

Science

FINDINGS

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“Science affects the way we think together.”

Lewis Thomas

Nature and Nurture: Genetics and Climate Influence the Timing of Flowering in Trees



Janet Prev  y

Technically, Douglas-fir are not flowering plants, but its young female cones, shown above, are often referred to as “flowers.” Genetic variation yields “flowers” of various hues; it also influences the timing of flowering in different populations. Knowing when Douglas-fir are going to flower helps seed orchards have staff ready for the labor-intensive pollination process that yields high-quality Douglas-fir seeds.

*“O, wind, if winter comes, can spring
be far behind?”*

—Percy Bysshe Shelley

Timing is everything, especially when it comes to tree sex.

To successfully produce viable seeds, conifers must open their female cones at the same time that other trees of the same species are releasing pollen from their male cones. The trees also need to flower during the “sweet spot” after the last killing frost, but early enough to benefit from favorable growing season conditions after pollination occurs.

Plants depend on signals, such as changes in seasonal temperature, to trigger the timing of reproduction in the spring.

The timing of biological events in relation to season or climate—such as flowering and leaf-out in plants or hibernation and migration in animals—is called phenology. Changes in phenology are among the most sensitive biological responses to climate, and accordingly are an early indicator of the ecological effects of climate change.

Phenology is also important to managers of commercially important tree species, such as Douglas-fir. “Managers want to make sure they plant Douglas-fir during the right climate conditions, so they’ll do well at the sites in which they are planted—which means they don’t start growing too early and suffer frost damage, but start growing early enough to take full advantage of the growing season,” says Janet Prev  y, a plant ecologist with the USDA Forest Service Pacific Northwest Research Station.

IN SUMMARY

To successfully reproduce, conifers must have impeccable timing—opening their female cones to receive pollen from the male cones of nearby trees. This timing is a response to temperature and other environmental cues. It is to the tree’s advantage to flower when risk of damaging frost is low, but early enough in the spring to take full advantage of the growing season.

Douglas-fir is ecologically important and the cornerstone of the timber industry in the Pacific Northwest. Seed orchard managers carefully breed different populations of the species to produce seedlings that will thrive in particular areas in need of replanting. Understanding the environmental cues that influence the timing of flowering is important for predicting how reproduction and survival of trees will change in the future. To address this need, a team of researchers with the USDA Forest Service Pacific Northwest Research Station developed a model that predicts, within an average of 5 days, when Douglas-fir will flower. Seed orchard managers are using the model to plan and schedule time-sensitive tasks related to flowering in the orchards.

The model highlights how both cool and warm temperatures influence the date of flowering for Douglas-fir. It can be used to predict how future changes in temperature could influence flowering times across the range of Douglas-fir under different climate predictions.

Douglas-fir are found across western North America from British Columbia to Mexico, and from the moist, temperate rainforests along the Pacific coast to the dry forests of the Rocky Mountains. Douglas-fir populations have adapted to a wide range of winter temperatures and amounts of summer precipitation. Understanding how these adaptations influence phenology is important for predicting how reproduction and survival of Douglas-fir will change in the future with changing temperature and moisture patterns.

All in the Timing

Prevéy, along with colleagues Connie Harrington and Brad St. Clair at the Pacific Northwest Research Station, recently developed a model that accurately predicts the day of flowering to within an average of 5 days of observed flowering dates. They also examined whether genetic variation in Douglas-fir influenced the timing of flowering.

The scientists worked with seed orchard managers in Oregon and Washington, who provided data on the flowering times in their orchards. All told, they used more than 4,500 flowering observations from 12 sites to develop the model. To make it a viable tool for predicting the timing of Douglas-fir flowering, Prévéy teamed up with a collaborator with the Washington Department of Fish and Wildlife, Ty Garber, to develop an interactive website based on the reproductive phenology model and real-time data from weather stations run by the National Oceanic and Atmospheric



KEY FINDINGS



- Winter temperatures were the strongest predictor of Douglas-fir flowering time. Fewer hours of forcing (warm) temperatures during the trees' dormant season were required for flowering on sites and during years that had many hours of chilling (cool) temperatures.
- Genetic variation within the species also influenced flowering. Genotypes from warmer, drier locations flowered earlier in common gardens than genotypes from colder, wetter locations.
- Warmer temperatures in the future will likely result in earlier flowering on sites that currently experience many hours of high chilling. Sites that currently experience low chilling may display no change or possibly even a delay in flowering.

