slower at the installation with the earliest budburst but the installations then switched ranks (Figure 5). It is not clear which environmental factors produced divergent growth patterns in the latter part of the growing season; however, plant water status may have played a role. Despite lower precipitation and higher temperatures at $L42_{LOW}$, soil water content did not decrease as much during the growing season as at $L46_{LOW}$. Competing vegetation was nearly completely eliminated at $L42_{LOW}$ and the soil contains a relatively impermeable hardpan that may have retained soil water at a depth that was accessible to the study trees. Basal-area growth in mid-September 2010 accelerated at $L46_{LOW}$ at about the same time as soil water began to recharge, indicating that growth had been limited in the latter part of the season or that the stems were not fully hydrated (or both).

The differences among installations in growth phenology did not correspond with differences in total growth. The $L42_{LOW}$ installation had far greater basal-area and height growth than the other installations despite having about the same period of basal-area growth and a shorter period of height growth. High summer temperatures, low humidity and low precipitation presumably caused height growth to cease early at the $L42_{LOW}$ installation, but did not cause a cessation of basal-area growth. Despite the short period of growth, the 2010 height increment was 60% greater at $L42_{LOW}$ than at any of the other installations. In contrast, the $L46_{HI}$ installation had about the same period of height growth as the $L46_{CST}$ and $L46_{LOW}$ installations but only ~60% as much height growth. These results suggest that resource limitations during different times in the growth period have a greater effect on total growth than the length of the growth period.

Relationships between phenology and seed-source environments

Several of the phenology metrics were strongly correlated with variables describing the seed-source environments, but there were important differences between the basal-area and height-growth metrics. The growth metrics related to the initiation and cessation of basal-area growth were not strongly correlated with any of the environmental variables, but BA_{50} was highly correlated with the minimum temperature during the growing season and the length of the frost-free period. In contrast, HT_{10} was strongly correlated with both measures of minimum temperature and precipitation during the growing season. Our results affirm those of previous studies that found that genetic variability in height-growth initiation in Douglas-fir is closely related to water availability during the growing season

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(St. Clair et al. 2005, Gould et al. 2011). The strong correlations found for BA_{50} suggests that minimum temperature has been more important to the evolution of cambial phenology than summer drought or other factors.

Several hypotheses can be proposed regarding the adaptive significance of variation in basal-area growth rates and its relation to seed-source environments. Slow growth is associated with high wood density (Vargas-Hernandez and Adams 1994, Devine and Harrington 2009), and the transition to slow growth relatively early in the growing season may mark an early transition from earlywood to latewood formation. Although we did not measure it here, in earlier work the timing of the earlywood–latewood transition has been found to differ more among families than the timing of growth initiation and cessation, and the length of the growth period (Vargas-Hernandez and Adams 1994). High wood density may be advantageous in dry environments as the small lumen diameters may reduce cavitation (Kavanagh et al. 1999), and high-density wood maintains stored water better than low-density wood under low stem water potential (Domec and Gartner 2002). Drought tolerance alone does not explain why the CA_{SIERRA} trees had slower growth than the ORS_{IL} trees that are also adapted to a dry environment. The CA_{SIERRA} environment is somewhat drier and considerably colder than the ORS_{IL} environment. The combination of low water potential and freeze–thaw cycles greatly increases the risk of cavitation and the loss of hydraulic conductivity (Pittermann and Sperry 2006, Wilson and Jackson 2006); thus, the combination of cold and drought may be the key factor differentiating the two seed sources. Slow growth in the latter part of the growing season among populations from cold environments could also reflect a necessary trade-off between growth and the development of cold hardiness in cambial cells (Sennerby-Forsse and Fircks 1987). Differences in above-ground growth may also indicate differences in allocation to roots or other carbon sinks (Krueger and Trappe 1967, Webb 1977, Reich et al. 1980). Populations from cold environments may shift the allocation of photosynthate to root growth relatively early in the season to compensate for a shorter period of root growth in the fall.

