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"Science affects the way we think together."
Lewis Thomas

The Future of Spring Bud Burst: Looking at the Possibilities

Connie Harrington

Winter temperatures and length of exposure influence the timing of spring bud burst for Douglas-fir. Understanding the interplay between the temperature-exposure relationship and genetic variation within the species is critical when assessing management options under future climate scenarios.

IN SUMMARY

Spring bud burst has been occurring earlier in the year for many plant species because of warmer winter and spring temperatures. Understanding the long-term effects of this shift and adapting forest management to accommodate it requires deeper insights into the dynamics of bud burst.

Scientists with the Pacific Northwest Research Station conducted several experiments that involved exposing many genetic varieties of Pacific coastal Douglas-fir seedlings to a range of winter conditions. Their results, in conjunction with findings from many previous studies on bud burst in other plant species, enabled the team to build a mathematical model demonstrating that an intricate interplay between temperatures during winter and spring months is involved in producing this critical first step in the growth cycle.

They found that moderately warmer winters will continue to trigger earlier bud burst, but much warmer winters could result in later bud burst than has occurred historically. This is because plants exposed to fewer hours of optimal chilling temperatures in winter need more hours of warmth to satisfy their genetically determined needs for bud burst. The scientists propose that this relationship governs bud burst in many plant species. This research offers a starting point for predicting bud burst for genetically different populations under future climate scenarios.

Winter Trees
All the complicated details
of the attiring and the
disattiring are completed!
A liquid moon moves gently among
the long branches.
Thus having prepared their buds
against a sure winter
the wise trees stand sleeping
in the cold.
—William Carlos Williams

We take for granted that perennial plants will burst bud and resume growth in the spring, but how they "know" the right time to do so, and why this happens earlier in some years and later in others, are questions that have long intrigued scientists. Many studies have suggested that plants perceive and "remember" environmental signals, but the specific mechanisms underlying these remarkable abilities have remained unclear. A better understanding of these fundamental processes is important to biological science, but also has practical applications in predicting the effects of global warming.

Some people have suggested that if and when climate warming makes plants less viable on their current home turf, assisted migration—bringing in varieties better adapted to warmer

conditions, such as those from farther south or lower elevations—could help compensate for warming effects. But forecasting how climate change may impact ecosystems, and developing management responses, requires more solid information on how weather relates to events in plant life cycles and better tools for predicting how different genetic varieties might respond under different conditions.

For many woody species that grow in mid-latitude temperate areas, the first step in spring growth—the bursting of buds—has been occurring earlier in the year as winter and spring generally have become warmer in recent decades. Given that bud burst is a key factor in shaping biological communities, its timing is important in forecasting the effects of climate change on individual species and their populations. Thus, a question of growing importance is how might increasingly mild winters and warmer springs affect this critical biological event?

Scientists at the Pacific Northwest Research Station recently addressed this question for coastal Douglas-fir, one of the most ecologically and economically important trees in western North America. Research foresters Connie Harrington and Peter Gould (based at the Olympia Forestry Sciences Laboratory) and research geneticist Brad St. Clair (at the Corvallis Forestry Sciences Laboratory) tested the effects of an array of winter environments on a range of Douglas-fir populations from Washington, Oregon, and California. Their findings revealed some intriguing surprises and provided the underpinnings for a novel model that promises to aid managers in predicting bud burst for different populations under various scenarios of future climate.

PEERING INTO THE "BLACK BOX" OF CHILLING AND WARMING

Connie Harrington

Scientists explored the consequences of a range of warmer winter conditions on the timing of bud burst. Above, a technician checks to see if bud burst has occurred.

Scientists have long appreciated that many woody species need a certain amount of exposure to cold temperatures in the winter (referred to as chilling), as well as adequate warming (called forcing), to trigger spring growth. Some species won't leaf out at all without enough chilling (Douglas-fir is one such plant). Other species are less particular but may have delayed bud burst, which can shorten the plant's growing season. Conversely, if bud burst happens too early, the plant could suffer damage from subsequent spring frosts. What wasn't known prior to this study was the intricate interplay between temperatures during the winter and spring months.

Research on fruit tree production has shown that certain varieties, if grown too far south, won't flower optimally or leaf out normally. In forestry, the focus has been more on what happens to trees during winter or to nursery seedlings in cold storage. "Many studies had hinted that there was a range of effectiveness in temperatures that might satisfy a plant's chilling requirement," Harrington notes. "We wanted to understand this better in order to predict how individual species might respond to different environments during winter and spring."