Administration (NOAA).

Controlled breeding of Douglas-fir in seed and breeding orchards is a complicated process designed to exert control over natural reproductive processes. Cloth bags are used to isolate young Douglas-fir cones from contamination by unwanted pollen. Once the cones break bud, pollen is carefully applied manually using small paintbrushes or eyedroppers. The pollen used for pollination has typically been collected from parent trees that were selected for characteristics such as growth, wood quality, and reduced susceptibility to insect and disease damage. The collected pollen is often considered so precious, it is applied grain by grain to selected conelets.

Until recently, Norah Young worked as a forester for the Washington Department of Natural Resources (WA DNR) at the Meridian

Seed Orchard in Olympia, Washington (she now works in the WA DNR small-forest land-owner office), and was responsible for the controlled pollination process at the orchard.

"Once a cone bud opens, we have about a week to complete cross-fertilization," Young says. "We try to apply pollen to each bud three times during the week with a day between each application."

Managers say there are months of preparation before breeding season, so it's critical for the breeders to know approximately when the trees are going to flower.

"Knowing the timeline helps us gear up," says Bill Marshall, the director of silviculture at Cascade Timber Consulting, Inc., in Sweet Home, Oregon. "When doing controlled breeding, we may hang 2,000 to 3,000 bags on clus-

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Norah Young

A Douglas-fir seed orchard in Washington. The cones of some trees have been bagged to prevent pollination by wind or insects. They will be selectively pollinated by hand.



Norah Young

A field technician pollinates Douglas-fir cones at Green Diamond's seed orchard. Seed orchard managers are trying to adjust to climate change and produce trees that will thrive in conditions 20 to 30 years from now.

ters of female flowers before the pollen starts to flow. That takes a lot of time and a lot of preparation to get crews and equipment in place.”

“This project was a really cool collaborative relationship where seed orchard managers provided us with a lot of data that allowed us to develop a model, and in exchange, we were able to give them something they could use to predict flowering in the future,” Prev  y says. “It’s been rewarding to produce science where people are saying, ‘Hey, I’m actually using this.’”

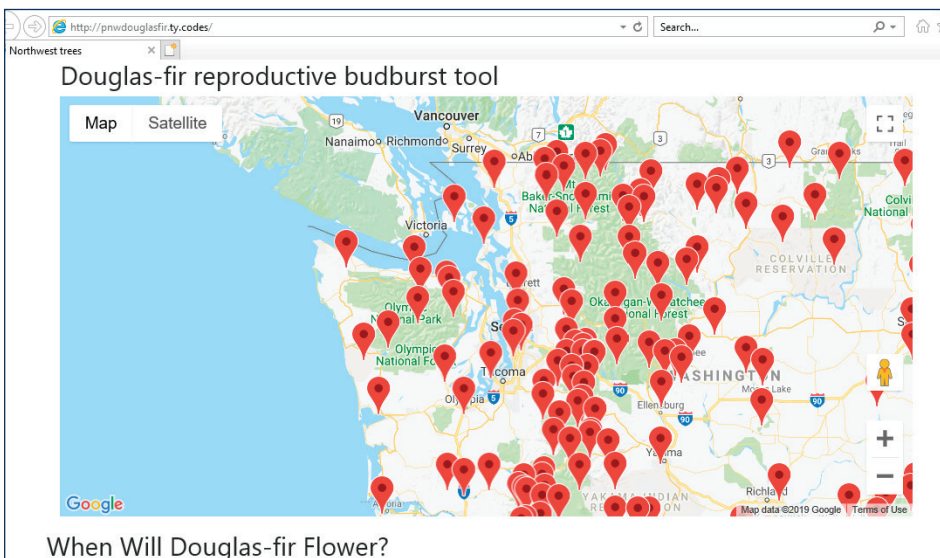
Prev  y, Harrington, and St. Clair combined the data from the seed orchards with in-house data from their ongoing Douglas-fir Seed-Source Movement Trial. The trial is designed to look at combinations of seed sources and test sites to evaluate various aspects of plant adaptation. In 2009, seedlings from 60 populations from a wide range of climates in western Washington and Oregon and northern California were planted at nine sites in Washington and Oregon. The planting sites represented the range of conditions experienced across the region. Over the years, the researchers have studied adaptive traits, such as growth, survival, cold hardiness, drought hardiness, and phenology, in relation to the source environments of the different populations and the environments in which they are growing.

