Phenology of Pacific Northwest Tree Species

Constance A. Harrington, Kevin R. Ford, and J. Bradley St. Clair

Research Forester, U.S. Department of Agriculture (USDA), Forest Service, Pacific Northwest (PNW) Research Station, Olympia, WA; Research Ecologist, USDA Forest Service, PNW Research Station, Olympia, WA; Research Geneticist, USDA Forest Service, PNW Research Station, Corvallis, OR.

Abstract

Phenology is the study of the timing of recurring biological events. For foresters, the most commonly observed phenological events are budburst, flowering, and leaf fall, but other harder to observe events, such as diameter-growth initiation, are also important. Most events that occur in the spring are influenced by past exposure to cool (chilling) temperatures and also to warm (forcing) temperatures. For trees in the Pacific Northwest, chilling temperatures generally promote earlier growth initiation, but species differ in their sensitivity to chilling and forcing and to whether some minimum amount of chilling is required for certain events, such as budburst, to occur at all. The initiation of diameter growth for the studied species does not require chilling and may begin 6 to 8 weeks before height growth. The timing of height growth may affect the pattern of diameter growth early in the season. The timing of reproductive events for conifers varies by species and can occur well before vegetative growth begins. This paper was presented at the annual meeting of the Western Forest and Conservation Nursery Association (Eugene, OR, October 26–27, 2015).

Introduction

Phenology is the study of the timing of recurring biological events such as growth initiation in plants, insect hatching, or bird migrations. The timing of these events is critically important, because it determines how well periods of activity are matched with periods of suitable environmental conditions. In trees, phenology represents a balancing act; if growth begins too early in the year, tender new tissues can be killed by frost, but, if growth begins late, the length of the growing season is shortened and opportunities are missed to grow under the favorable temperature and moisture conditions of spring and early summer. These missed opportunities may be especially costly in temperate climates with short growing seasons due to cold or drought, or both. Trees in temperate regions rely on winter chilling, photoperiod, and warm temperatures to control phenological events, but species differ in the number of factors which control an event such as budburst (Körner and Basler 2010).

An understanding of tree phenology is important for effective nursery and forest management. Many physiological processes in temperate trees occur seasonally, including spring budburst, the initiation and progression of diameter growth, sap flow, flowering, development and dispersal of seeds, fall budset or growth cessation, the development of leaf color and leaf fall, and the timing of root growth. Understanding what determines when these key processes occur is fundamental to our understanding of tree function, and it helps us predict how changes in the environment will affect forest productivity and health. This may be particularly important for understanding the impacts of predicted changes in future climate (IPCC 2014), including evaluating possible management options. In addition, the effectiveness of management actions, such as fertilizer or pesticide application, depends on the timing of those treatments relative to tree activity and development. An understanding of tree phenology can help optimize treatment effects.

Phenological events in trees are typically triggered by cues from their environment, but the relationship between phenology and the environment can be complex. At mid to high latitudes, temperature is often the primary signal for phenological events, particularly in the spring. Exposure to warm temperatures accumulated over the fall, winter, and spring, referred to as "forcing," typically triggers budburst, flowering, and cambial reactivation; however, exposure to cool temperatures while the tree is dormant, referred to as "chilling," also plays a critical role (Romberger 1963, Sarvas 1974, Vegis 1964). In some cases, a phenological event in the spring cannot occur unless a tree has experienced a sufficient amount of chilling. Also, regardless of whether a tree has a minimum or obligate chilling requirement, the amount of chilling can influence how much forcing is required, with the amount of required forcing generally declining with greater chilling (Carlson 1985, Harrington et al. 2010, Ford et al. 2016). As a consequence, warmer temperatures brought on by climate change can either delay or promote phenological events, depending on the decrease in chilling relative to the increase in forcing, respectively. Other factors, such as photoperiod and plant nutrient status, can also influence phenology, and the relationships between phenology and environmental cues can differ by species and genotype (Gould et al. 2011, Harrington and Gould 2015).

In this article, we summarize some recent information we have learned about the phenology of several of our native trees in the Pacific Northwest. We focus on initiation and seasonal progression of height and diameter growth, including the timing of spring budburst and cambial activation. We also briefly discuss flowering phenology, including seed cone receptivity and pollen shed.

Budburst and the Initiation of Height Growth

In most Pacific Northwest trees, shoot growth begins in the spring with the resumption of cell division and cell elongation from the shoot apical meristem within a bud formed during the previous growing season (cf. Allen and Owens 1972). As spring progresses, the expansion of the needle tissues can no longer be contained inside the bud and the new shoot bursts through the bud scales. In our studies, we determined the initiation of height growth for several species by observing the timing of when the bud scales of the terminal bud had parted sufficiently to enable us to view green leaf tissue. In the case of western redcedar (*Thuja plicata* Donn ex D. Don), which does not form vegetative buds, we determined height growth initiation by measuring shoot length periodically during the spring.

The timing of budburst can vary substantially due to differences in the environment or genetics, or both. For example, results from the Douglas-fir Seed-Source Movement Trial (Gould et al. 2012) show that the range in date of terminal budburst of individual trees from one seed source (represented by the progeny of two mother trees from each of five populations with similar adaptive characteristics and from an area of similar climates) of coast Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*) was about 20 days over 6 years at a single low-elevation site in Washington (classified as "medium" in terms of climate; figure 1, table 1). The range in date of budburst for that same seed source was more than 40 days during 1 year across three test sites that differ greatly with respect to temperature. The range in date of budburst across three sites and three different seed sources was over 50 days in 1 year. The coldest site resulted in the latest budburst and the narrowest range in budburst dates (figure 1). These results from the Douglas-fir Seed-Source Movement Trial illustrate that the range of initial dates of budburst and also the range in time to complete budburst can vary substantially among sites and among seedlots at a single site.

Tradeoffs exist between bursting bud late and bursting bud early. Bursting bud late helps a tree avoid spring frosts and foliar pathogens that thrive on new tissues

Table 1. Geographic and climate summaries for the study locations.

Site	Name	Latitude	Longitude	Elevation (m)	MAT (°C)	MWMT (°C)	MCMT (°C)	MAP (mm)
Cold	Doorstop	46.9° N.	122.0° W.	860	7.5	15.2	1.2	1821
Medium	Buckhorn2	46.5° N.	123.0° W.	240	10.3	17.7	3.8	1470
Hot	Stone	42.3° N.	122.9° W.	415	12.2	21.9	4.0	503
Olympia	OFSL	47.0° N.	123.0° W.	58	10.6	18.0	4.2	1266

C = Celsius. m = meter. MAP = mean annual precipitation. MAT = mean annual temperature. MCMT = mean coldest month temperature. mm = millimeter. MWMT = mean warmest month temperature. OFSL = Olympia Forestry Sciences Laboratory.