To begin with, Harrington reviewed about 100 studies that investigated the effectiveness of various temperatures for activating bud burst or seed germination—generally described as hours of exposure to certain temperatures—in plants ranging from winter rye to peach trees to birch and Douglas-fir. It appeared that the same temperatures were effective for diverse plant types. "Those results led to our hypothesis that, while plants might differ by species or genetic variety in their chilling and forcing needs, many plants likely use the same biochemical system to sense temperatures." During the winter of 2007–2008, the team set up several sets of experiments using outside areas and greenhouses in Olympia, Washington, and Corvallis, Oregon—locations different enough to provide a wide scope of environmental conditions.

KEY FINDINGS

- Douglas-fir seedlings require both cold and warm temperatures during the winter, accumulating chilling and forcing (warming) signals, which ultimately induces bud burst.
- Many different combinations of warm and cool temperatures can result in bud burst. Plants exposed to fewer hours of optimal chilling temperatures in winter need more hours of warmth to satisfy their genetically determined needs for bud burst. Conversely, after a winter with many hours of chilling, plants require fewer hours of warm temperatures for buds to burst.
- Moderately warmer winters will continue to trigger earlier bud burst. However, much warmer winters could result in later bud burst than has occurred historically.
- The range of possible temperature combinations resulting in bud burst varies for different species and genetic varieties and is based on seed origin. Trees from the southern part of the species' range that are adapted to drier environments will break bud earlier than local varieties when they are planted farther north.

Purpose of PNW Science Findings

To provide scientific information to people who make and influence decisions about managing land.

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Peter Gould

Bud burst!

Earlier studies led by St. Clair had explored the links between genetic variation in Douglas-fir and the climates of seed source locations in western Oregon and Washington. That work indicated that seedlings from populations originating in drier climates and higher elevations burst bud earlier when grown in a common environment. "We wanted to explore the consequences of a range of warmer winter conditions on the timing of bud burst in a subset of the populations from the earlier study," says St. Clair. To do this, the team used seeds from 109 families (each progeny of a single mother), originating from 59 areas in western Oregon, western Washington and northern California. "This gave us a wide sampling of genetic differences across a big part of the species' range," he explains.

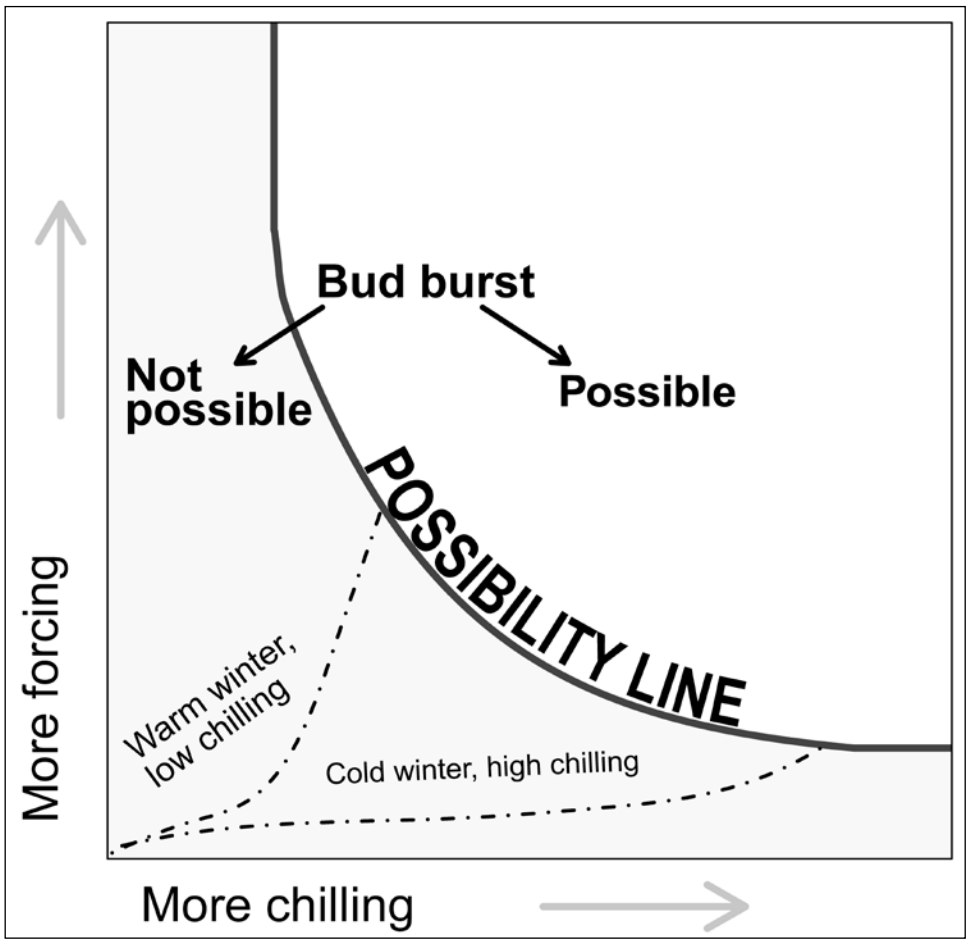
After the seedlings finished their first year of growth, the researchers divided them into groups—each including representatives from all populations—and began to manipulate their winter environments. Based on hourly temperature monitoring, three seedling groups were moved in and out of the greenhouses at each location according to different, predetermined programs for exposure to temperatures between 32 ˚F and 41 ˚F, the range considered optimal for chilling. One group at each location remained outside throughout the winter, thus receiving the maximum amount of chilling. A separate experiment tested the effects of timing of chilling during the dormant season. All populations of seedlings were subjected to eight different winter environments, and a subset of populations was treated to five other environments.