Implications for climate change

Our results provide a clearer understanding of growth phenology of Douglas-fir that can aid in predicting some impacts of climate change and in the development of mitigation strategies. Growth phenology exhibits a high degree of plasticity in response to the environment. Individual trees can be expected to exhibit different patterns of basal-area and height growth as the climate changes. Some changes, such as earlier growth initiation with rising temperatures, may help individuals cope with climate change as the growth period may be better coordinated with the period of high soil moisture that precedes summer drought in the Pacific Northwest. Other changes, such as an earlier shift to slow basal growth in response to lower soil water content in the summer, may result in reduced growth. It is not clear to what degree changes in phenological events such as the timing of basal-area and height-growth initiation and cessation will affect forest productivity. In the present study, total growth was not closely related to the length of the growth period. Although changes to phenology are potentially important, accurately predicting climate change impacts requires a better understanding of how genotypes respond to environmental conditions throughout the growing season.

Genetic variation in growth phenology is a potentially important resource for mitigating some of the effects of climate change. Phenological traits can be considered with other factors in determining whether a genotype is well adapted to a particular environment. Distinction should be made between different aspects of growth phenology. Variation in diameter-growth phenology appears to be an adaptation to a different set of environmental factors than budburst or height-growth phenology. It should not be assumed that a population that is well adapted to an environment based on budburst phenology will also be well adapted based on diameter-growth phenology. It is also important to better understand how traits may interact with one another and with a changing environment. The current study was too limited to draw general conclusions about which populations may be best adapted to future climates. Diameter-growth phenology is more difficult to measure than other traits; however, some simple cambial phenology metrics such as BA_{AUG1} can be calculated with relatively little effort (e.g., based on a measurement before growth starts, on 1 August, and after growth is completed). It may be feasible to predict different aspects of growth phenology based on the climate of the seed source, and on environmental factors at the planting location. The model for budburst phenology developed by Gould et al. (2011) could be a template for models to predict growth phenology. A much larger sample of seed sources needs to be measured to develop these models. High-resolution measurements, such as those made with dendrometers, are also helpful for understanding when and how populations differ in growth phenology.

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References

Barnett JR, Miller H (1994) The effect of applied heat on graft union formation in dormant *Picea sitchensis* (Bong.) Carr. J Exp Bot 45:135–143.

Begum S, Nakaba S, Oribe Y, Kubo T, Funada R (2007) Induction of cambial reactivation by localized heating in a deciduous hardwood hybrid poplar (*Populus sieboldii* × *P. grandidentata*). Ann Bot 100:439–447.

Begum S, Nakaba S, Bayramzadeh V, Oribe Y, Kubo T, Funada R (2008) Temperature responses of cambial reactivation and xylem differentiation in hybrid poplar (*Populus sieboldii* × *P. grandidentata*) under natural conditions. Tree Physiol 28:1813–1819.

Bhella HS, Roberts AN (1975) Bud and cambial activity in Douglas-fir as related to stem cutting rootability. For Sci 21:269–275.

Camm E (1993) Photosynthetic responses in developing and year-old Douglas-fir needles during new shoot development. Trees Struct Funct 8:61–66.

Campbell RK (1974) Use of phenology for examining provenance transfers in reforestation of Douglas-Fir. J Appl Ecol 11:1069–1080.

Campbell RK, Sorensen FC (1973) Cold-acclimation in seedling Douglas-fir related to phenology and provenance. Ecology 54:1148–1151.

Campbell RK, Sugano AI (1975) Phenology of bud burst in Douglas-fir related to provenance, photoperiod, chilling, and flushing temperature. Bot Gazette 136:290–298.

Campbell RK, Sugano AI (1979) Genecology of bud-burst phenology in Douglas-fir: response to flushing temperature and chilling. Bot Gaz 140:223–231.

Chuine I (2010) Why does phenology drive species distribution? Philos Trans R Soc B Biol Sci 365:3149–3160.

Crookston NL (2008) Current climate data for western North America. Moscow, ID: USDA Forest Service, Rocky Mountain Research Station. http://forest.moscowfsl.wsu.edu/climate/currentClimate.html (21 December 2008, date last accessed).

Daubenmire RF (1950) A comparison of season of cambial growth in different geographic races of *Pinus ponderosa*. Bot Gaz 112:182–188.

Deslauriers A, Rossi S, Anfodillo T, Saracino A (2008) Cambial phenology, wood formation and temperature thresholds in two contrasting years at high altitude in southern Italy. Tree Physiol 28:863–871.