Note: All climate variables refer to the 1981-to-2010 normals.

Source: All climate variables were taken from ClimateWNA (Wang et al. 2012).

in cool, moist conditions. Bursting bud early allows for trees to capture favorable growing conditions in the earlier parts of the growing season when they begin to experience warm temperatures while still having access to abundant soil moisture. These tradeoffs can lead to differences among populations in date of budburst due to differential natural selection. When grown in a common garden, trees from drier and colder climates tend to burst bud earlier (St. Clair et al. 2005, Gould et al. 2011; see also the “hot” and “cold” seed sources in figure 1, respectively), while those from mild climates burst bud later (the “medium” seed source in figure 1). One possible explanation for this pattern is that the growing season is short in both dry and cold locations. In dry locations, parents that burst bud early and grew quickly during the early part of the growing season before the onset of drought in the summer were able to outcompete those that burst bud late, and, thus, were better able to survive and reproduce and to pass on the inherited characteristics of early budburst to their offspring (St. Clair et al. 2005, White et al. 1979). In cold locations, early bud burst may have resulted from selection for lower chilling requirements or lower flushing requirements, or both (Howe et al. 2003). The later arrival of spring at colder locations resulted in selection of those parents that can start growing more quickly to take advantage of the shorter growing season. At mild sites with a longer growing season and adequate moisture later in summer, trees are under less pressure to start growth earlier in the year and may increase their fitness by delaying budburst to avoid frost and leaf pathogens that can be important stressors in

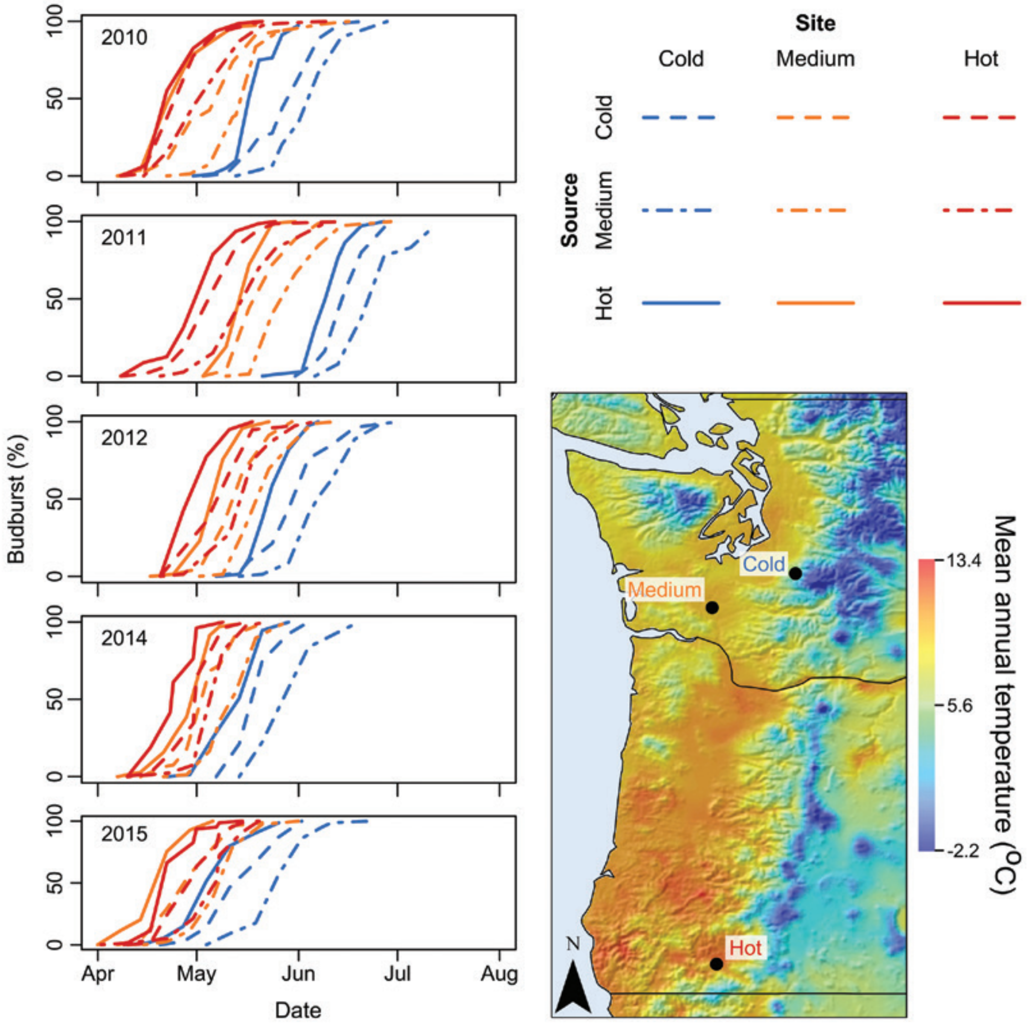

Figure 1. Progression of terminal budburst over 5 years in three seedlots of Douglas-fir grown in three common gardens. The common garden locations were Stone, a hot, dry site near Medford, OR; Buckhorn2, a mild site near Centralia, WA; and Doorstop, a cold, wet site near Mount Rainier National Park, WA. The seedlots shown were chosen to be ones that would be considered local for each location: a low-elevation Oregon Siskiyou Mountains source for Stone, a Washington Coast source for Buckhorn2, and a high-elevation Washington Cascades source for Doorstop. Each seedlot consisted of trees from five populations, with collections of seed from two mother trees per population.

the cool and damp conditions of early spring.

Faster growth rates can sometimes compensate for later budburst, allowing for trees to avoid early-season stresses while still achieving high productivity (Gould et al. 2012). The trees shown in figure 2 are representative of this possibility. Here we can see that budburst occurred much earlier in the Douglas-fir sapling from a southern Oregon Coast seedlot than in the tree from a Washington Coast seedlot, but, by the end of this particular year, the two trees both had grown the same amount. In this example, the tree from the Oregon Coast seedlot also stopped growing in height briefly, set bud, and then reflushed. The tree from the Washington Coast seedlot burst bud much later than the Oregon Coast seedlot, then grew faster during the early summer; it grew more continuously and, thus, avoided the brief period of summer budset evidenced by the other source. Different growth strategies have benefits and risks related to frost, drought, and second flushing and no one strategy will be best for all conditions.