In March, all the seedlings were moved outside, where the team tracked their bud burst dates. "One obvious result was that some seedlings that had spent a lot of time inside the greenhouse and thus received very little chilling took quite a long time to burst bud," St. Clair recounts. "These groups represented an extreme such as might occur with considerable climate warming," he says.

SEEING THE "WHOLE ELEPHANT"

When all the temperature and bud burst data were in, the researchers mathematically tested different combinations of assumptions and hypotheses to find a plausible explanation for the results. "We considered several ideas from earlier, more data-limited studies," Harrington says. "Some researchers had suggested that all the chilling needed to satisfy or release plants from dormancy had to occur in the fall. Some said mid-winter. Others speculated that only warming after March 1 mattered, or that only temperatures above or below specific cutoff levels were effective."

While all these suggestions seemed to fit some plants growing under some temperature conditions, none seemed to be true under all circumstances. As Harrington describes it, "It was like various studies were touching on different parts of the proverbial elephant, but none seemed to explain the broader picture of plant responses to winter and spring temperatures revealed by our data. In the end, we were surprised to find that we could make the best predictions of bud burst timing only if we assumed that beyond a minimum, required level of chilling, many combinations of temperatures can result in spring bud burst. During winters with fewer hours in the optimum range for chilling—as with the experimental seedlings that spent the longest periods in the greenhouse—plants will require more hours of warmth to cross the line. On the other hand, in winters with lots of chilling, it will take fewer hours of effectively warm temperatures to set off bud burst."



Different combinations of warm and cool winter temperatures can result in bud burst. Plants exposed to fewer hours of optimal chilling temperatures need more hours of warmth to burst bud, whereas winters with many hours of chilling require fewer hours of warm spring temperatures for bud burst.

After much number crunching and brainstorming, the researchers developed a model that produced a "possibility line." The graphed output showed a smooth, gradual tradeoff between chilling and forcing temperatures that set the stage for bud burst. "Interestingly, it appears from the data that both signals were being sensed and tracked during the same time period, and that the effective range of temperatures is wider than previously suggested," says Harrington.

To test the model for historical accuracy, the team used an independent data set of winter temperatures and the observed dates of bud burst for the years 2001, 2002, and 2004, from a plantation west of Centralia, Washington. "The model predicted the timing of past bud burst quite accurately, even though bud burst occurred 21 days later in 2002 than in 2004. The maximum difference between predicted and observed date of bud burst was 5 days and average difference between the predictions and the observed bud burst dates was less than 1 day," Harrington says. "So we have more confidence that this model can allow forest managers to calculate when plants will burst bud under different climate scenarios."

Although it might seem improbable that Douglas-firs and other plants are able to sense chilling and forcing signals over the same time period and essentially keep a running total on each, there are other instances in which nature has evolved a flexible system with a range of responses, Harrington notes. One case in point is the proven mechanism that determines the timing of flower production (a separate event from leaf bud burst). In the system for flowering, different photoreceptors in plant tissues sense light of different wavelengths, and once an optimal balance between them is reached, the bloom is on.

In contrast, the biological system underlying the capability of plants to sense and "remember" temperatures in their progression to bud burst is still somewhat of a mystery.

Nonetheless, the researchers' findings have considerable implications for predicting potential plant responses under future climate change.