Chilling and Forcing

Temperate tree species enter a dormant period in late fall that continues through winter and early spring. Previous research has shown that the timing of vegetative budburst, often called “leaf-out,” depends on the accumulation of both chilling (cool) and forcing (warm) temperatures during the dormant period. Although researchers know that chilling and forcing are important, the biochemical mechanisms underlying bud dormancy and growth are not well understood at this point.

The researchers hypothesized that both chilling and forcing temperatures would be principal drivers in the timing of flowering. Based on findings from prior studies associated with the Douglas-fir Seed-Source Movement Trial, they assumed that longer periods of cool temperatures during the winter would result in fewer warm days in the spring needed to trigger budburst, whereas shorter periods of cool temperatures would require more warm days to induce budburst.

They adapted chilling and forcing effectiveness functions previously developed in Harrington’s vegetative budburst model for Douglas-fir to generate a “possibility line” for reproductive budburst of Douglas-fir. Reproductive budburst occurs prior to vegetative budburst in Douglas-fir, so the func-



A screen shot of the Douglas-fir Reproductive Budburst Tool. Users can click on a red marker to see when budburst is likely to happen in that location. The tool uses equations adapted from a reproductive phenology model and daily temperature data.

tions were changed to reflect this difference in timing.

“Both chilling and forcing temperatures influence budburst timing—and many combinations can result in budburst,” says Prevéy.

“Our model produces a ‘flowering possibility line’ for Douglas-fir, which shows the relationship between the amount of warm or forcing temperatures needed for flowering at any level of cool or chilling temperatures,” says Harrington. “Prevéy and Garber developed a visualization tool that allows managers to see how the past weather conditions at a specific location are approaching the possibility line. Once the specific site tracking line approaches the possibility line, they know it’s possible for Douglas-fir to flower at that site.”

The model demonstrated that fewer hours of forcing temperatures were required for flowering on sites and during years that had many hours of chilling temperatures.

“Over the winter, the tree needs to experience some combination of cool and warm temperatures to convince it that winter is over and it is now spring and time to flower,” Prevéy says. “You can have a very cold winter and then a little bit of warm temperatures and the trees say, ‘OK, time to flower.’ Whereas if you have a really warm winter, it’s going to take a lot more warm temperatures to convince the tree it’s time to flower.”

In the past, Harrington explains, researchers believed sufficient chilling temperatures were needed first “to turn the key in the lock;” after that occurred, the tree began accumulating forcing temperatures that led to budburst.

“What we found in looking at these different datasets is that it appears the plants are able to benefit from both forcing and chilling intermingled through the dormant season,” Harrington says. “And that’s obviously more likely to be occurring with the type of climate in the Pacific Northwest where we have a lot of days with temperatures in the high 30s, 40s, and low 50s in the winter, as opposed to places at higher elevations or further north, where once winter comes it may be very cold for months on end.”

The study results also led the team to a set of conclusions about the effects of climate change that may seem counterintuitive.

Warmer temperatures in the future will likely result in earlier flowering on sites that currently have high chilling. But sites that currently experience low chilling may display no change or possibly even a delay in flowering. In other words, higher temperatures during the winter could lead to later budburst in the spring in some places, rather than earlier, owing to the lack of chilling.

“If the tree experiences a lot of warm days over winter, then it may take a stronger warm signal to break it out of dormancy,” Prevéy says.

Prevéy says that one of the weaknesses of the Douglas-fir study is it’s based solely on observational data, with no control over conditions, such as those that could be achieved in a greenhouse study. If they wanted to pick apart the differences between, for example, climate and photoperiod or day length, the researchers would need to do a controlled-environment study. But, of course, it is impossible to put large flowering trees into growth chambers because of their size.

To get around this problem, and to test their hypotheses on a deciduous species native to the Pacific Northwest, the researchers took cuttings from mature red alder trees and put them in growth chambers under regulated conditions—one colder and one warmer.