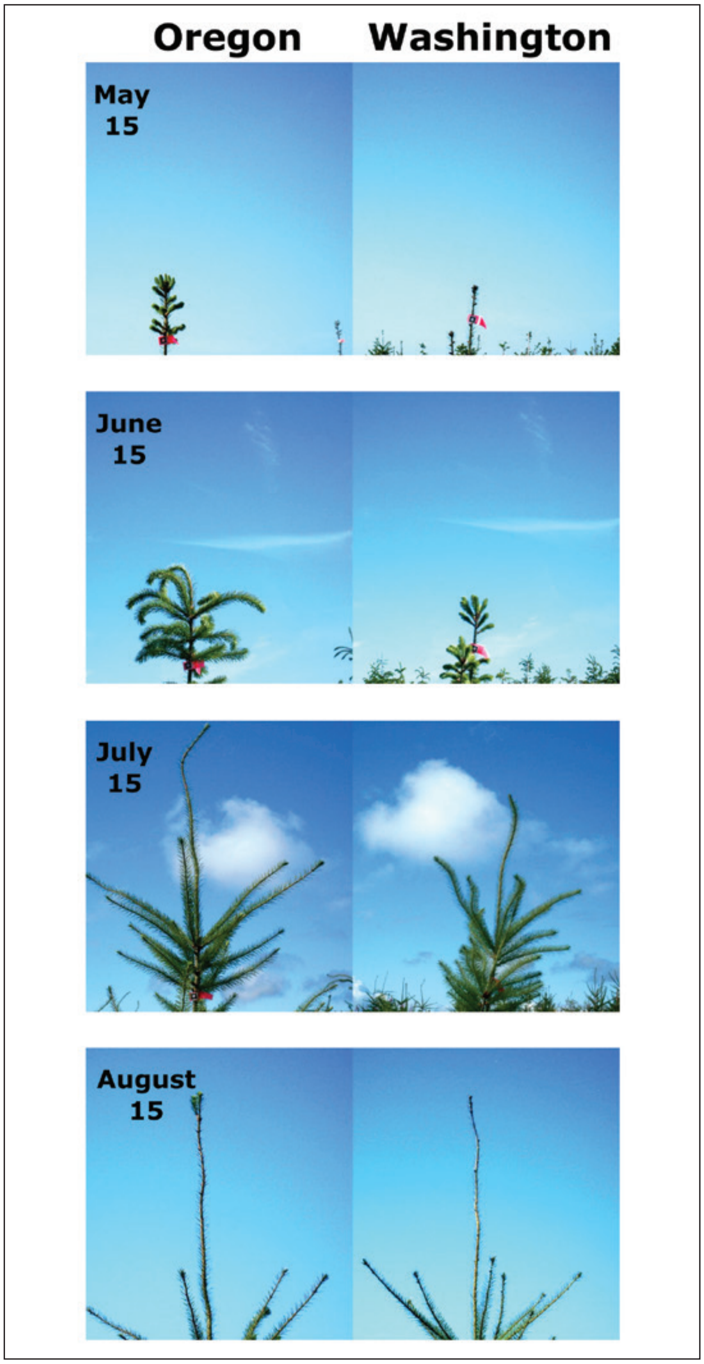

Figure 2. Time-lapse cameras can be used to follow budburst, the seasonal progression of height growth, and development of multiple flushing or other traits. In this example, we followed trees from two seed sources (southern Oregon Coast and Washington Coast) planted in the Buckhorn2 common garden near Centralia, WA. Cameras were located to the south of each tree being followed. The trees were in their fourth growing season after planting. A video clip of the full season of time-lapse images is available at https://youtu.be/KipZfWnjkB4.

Understanding the timing of budburst for different tree species and how the risks and opportunities trees face change over the year can inform decisions, such as selecting seed sources or planting windows or scheduling herbicide or pesticide applications. In addition, understanding the presence of alternative growth patterns within a species may provide tree breeders with additional traits to consider.

The relationship between temperature and terminal budburst also differs greatly among species. Some species must experience some minimum amount of chilling after budset before budburst can occur and are said to have an obligate or absolute chilling requirement. In the Pacific Northwest, these species include Douglas-fir, true firs (*Abies* spp.), western larch (*Larix occidentalis* Nutt.), and western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) (Harrington and Gould 2015, Nelson and Lavender 1979, Wommack 1960). Pacific madrone (*Arbutus menziesii* Pursh), on the other hand, can burst terminal bud in the spring without chilling (Harrington and Gould 2015). Western redcedar does not have vegetative buds and also resumes height growth without chilling (Harrington and Gould 2015). In addition, species differ in their relationships between the amount of chilling received and the amount of forcing required for budburst to occur. For all Northwest tree species we studied, increased chilling reduces the amount of forcing needed to initiate height growth in the spring, regardless of whether the species has an obligate chilling requirement or not.

Ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) is complicated in its response to chilling, with some seed sources exhibiting an obligate chilling requirement (Omi et al. 1991, Sloan 1991) and others not (Burr et al. 1989, Wenny et al. 2002). In our seedling trials, we observed that the amount of winter chilling influenced the initiation of budburst in eight seedlots of ponderosa pine, the length of time the budburst lasted, the rank order of sources to begin or complete budburst, and the completeness of budburst in the population (figure 3). For example, under the highest chilling level (a lath house in Olympia, WA), the beginning of budburst differed by 20 days among seedlots, and all lots burst bud completely and quickly. With slightly warmer conditions (4 days per week in a greenhouse), all seedlots were still adequately chilled and they all achieved 100 percent budburst. Under warmer winter environments, budburst took much longer for all trees in a population, and the seedlots diverged into groups with complete budburst and groups with substantial percentages of seedlings not bursting their terminal bud. In the warmest environment (plants in a heated greenhouse all winter) only one high-elevation lot from southwest Oregon had 100 percent of seedlings bursting bud, and only 40 percent or fewer of the seedlings from two of the three Washington sources burst bud at all.