"With moderately warmer winters, we think the trend of earlier spring bud burst that has been observed for lilacs and other plants worldwide will continue. But if winters grow increasingly warmer, this trend could reverse and eventually result in later bud burst than has occurred historically, or even no bud burst at all," Harrington explains. For trees in soil water-limited conditions, such as commonly occurs during summers in the Pacific Northwest, later bud burst could also mean more limited growth before soil moisture is depleted, she says. Furthermore, climatologists have warned that severe spring frosts could still occur, so trees that break bud sooner than in the past will be more vulnerable to damage by frost or other ill effects, such as stunted growth.

FOCUSING ON POPULATION DIFFERENCES

The original "possibility line" had incorporated only some of the greenhouse results. In the second stage of research, the scientists expanded their model to reflect data from all 59 populations in the experiment to learn how the possibility lines for different populations might differ. "The modeling results showed the possibility lines for individual genotypes shifted upward or downward from the original line. Thus, our general bud burst model was modified to account for population differences," says Gould.

Once again, the team sought to interpret the findings based on natural phenomena. One hypothesis supported by the expanded model involved summer drought—a reality for a significant portion of the species' range represented in the research. "During the greenhouse studies, we found that within groups exposed to the same regime of winter temperatures, some seedlings burst bud earlier," St. Clair says. "The model shows that possibility lines of the earliest populations to burst bud are shifted below the average line—they needed less forcing. Matching the results from earlier common-environment studies, these populations were of genetic varieties from more southerly or higher elevation locations that have relatively dry and/or cold climates."

"In cold climates, plants need to take advantage of the shorter growing season; it doesn't take much warming to promote bud burst. In addition, high-elevation sites may actually receive less chilling than their lower elevation counterparts since temperatures much below freezing are not effective in satisfying chilling. Likewise, at southern, more arid sites, plants burst bud and begin active growth earlier, so that most of their growing is completed by the time soil moisture becomes limited. In other words, natural selection has given rise to earlier bud burst for populations from colder climates and from drier climates. Those parents that burst bud earlier grew more and were more likely to survive and reproduce, thus passing on those genes which conferred early bud burst to their progeny," St. Clair explains.

Brad St. Clair

The seedlings on the left were exposed to typical current winter conditions. The seedlings on the right were exposed to much warmer conditions, resulting in delayed bud burst.

The research findings are highly relevant to the development of strategies for assisted migration or seed transfer, Gould notes. While past studies have suggested that local seed sources were best for establishing new plantations, that research assumed that climate would be more consistent over time. Now, with climate forecasts for the Pacific Northwest pointing to warmer seasons year-

round and unchanged or slightly lower summer precipitation, summer drought will likely arrive sooner and be more severe in many parts of the Douglas-fir range. "Although combinations of traits must be considered, genetic varieties equipped with earlier dates of bud burst could be better adapted to future climates than local populations," Gould suggests. "Our model can be used to test 'virtual' seed transfers and changes to bud burst under different climates."

The possibility-line approach pioneered by Harrington, Gould, and St. Clair represents a new paradigm in modeling the effects of winter temperature on the emergence of plants from winter dormancy. Because the researchers' models of temperature effectiveness were initially based on studies from multiple species, the possibility approach may well apply to many, if not all, plant species with chilling requirements, although with variations by species and geographic origins of populations. The scientists plan to evaluate the model further, based on data from other species.

Another step in this ongoing research is to test ideas about seed-transfer strategies and responses to climate by actually moving populations between markedly different climates. Using the seedlings from the bud burst study, the team has now established trials at nine sites in Washington and Oregon and is evaluating bud burst and other adaptive traits for their responses to weather as measured at each of the sites. Results from these studies will be used to assess management options for maintaining adapted Douglas-fir populations in the face of changing climates.

"It's all about timing."
—Carl Lewis

Connie Harrington

A technician records weather data at a site where local and nonlocal sources of Douglas-fir have been planted.

LAND MANAGEMENT IMPLICATIONS

- Trees that burst bud earlier than the species' historical norm may be at risk for damage by late spring frosts.
- Substantially warmer winters could reduce tree height growth, as trees could encounter soil-moisture limitations sooner after the onset of bud burst.
- The temperature effectiveness models developed for chilling and forcing can be used to predict future bud burst under various models of future climate; the possibility line for bud burst can be adjusted to compare the responses of local and nonlocal genotypes.
- Planting nonlocal genetic varieties may be a viable management response to climate change, but field trials are needed to test plant responses to different environments.

FOR FURTHER READING

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