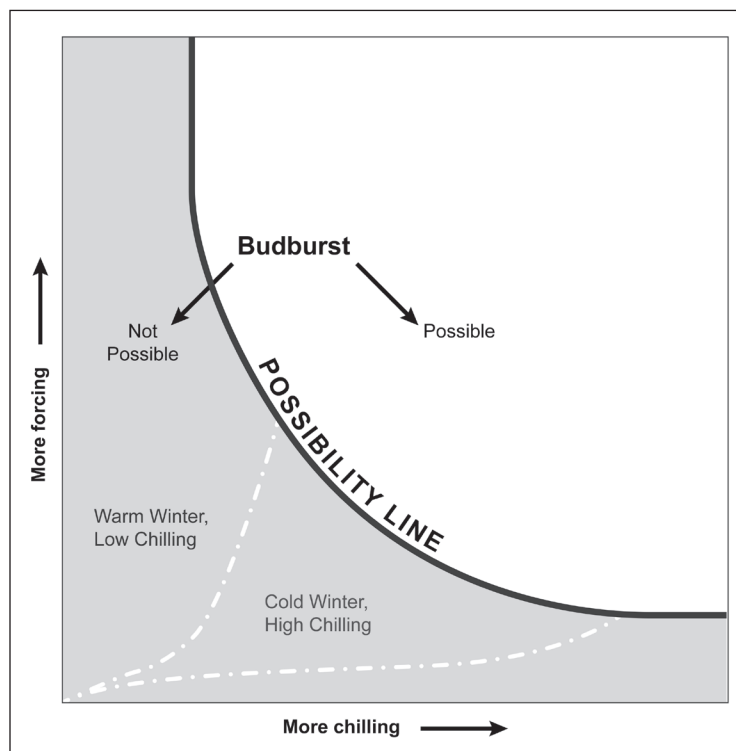
“We just tried to convince the cuttings they were still attached to the rest of the tree all winter,” Prevéy says.

The red alder trial demonstrated that trees which experience cooler temperatures over the winter need less warm temperatures to flower in the spring, and this result was consistent with findings from their research on Douglas-fir phenology.

Nature and Nurture

The second question the team addressed was: Does heredity influence the relationship between temperature and flowering dates for trees from different seed sources?

They found that genotypes from warmer, drier locations flowered earlier in common gardens than genotypes from colder, wetter locations.



When will budburst occur? This schematic illustrates that both chilling (cool) and forcing (warm) temperatures influence reproductive budburst (i.e., flowering). Many combinations can result in budburst.

St. Clair says that’s an adaptation to drought and aridity in the summertime.

“Basically, parent trees in dry places produced flowers early and got their reproduction done before the drought commenced in the later summer,” St. Clair says. “They were the ones that successfully survived and reproduced and passed their genes for early flowering on to the next generation. So, when we take seedlings of the parents from these different sources, and put them in a common environment, those from the drier locations are the ones that flower first.”

The relationship between seed source climate and phenology is stronger for drought than for winter or spring temperature, indicating that summer drought was a more important factor for natural selection than avoiding early frost.

“Genotypes that came from areas that have very droughty summers have evolved to burst bud earlier and take advantage of the favorable early growing conditions because conditions are going to become a lot less favorable for tree growth later in the season,” Harrington says. “So there’s been more evolutionary pressure to push flowering earlier in particular, requiring less forcing.”

The researchers concluded that Douglas-fir can respond to the conditions it’s experiencing at a site, but a particular seed source is also limited by its genetic history, as determined by the past climate of its source environment.

In this study, even though the trees from drier seed sources would generally flower earlier, the temperature over the winter at the site they were growing was also a really important determinant of when they would flower. As St. Clair says, “It is both nature and nurture that determine when a Douglas-fir tree will flower. There are genetic effects driven by drought avoidance, but there are also local environmental effects of temperature in the spring and winter that help trees adjust to avoid frost damage.” This has important implications for climate change.

“If the climate changes rapidly, trees may not be able to adjust their phenology that quickly,” Prev y says. “Pretty soon, there might be mismatches between the climate where the parent trees evolved and the climate where their progeny are growing.”

These results can be used to predict regions where future climate could advance or delay flowering, and predict optimal locations for

	LAND MANAGEMENT IMPLICATIONS	
•	Seed orchard managers can use the reproductive phenology model to help plan time-sensitive management decisions, such as applying pollen to receptive reproductive buds for controlled breeding programs.	
•	The model can be used to predict where future climate could advance or delay flowering, and predict optimal locations for new seed orchards. Warmer temperatures may cause earlier flowering, requiring changes in seed orchard management.	
•	The modeled relationship between chilling and forcing temperatures can also be used to predict how the timing of reproductive budburst of other important tree species, such as red alder, may be affected by climate, and inform replanting and restoration efforts.	

new seed orchards. In addition, warmer temperatures may change the traditional dates of flowering, requiring changes in the timing of seed orchard management practices.