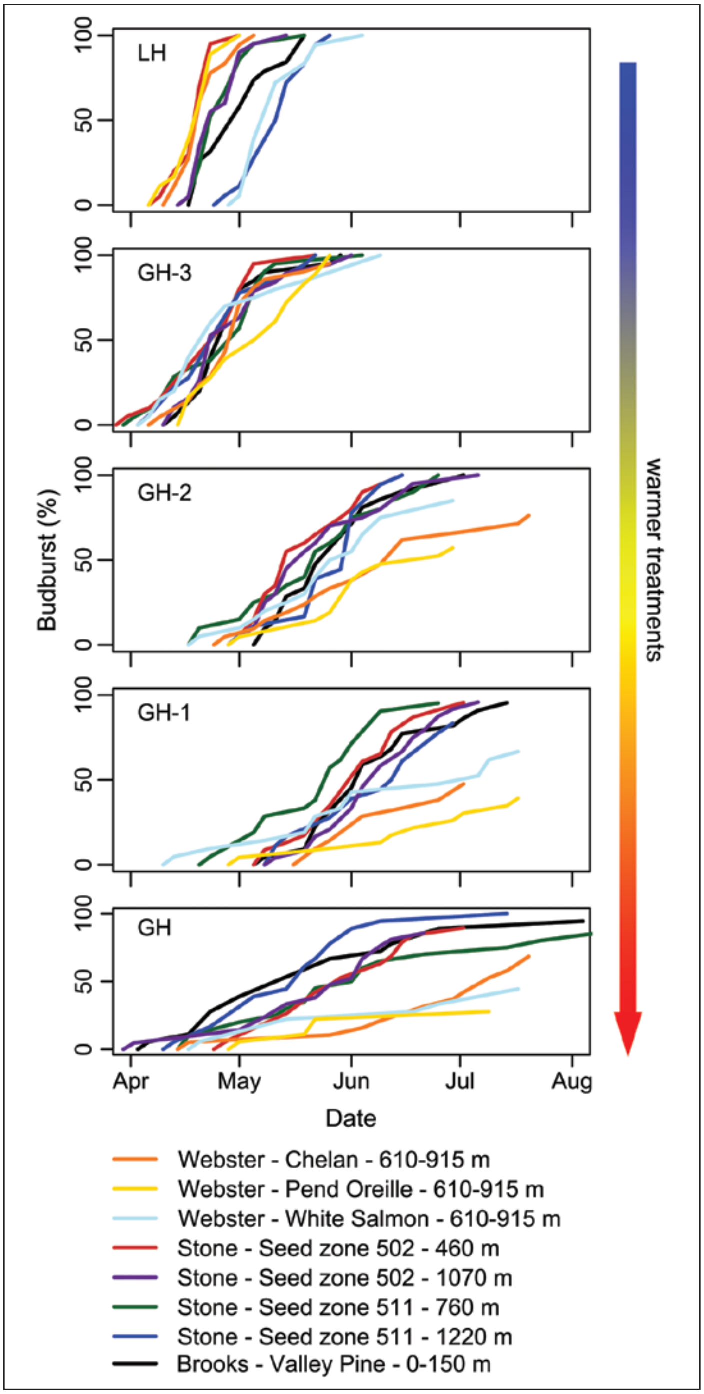

Figure 3. Patterns of the progression of terminal bud burst in eight ponderosa pine seedlots grown under five different temperature environments. These data came from a trial conducted during fall and winter 2014 and spring and summer 2015 at the Olympia Forestry Sciences Laboratory near Olympia, WA. Potted seedlings were kept under outside ambient conditions (LH = lath house), in a greenhouse where air temperature did not drop below 15 ˚C (GH), or moved back and forth weekly between the two environments (e.g., GH-3 means plants were moved outside the greenhouse 3 days per week).

Understanding the relationships between temperature and budburst enables us to predict the timing of budburst under different climatic conditions (e.g., Harrington et al. 2010) and, thus, enables us to predict when budburst occurred in the past and also predict when budburst will likely occur in the future based on climate projections (Harrington and Gould 2015). Although budburst can vary substantially from year to year (by 30 days or more at a location), the trend for Douglas-fir over the past half century or more has been for earlier budburst (figure 4). For Salem, OR, we predicted that the date of 50 percent of individuals reaching terminal budburst for Douglas-fir ranged from April 12 to May 11 and that the date advanced an average of approximately 2 days per decade from 1949 to 2015: this is similar to the 2.5 days per decade observed for budburst and flowering of plant species in nine European countries from 1971 to 2000 (Menzel et al. 2006) . The predicted date of terminal budburst for Douglas-fir in Olympia, WA ranged from April 23 to May 23, and budburst also advanced over time. This response of advancing budburst with warmer temperatures is typical of sites with substantial chilling. Studies of responses to recent warming found that growth initiation is occurring earlier in the year, on average, likely due to increased forcing in locations that have continued to experience sufficient

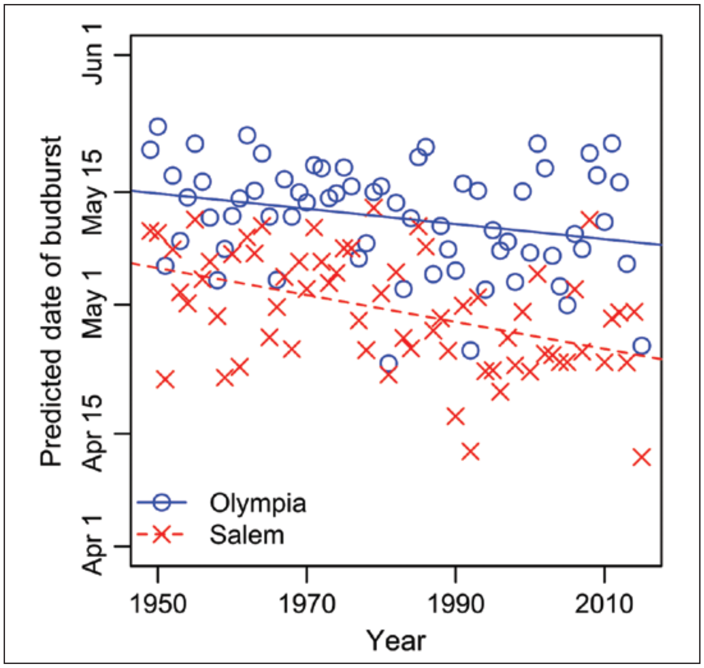

Figure 4. The date of terminal budburst for Douglas-fir was predicted from daily records of hourly temperature from Salem, OR, and Olympia, WA. Mean date of budburst was always predicted to be earlier in Salem than in Olympia and was quite variable from year to year. The slope of the line between year and predicted date of budburst was negative, indicating, on average, the date of budburst has advanced by 2 days per decade during this time period.

chilling (Wolfe et al. 2005). Many examples exist, however, of species that are not responding to warming temperatures or are even initiating growth later, a result often attributed to reductions in chilling (Cook et al. 2012, Parmesan 2007). In addition, trees are more likely to respond to loss of chilling with delays in budburst in environments where chilling is already low (Harrington et al. 2010). Therefore, locations with already warm winters may be the most likely to experience delays in budburst in response to climate change, and this response may become more prevalent as warming progresses. Thus, uniform advances in budburst in response to climate change are unlikely. Instead, budburst responses will likely vary by species, within the ranges of individual species, and over time with increasing warming.