Devine WD, Harrington C (2009) Relationships among foliar phenology, radial growth rate, and xylem density in a young Douglas-fir plantation. Wood Fiber Sci 4:300–312.

Dietrichson J (1964) The selection problem and growth-rhythm. Silvae Genet 13:178–184.

Dimock EJ (1964) Simultaneous variations in seasonal height and radial growth of young Douglas-fir. J For 62:252–255.

Domec JC, Gartner BL (2002) How do water transport and water storage differ in coniferous earlywood and latewood? J Exp Bot 53:2369–2379.

Dutilleul P (1993) Modifying the t test for assessing correlation between two spatial processes. Biometrics 49:305–315.

Emhart VI, Martin TA, White TL, Huber DA (2006) Genetic variation in basal area increment phenology and its correlation with growth rate in loblolly and slash pine families and clones. Can J For Res 36:961–971.

Emmingham WH (1977) Comparison of selected Douglas-fir seed sources for cambial and leader growth patterns in four western Oregon environments. Can J For Res 7:154–164.

Glock WS (1951) Cambial frost injuries and multiple growth layers at Lubbock, Texas. Ecology 32:28–36.

Gonzalez-Benecke CA, Martin TA, Clark A III, Peter GF (2010) Water availability and genetic effects on wood properties of loblolly pine (*Pinus taeda*). Can J For Res 40:2265–2277.

Gordon JC, Larson PR (1968) Seasonal course of photosynthesis, respiration, and distribution of 14C in young *Pinus resinosa* trees as related to wood formation. Plant Physiol 43:1617–1624.

Gould PJ, Harrington CA, St. Clair JB (2011) Incorporating genetic variation into a model of budburst phenology of coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*). Can J For Res 41:139–150.

Griffith BG (1960) Growth of Douglas-fir at the University of British Columbia research forest as related to climate and soil. University of British Columbia Faculty of Forestry, Forestry Bulletin 2, 58 pp.

Hamann A, Gylander T, Chen P-y (2011) Developing seed zones and transfer guidelines with multivariate regression trees. Tree Genet Genomes 7:399–408.

Harrington CA, Gould PJ, St. Clair JB (2010) Modeling the effects of winter environment on dormancy release of Douglas-fir. For Ecol Manage 259:798–808.

Hermann RK, Lavender DP (1990) *Pseudotsuga menziesii* (Mirb.) Franco Douglas-fir. In: Burns RM, Honkala BH (tech. coords) Silvics of North America: 1. Conifers. Agriculture handbook 654. USDA Forest Service, Washington, DC. Vol. 1, pp 527–540.

Howe GT, Aitken SN, Neale DB, Jermstad KD, Wheeler NC, Chen TH (2003) From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees. Can J Bot 81:1247–1266.

Jayawickrama KJS, McKeand SE, Jett JB (1998) Phenological variation in height and diameter growth in provenances and families of loblolly pine. New For 16:11–25.

Kavanagh KL, Bond BJ, Aitken SN, Gartner BL, Knowe S (1999) Shoot and root vulnerability to xylem cavitation in four populations of Douglas-fir seedlings. Tree Physiol 19:31–37.

Khan SR, Rose R, Haase DL, Sabin TE (1996) Soil water stress: its effects on phenology, physiology, and morphology of containerized Douglas-fir seedlings. New For 12:19–39.

Kozlowski TT, Peterson TA (1962) Seasonal growth of dominant, intermediate, and suppressed red pine trees. Bot Gaz 124:146–154.

Krueger KW, Trappe JM (1967) Food reserves and seasonal growth of Douglas-fir seedlings. For Sci 13:192–202.

Legendre P, Dale MRT, Fortin M-J, Gurevitch J, Hohn M, Myers D (2002) The consequences of spatial structure for the design and analysis of ecological field surveys. Ecography 25:601–615.

Li P, Adams WT (1994) Genetic variation in cambial phenology of coastal Douglas-fir. Can J For Res 24:1864–1870.

Loopstra CA, Adams WT (1989) Patterns of variation in first-year seedling traits within and among Douglas-fir breeding zones in southwest Oregon. Silvae Genet 38:235–243.