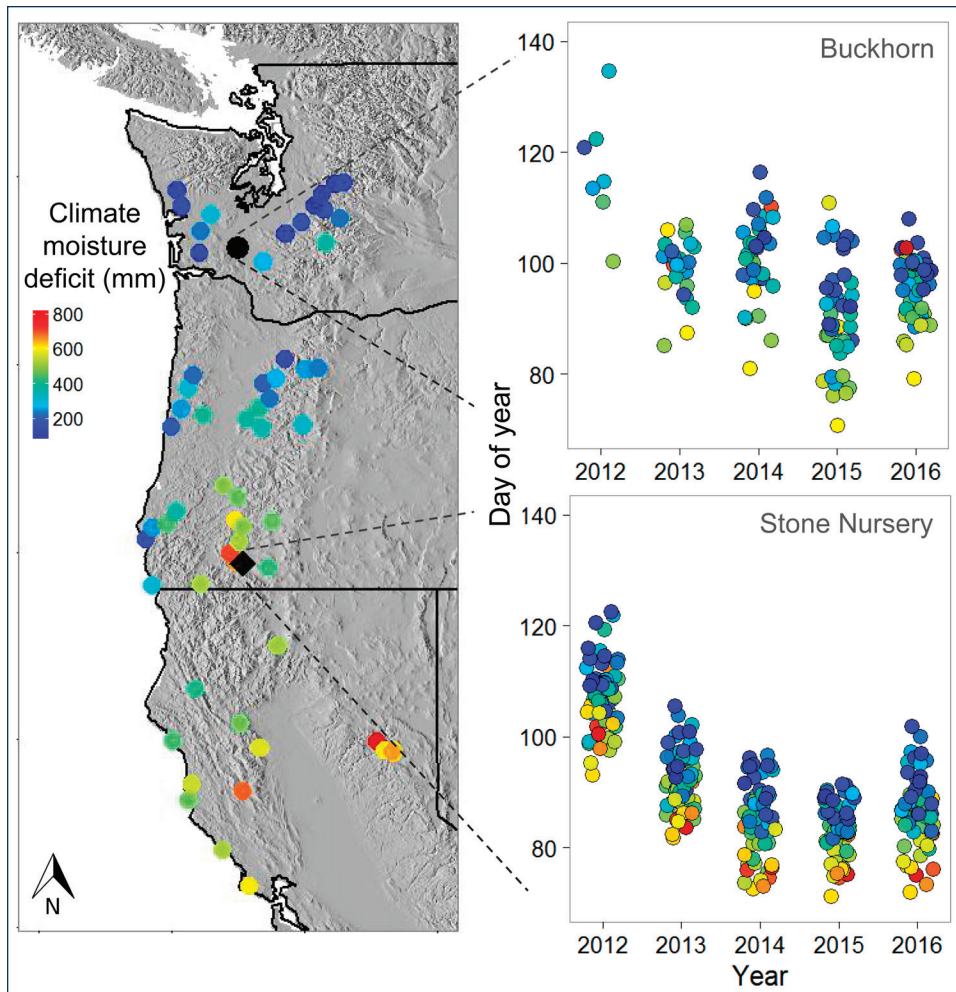
Bill Marshall with Cascade Timber Consulting, Inc. says seed orchard manag-

ers are trying to adjust to climate change and make management decisions based on how conditions will be 20 to 30 years in the future.

“In the past, people were very conservative with moving seeds,” Marshall says. “They believed each canyon had its own genotype, but the Seed-Source Movement Trial and the models created in the most recent study are going to allow people to feel more confident in moving seed around and seeing what the limits are.”

“No winter lasts forever; no spring skips its turn.”

— Hal Borland



Genetic variation in Douglas-fir, along with temperature, influenced when the trees flowered. Genotypes from warmer, drier locations (warmer colors) flowered earlier than genotypes from colder, wetter locations (cooler colors) regardless if they were growing in the Buckhorn site or 400 miles to the south in Stone Nursery.

Further Resources

Prev y, J.S.; Garber, T. 2019. The Douglas-fir reproductive budburst tool: <http://pnw-douglasfir.ty.codes>

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