Diameter Growth

The initiation of diameter growth follows reactivation of the vascular cambium, reactivation of the bark cambium, and rehydration of stem and bark cells. We determined the initiation, progression, and cessation of diameter growth for Douglas-fir, western redcedar, and Sitka spruce (*Picea sitchensis* [Bong.] Carrière) by observing changes in the diameters of these trees over the growing season using electronic dendrometers, sensitive instruments that can detect very small changes in stem diameter.

The timing of diameter growth initiation and progression is strongly affected by seasonal weather and other environmental conditions. Based on data from dendrometers at several sites, diameter growth for Douglas-fir seedlings generally begins in March or early April at low-elevation sites in western Washington and Oregon (figure 5) but may be delayed until May at higher elevations (figure 6). Differences in the timing of diameter-growth initiation and progression between seed sources at a location tend to be smaller than differences in the timing of budburst, but they are still present (figure 5a) and statistically significant (Gould et al. 2012). Like budburst, the timing of diameter-growth

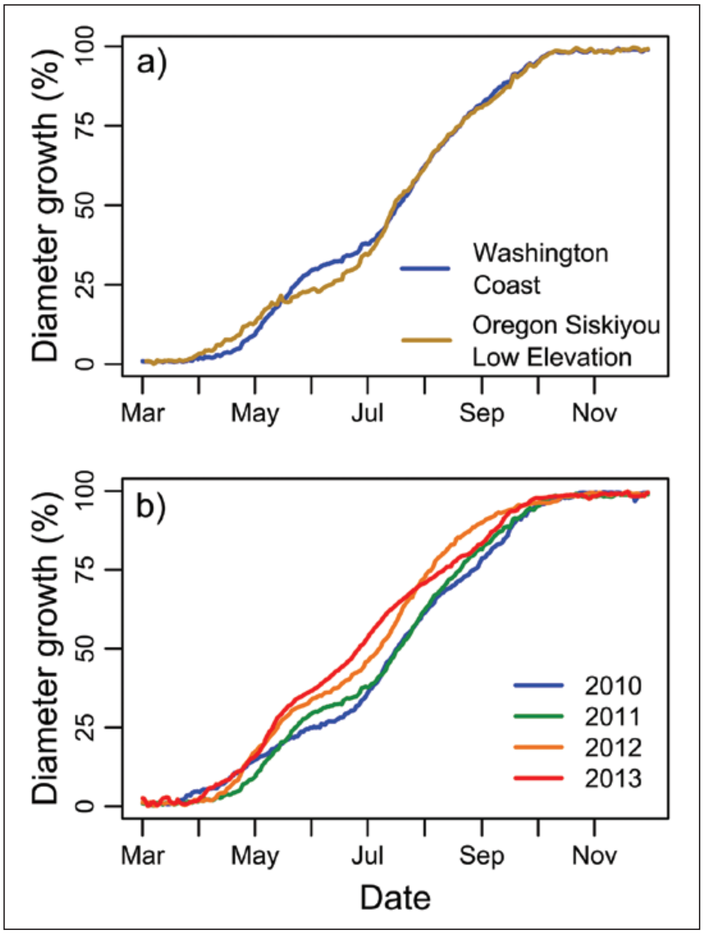

Figure 5. Electronic dendrometers measured (a) diameter growth patterns in 2011 for two seedlots (Washington Coast and low-elevation Oregon Siskiyou Mountains) of Douglas-fir planted at the Buckhorn2 common garden site near Centralia, WA. Diameter growth initiation began sooner for the low-elevation Oregon Siskiyou Mountains seedlot and had an earlier slowdown in growth than for the Washington Coast seedlot. Relative growth rates later in the season were very similar for the two sources. In addition, (b) diameter growth patterns for one seedlot (Washington Coast) of Douglas-fir in multiple years were measured at the same site. Patterns differed from year to year, with variation in temperature and precipitation.

initiation is influenced by both chilling and forcing, though there does not appear to be a minimum chilling requirement (Ford et al. 2016). Differences in patterns among years can be much larger than differences between sources (cf. figure 5a versus 5b); for example, the date when 30 percent of seasonal diameter growth had occurred varied by about 45 days in one seed source at one site across 4 years (figure 5b). Differences among years are associated with patterns of temperature and precipitation and their influence on the date of diameter growth initiation and diameter growth rates; in a similar way, diameter growth phenology for a seed source differs across locations with different climates (figure 6a). Diameter growth in seedlings is often sharply curtailed around the time of budburst and the early stages of height growth, suggesting that seedlings could be preferentially allocating photosynthate or other resources to cell division to support expansion of needle primordia and shoot growth, and not diameter growth, at this time (figure 7). The seasonal progression of diameter growth for western redcedar and Sitka spruce, in general, is similar to that of Douglas-fir (figure 8). Western redcedar has indeterminant growth, however, and tends to exhibit a more linear progression of growth during the season (if environmental conditions are favorable) than do either Sitka spruce or Douglas-fir. This growth pattern means that more of the seasonal growth occurs earlier and later in the season for western redcedar than for the other two species.

Understanding the phenology of diameter growth can inform decisions about the timing of repeated measurements, especially for short time intervals. For example, it could be important to ensure that the timing of repeated measurements for a 1- or 2-year measurement interval happens when the trees are not growing in diameter, but care in the timing of a 5- or 10-year measurement interval would be less important.