Mellerowicz EJ, Coleman WK, Riding RT, Little CHA (1992) Periodicity of cambial activity in *Abies balsamea*. I. Effects of temperature and photoperiod on cambial dormancy and frost hardiness. Physiol Plant 85:515–525.

Menzel A, Sparks T (2006) Temperature and plant development: phenology and seasonality. In: Morison JIL, Morecroft MD (eds) Plant growth and climate change. Blackwell Publishing Ltd, Oxford, pp 70–95.

Menzel A, Sparks TH, Estrella N et al. (2006) European phenological response to climate change matches the warming pattern. Glob Change Biol 12:1969–1976.

Millar CI, Stephenson NL, Stephens S (2007) Climate change and forests of the future: managing in the face of uncertainty. Ecol Appl 17:2145–2151.

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Neter J, Kutner MH, Nachsheim CJ, Wasserman W (1996) Applied linear statistical models, 4th edn. WCB McGraw Hill, Burr Ridge, IL.

Oribe Y, T. Kubo (1997) Effect of heat on cambial reactivation during winter dormancy in evergreen and deciduous conifers. Tree Physiol 17:81–87.

Ott L (1993) An introduction to statistical methods and data analysis, 4th edn. Duxbury Press, Belmont, CA.

Pittermann J, Sperry JS (2006) Analysis of freeze-thaw embolism in conifers. The interaction between cavitation pressure and tracheid size. Plant Physiol 140:374–382.

R Development Core Team (2006) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. http://www.R-project.org.

Rehfeldt GE (1978) Genetic differentiation of Douglas-fir populations from the northern Rocky Mountains. Ecology 59:1264–1270.

Rehfeldt GE (2006) A spline model of climate for the Western United States. Gen. Tech. Rep. RMRS-GTR-165. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, 21 pp.

Reich PB, Teskey RO, Johnson PS, Hinckley TM (1980) Periodic root and shoot growth in oak. For Sci 26:590–598.

Repo T, Zhang G, Ryyppo A, Rikala R, Vuorinen M (2000) The relation between growth cessation and frost hardening in Scots pines of different origins. Trees Struct Funct 14:456–464.

Reukema DL (1965) Seasonal progress of radial growth of Douglas-fir, western redcedar, and red alder. PNW Old Series Research Paper PNW-26, 14 pp.

Sennerby-Forsse L, Fircks HA (1987) Ultrastructure of cells in the cambial region during winter hardening and spring dehardening in *Salix dasyclados* Wim. grown at two nutrient levels. Trees Struct Funct 1:151–163.

Seo J, Eckstein D, Jalkanen R, Rickebusch S, Schmitt U (2008) Estimating the onset of cambial activity in Scots pine in northern Finland by means of the heat-sum approach. Tree Physiol 28:105–112.

Sorensen FC (1983) Geographic variation in seedling Douglas-fir (*Pseudotsuga menziesii*) from the western Siskiyou mountains of Oregon. Ecology 64:696–702.

St. Clair JB, Howe GT (2007) Genetic maladaptation of coastal Douglas-fir seedlings to future climates. Glob Change Biol 13:1441–1454.

St. Clair JB, Mandel NL, Vance-Borland KW (2005) Genecology of Douglas-fir in western Oregon and Washington. Ann Bot 96:1199–1214.

Vargas-Hernandez J, Adams WT (1994) Genetic relationships between wood density components and cambial growth rhythm in young coastal Douglas-fir. Can J For Res 24:1871–1876.

Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416:389–395.

Webb WL (1977) Seasonal allocation of photoassimilated carbon in Douglas fir seedlings. Plant Physiol 60:320–322.

Wilczek AM, Burghardt LT, Cobb AR, Cooper MD, Welch SM, Schmitt J (2010) Genetic and physiological bases for phenological responses to current and predicted climates. Philos Trans R Soc B Biol Sci 365:3129–3147.

Wilson CJ, Jackson RB (2006) Xylem cavitation caused by drought and freezing stress in four co-occuring *Juniperus* species. Physiol Plant 127:374–382.

Worrall, J (1971) Absence of 'rest' in the cambium of Douglas-fir. Can J For Res 1:84–89.

Worrall, J (1975) Provenance and clonal variation in phenology and wood properties of Norway spruce. Silvae Genet 24:2–5.

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