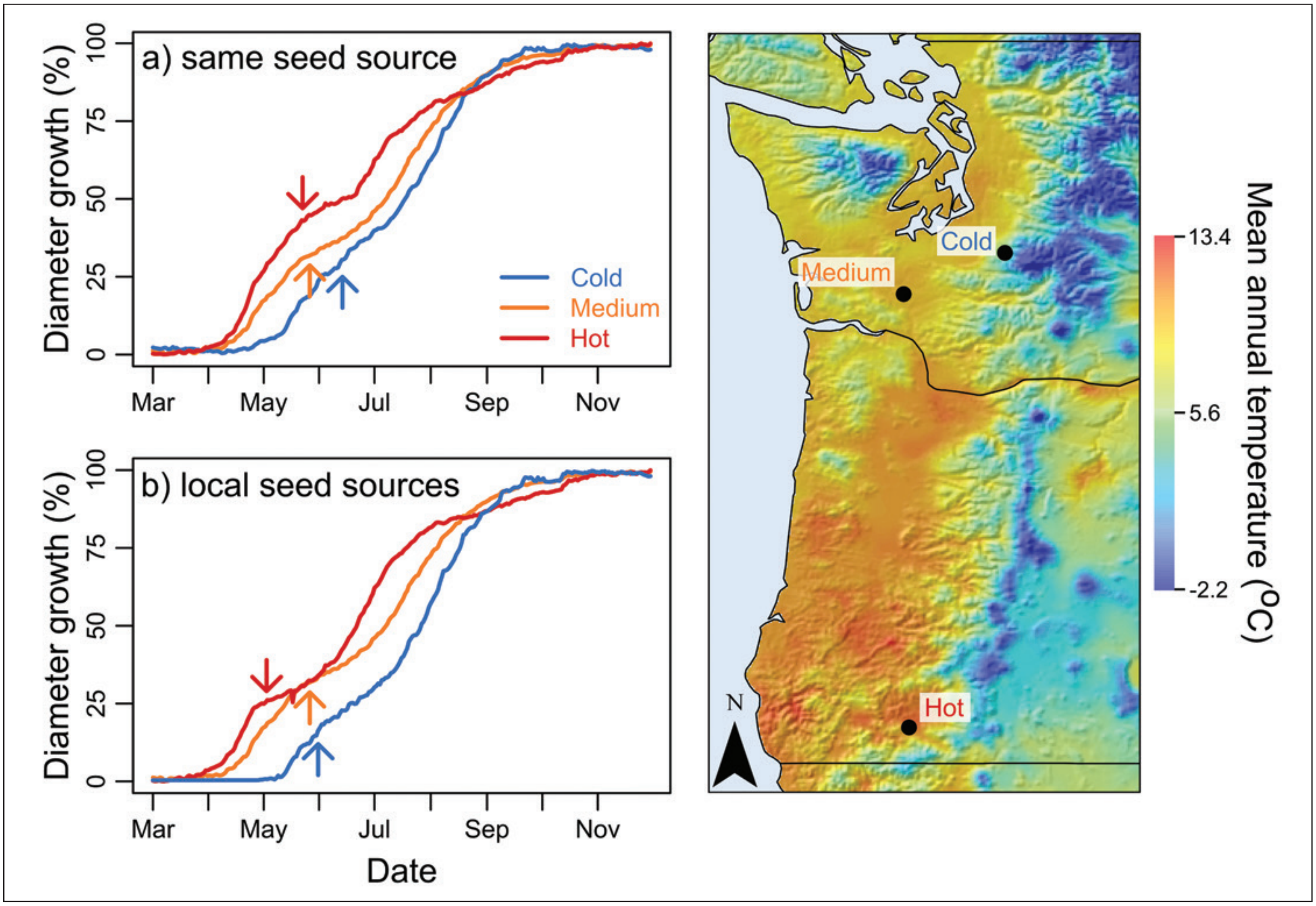

Figure 6. Diameter growth patterns for Douglas-fir in 2012 varied by both seed source and outplanting location (site). (a) The same seed source was planted (source = Washington Coast) at all three sites. The date of budburst is marked by arrows for the three sites. (b) Diameter growth for the local seed sources was monitored at three sites with a range in mean annual temperature. The date of budburst for the local seed source is marked on each dendrometer trace.

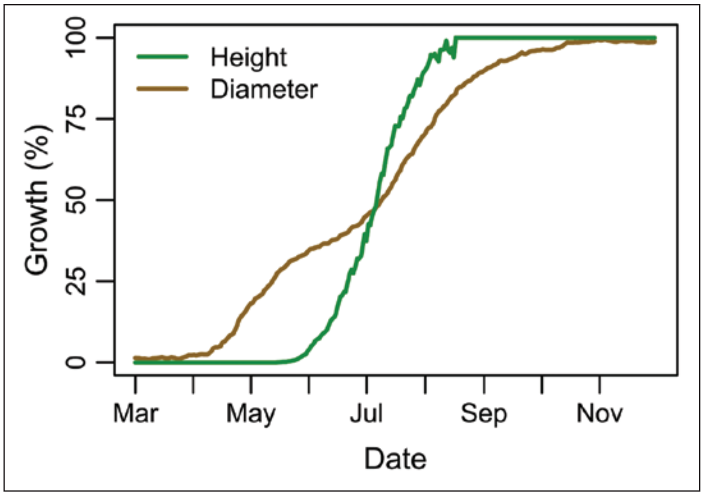

Figure 7. Relative patterns of height and diameter growth for Douglas-fir in 2012, based on eight trees from a Washington Coast seedlot planted at the Buckhorn2 site located near Centralia, WA (site labeled as "Medium" in figure 1). Note that significant diameter growth occurred before the beginning of height growth.

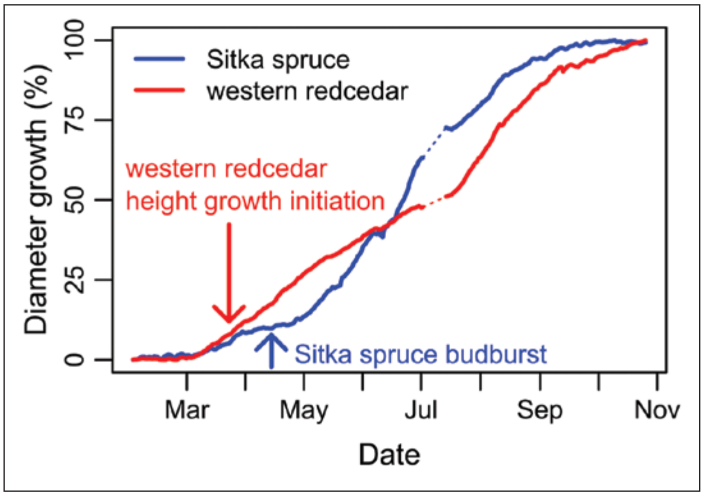

Figure 8. Within-season patterns of diameter growth for Sitka spruce and western redcedar in 2015 in a lath house at the Olympia Forestry Sciences Laboratory near Olympia, WA. Bareroot seedlings were obtained from the Washington Department of Natural Resources, L.T. Mike Webster Nursery (spruce seedlot = Twin Harbors, 0–2745 m; western redcedar seedlot = Skagit, 610–1220 m) in 2014 and transplanted into pots. Each line is the mean of six trees. The dotted portion of the lines indicates when the dendrometers were removed from the seedlings to move them to larger pots.

Reproductive Phenology

Reproductive phenology is key to successful seed production. As with vegetative phenology, early flowering runs the risk of frost damage and late flowering reduces the time period for cone development and seed filling. In addition, the synchrony of pollen release and female flower receptivity is key to the production of viable seeds for trees with separate male and female flowers, which is the case for dioecious species (male and female organs on separate plants; e.g., *Fraxinus, Populus,* and *Salix* species) and monecious species (male and female reproductive organs in different structures but on the same tree; e.g., most conifers and many angiosperms such as Alnus and Acer species). Local managers of seed orchards are well aware of variation within their orchards from year to year, and general ranges in characteristics such as flowering, cone ripening, and seed dispersal have been documented for most woody species in the United States and elsewhere (cf. Bonner and Karrfalt 2008).

As with the initiation of vegetative growth, the timing of reproductive stages in Douglas-fir and western redcedar can vary substantially from year to year (figure 9; El-Kassaby 1999) and is presumably responding to climate cues and past conditions. Our observations of pollen release and female flower receptivity for these two monecious species suggest that these events are well-synchronized under the current climate. It is unknown if these phenological processes could

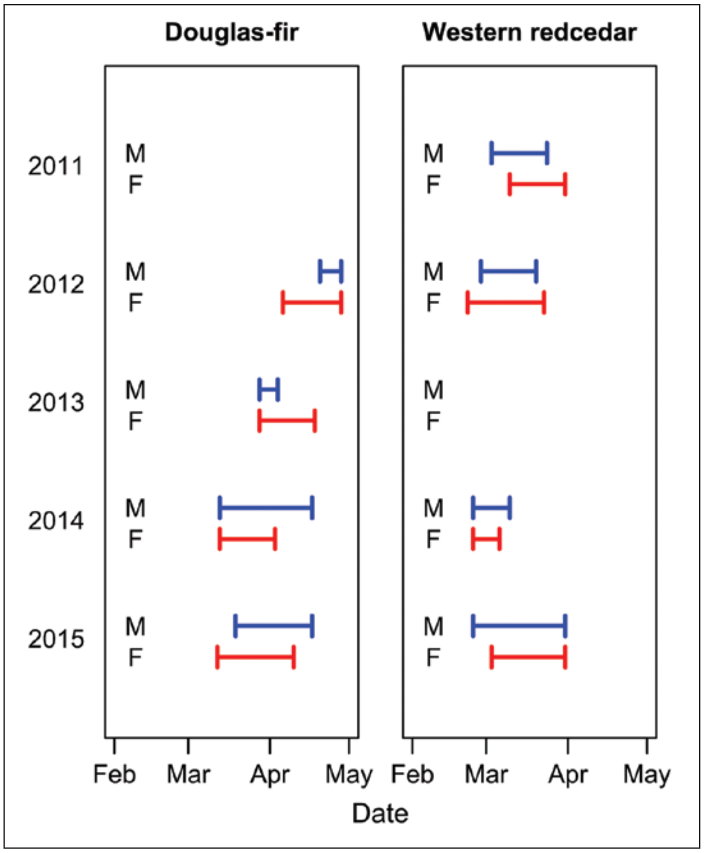

Figure 9. Reproductive status was monitored for Douglas-fir saplings in the Stone common garden near Medford, OR, and for clones of western redcedar at the Washington State Department of Natural Resources, Meridian Seed Orchard near Olympia, WA. The Douglas-fir saplings, planted in the fall of 2008, were from seed sources that would be considered local for that location (low-elevation Oregon Siskiyou Mountains). The western redcedar plants were established from rooted cuttings of eight clones planted in 2001 or 2005 (locations of parent trees ranged from 60 to 600 m in western Washington). Shown is the date range for female receptivity and pollen shed.

respond differently to warming and become decoupled in the future, leading to phenological mismatches due to climate change. Changes in climate disrupting the synchrony of male and female flower phenology could lead to a small percentage of individuals providing pollen in a seed orchard at the time when female flowers are receptive (e.g., Alizoti et al. 2010), which could potentially reduce genetic diversity or, in a worst case scenario, result in little or no pollen being available at the time it is needed, reducing the production of viable seed. We hope to continue to expand our work on phenology to understand the factors controlling reproduction so we can better predict which processes, species, and sites might be at risk under future climates, and so we can learn if there are ways to reduce these risks.

Conclusions

Most foresters are well aware that the timing of biological events can vary substantially across years, locations, species, or genotypes, and they appreciate that these observations can have practical significance. We understand that phenological responses to climate change will differ, depending on the species and genotype and the position on the landscape (in terms of current and predicted changes in climate). Furthermore, some phenological traits may be more sensitive to climate change than others; for example, the timing of budburst varies more among populations than the initiation of diameter growth. Most information on phenology of tree species has focused on budburst and flowering. Predicting how trees respond to their current and future environments will require much more information on plant functions such as growth, form, and reproduction as well as interactions with other species. For example, some species or locations may gain a competitive advantage in terms of a longer effective growing season; trees in some areas may become less or more valuable due to changes in stem taper or wood characteristics, while others may see changes in interactions with insect or fungal pests as a result of phenological mismatches. We hope that future work on phenology will (1) document phenological changes over time for many species and locations, including the phenology of organisms that interact with trees, and (2) collect detailed observations of phenological events along with monitoring of environmental conditions to develop models that can be used to predict how phenology of trees in the Pacific Northwest will change in the future. Phenological studies should help foresters in their day-to-day activities, including developing recommendations for adapted seed sources or for the timing of activities such as planting, sowing, or vegetation control. In addition, such studies should increase our understanding of range limitations for individual species and competitive interactions in stands with mixtures of tree species.

Address correspondence to—

Constance A. Harrington, USDA Forest Service, Pacific Northwest Research Station, 3625 93rd Avenue SW, Olympia, WA 98512; e-mail: charrington@fs.fed.us; phone: 360-753-7670.

Acknowledgments

The authors thank George McFadden, Oregon State Office, U.S. Department of the Interior, Bureau of Land Management for financial support of the study; Washington State Department of Natural Resources, Port Blakely Tree Farms, USDA Forest Service J. Herbert Stone Nursery, Hancock Resources, Cascade Timber Consulting, Roseburg Resources, Giustina Land and Timber, and Starker Forests for access to their land and assistance; and our coworkers, especially Chris Poklemba, Teresa Vail, Peter Gould, Leslie Brodie, and David Thornton for data collection and processing.

REFERENCES

Alizoti, P.G.; Kilimis, K.; Gallios, P. 2010. Temporal and spatial variation of flowering among Pinus nigra Arn. clones under changing climatic conditions. Forest Ecology and Management. 259(4): 786–797.

Allen, G.S.; Owens, J.N. 1972. The life history of Douglas-fir. Ottawa, QC, Canada: Information Canada. 139 p.

Bonner, F.T.; Karrfalt, R.P., eds. 2008. The woody plant seed manual. Agric. Handb. 828. Washington, DC: U.S. Department of Agriculture, Forest Service. 1223 p.

Burr, K.E.; Tinus, R.W.; Wallner, S.J.; King, R.M. 1989. Relationships among cold hardiness, root growth potential and bud dormancy in three conifers. Tree Physiology. 5(3): 291–306.

Carlson, W.C. 1985. Effects of natural chilling and cold storage on budbreak and root growth potential of loblolly pine (Pinus taeda L.). Canadian Journal of Forestry Research. 15(4): 651–656.

Cook, B.I.; Wolkovich, E.M.; Parmesan, C. 2012. Divergent responses to spring and winter warming drive community level flowering trends. Proceedings of the National Academy of Sciences of the United States of America. 109(23): 9000–9005.

El-Kassaby, Y. 1999. Phenotypic plasticity in western redcedar. Forest Genetics. 6(4): 235–240.

Fitter, A.H.; Fitter, R.S.R. 2002. Rapid changes in flowering time in British plants. Science. 296(5573): 1689–1691.

Ford, K.R.; Harrington, C.A.; Bansal, S; Gould, P.J.; St. Clair, J.B. 2016. Will changes in phenology track climate change? A study of growth initiation timing in coast Douglas-fir. In press: Global Change Biology. doi: 10.1111/gcb.13328

Gould, P.J.; Harrington, C.A.; St. Clair, J.B. 2011. Incorporating genetic variation into a model of budburst phenology of coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*). Canadian Journal of Forest Research. 41(1): 139–150.

Gould, P.J.; Harrington, C.A.; St. Clair, J.B. 2012. Growth phenology of coast Douglas-fir seed sources planted in diverse environments. Tree Physiology. 32(12): 1482–1496.

Harrington, C.A.; Gould, P.J. 2015. Tradeoffs between chilling and forcing in satisfying dormancy requirements for Pacific Northwest tree species. Frontiers in Plant Science. doi:10.3389/fpls.2015.00120.

Harrington, C.A.; Gould, P.J.; St. Clair, J.B. 2010. Modeling the effects of winter environment on dormancy release of Douglas-fir. Forest Ecology and Management. 259(4): 798–808.

Howe, G.T.; Aitken, S.N.; Neale, D.B.; Jermstad, K.D.; Wheeler, N.C.; Chen, T.H.H. 2003. From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees. Canadian Journal of Botany. 81(12): 1247–1266.

Intergovernmental Panel on Climate Change (IPCC). 2014. Climate change 2014: impacts, adaptation, and vulnerability. Part A: global and sectoral aspects. In: Field, C.B.; Barros, V.R.; Dokken, D.J.; Mach, K.J.; Mastrandrea, M.D.; Bilir, T.E.; Chatterjee, M.; Ebi, K.L.; Estrada, Y.O.; Genova, R.C.; Girma, B.; Kissel, E.S.; Levy, A.N.; MacCracken, S.; Mastrandrea, P.R.; White, L.L., eds. Fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge, United Kingdom; New York: Cambridge University Press. 1,132 p.

Körner, C.; Basler, D. 2010. Phenology under global warming. Science. 327(5972): 1461–1462.

Menzel, A; Sparks, T.H.; Estrella, N.; Koch, E,; Aasas, A,; Ahas, R.; Alm-Kübler, K.; Bissolli, P.; Braslavská, O.; Briede, A.; Chmielewski; Crepinsek, Z.; Curnel, Y., Dahl, Å; Defila, C.; Donnelly, A.; Filella, Y., Jatczak, K.; Måge, F.; Mestre, A.; Nordli, Ø.; Peñuelas, J.; Pirinen, P.; Remišová, V.; Scheifinger, H.; Striz, M.; Susnik, A.; Van Vliet, A.; Wielgolaski, F.; Zach, S.; Zust, A. 2006. European phenological response to climate change matches the warming pattern. Global Change Biology 12 (10): 1969-1976.

Nelson, E.A.; Lavender, D.P. 1979. The chilling requirement of western hemlock seedlings. Forest Science. 25(3): 485–490.

Omi, S.K.; Rose, R.; Sabin, T.E. 1991. Effectiveness of freezer storage in fulfilling the chilling requirement of fall-lifted ponderosa pine seedlings. New Forests. 5(4): 307–326.

Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Global Change Biology. 13(9): 1860–1872.

Romberger, J.A. 1963. Meristems, growth and development in woody plants: an analytical review of anatomical, physiological, and morphogenic aspects. USDA For. Serv. Tech. Bull. 1293. Washington, DC: U.S. Government Printing Office. 214 p.

Sarvas, R. 1974. Investigations on the annual cycle of development on forest trees active period. II. Autumn dormancy and winter dormancy. Helsinki, Finland: Communicationes Instituti Forestalis Fenniae. 84 p.

Sloan, J.P. 1991. Ponderosa and lodgepole pine seedling bud burst varies with lift date and cultural practices in an Idaho nursery. USDA For. Serv. Res. Note INT–397. Ogden, UT: Intermountain Research Station. 9 p.

St. Clair, J.B.; Mandel, N.L.; Vance-Borland, K.W. 2005. Genecology of Douglas-fir in western Oregon and Washington. Annals of Botany. 96(7): 1199–1214.

Vegis, A. 1964. Dormancy in higher plants. Annual Review of Plant Physiology. 15: 185–224.

Wang, T.; Hamann, A.; Spittlehouse, D.L.; Murdock, T.Q. 2012. ClimateWNA: high-resolution spatial climate data for western North America. Journal of Applied Meteorology and Climatology. 51: 16–29.

Wenny, D.L.; Swanson, D.J.; Dumroese, R.K. 2002. The chilling optimum of Idaho and Arizona ponderosa pine buds. Western Journal of Applied Forestry. 17(3): 117–121.

White, T.L.; Ching, K.K.; Walters, J. 1979. Effects of provenance, years, and planting location on bud burst of Douglas-fir. Forest Science. 25(1): 161–167.

Wolfe, D.W.; Schwartz, M.D.; Lakso, A.N.; Otsuki, Y.; Pool, R.M.; Shaulis, N.J. 2005. Climate change and shifts in spring phenology of three horticultural woody perennials in Northeastern USA. International Journal of Biometeorology. 49(5): 303–309.

Wommack, D.E. 1960. Effect of winter chilling and photoperiod on growth resumption in Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco. Corvallis, OR: Oregon State College. 82 p. M.S. thesis.