

Science

FINDINGS

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“Science affects the way we think together.”

Lewis Thomas

Done for the Season: How Do Douglas-fir Know When to Stop Growing?



Connie Harrington

Researcher Kevin Ford collects weather data from a study site in a Douglas-fir plantation in Washington. New research is revealing how changes in daily mean temperature may influence when Douglas-fir stops growing for the season.

“No great discovery was ever made without a bold guess.”

—Sir Isaac Newton

2015 was a notorious warm and dry year in the Pacific Northwest. In Medford, Oregon, June 2015 was the hottest of the 99 years on record at the municipal airport. While summer temperatures in the 90s and low 100s are not uncommon in Medford, a heat wave in late June 2015 brought 100-degree days that coincided with long daylight hours around the summer solstice. By early July, 9 of 12 closely monitored trees growing near Medford stopped growing for the season.

“We were not expecting this because diameter growth usually goes into October,” says Connie Harrington, a research forester with the USDA Forest Service Pacific Northwest (PNW) Research Station. “This was quite a surprise.”

This serendipitous observation was part of a larger study on the environmental cues that trigger growth cessation in Douglas-fir. Compared to budburst—the visible signal that trees are beginning their spring growth—less is known about the mechanisms that trigger phenological events underneath the bark, particularly what causes trees to stop growing. “Budburst is something that captures poets’ hearts,” says Kevin Ford, a former

IN SUMMARY

Diameter growth is seasonal in Douglas-fir, the evergreen tree found in much of western Washington, Oregon, and northern California. Initiation and cessation of diameter growth are both triggered by environmental cues. The tree responds to these cues to improve its chances of growing under favorable conditions. As environmental conditions change, however, land managers want to know how warmer summers and falls may affect diameter growth in Douglas-fir.

Forest Service scientists Connie Harrington, Brad St. Clair, and Kevin Ford conducted a study to examine the environmental cues that drive diameter-growth cessation in Douglas-fir under the current climate. They also modeled seasonal cessation into the future, assuming increasing emissions of greenhouse gasses. In the warmer parts of Oregon and northern California, day length will be the limiting factor, preventing an extended fall growing season. In the cooler parts of Oregon and Washington, growth may extend nearly 4 weeks into fall by 2100 because low temperatures are currently the limiting factor.

Data gathered during record-high temperatures in 2015 revealed that Douglas-fir appears to stop growing when high temperatures coincide with long daylight hours. Research continues on this summer growth-cessation pathway, which currently may be occurring across 2 percent of the coast Douglas-fir range, but by 2100 may affect more than 30 percent of the area.

PNW Research Station ecologist now with the Bureau of Land Management. “Diameter-growth cessation is more difficult to observe. We don’t really understand the basic drivers.”

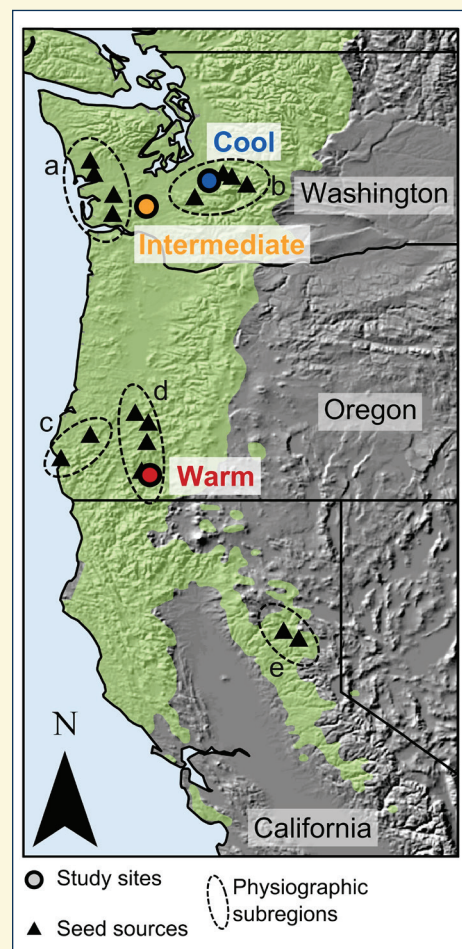
Ford, Harrington, and Brad St. Clair, a research geneticist with the station, designed a study to learn more about this fundamental aspect of tree physiology. They used a subset of trees and sites within the larger Douglas-fir Seed-Source Movement Trial, a large-scale common garden trial covering a range of sites and seed-source environments in Washington, Oregon, and northern California. The larger study has yielded many insights about the adaptive potential of Douglas-fir populations in different environments. Now it is revealing why diameter growth ceases earlier at cooler sites than at warmer sites, and how photoperiod cues, patterns in genetic variation, and summer heat waves may limit the ability of Douglas-fir to acclimate to climate change in the warmer parts of its range.

Key to studying diameter-growth cessation is a measuring device called a dendrometer, which is fitted around a tree’s trunk. A tree trunk—or stem—expands and contracts each day. This pulse is driven by water. When water is plentiful and moving up from roots to leaf tips for use in photosynthesis, the stem swells. It shrinks as transpiration releases water into the air at a faster rate than the tree can draw it from the soil. As the sun goes down, the tree is able to recover and catch up with its water needs. A stem is at its maximum diameter in early morning after a full

KEY FINDINGS	
• Cessation of diameter (cambial) growth in Douglas-fir appears to follow one of two possible pathways: the more typical “fall cessation” pathway or a “summer cessation” pathway.	
• In fall, fewer daylight hours (photoperiod) and cooler daily mean temperature both appear to cue the cessation of diameter growth in Douglas-fir.	
• In California and on low-elevation sites in Oregon and Washington, the date of diameter-growth cessation is expected to change very little even if future fall conditions become warmer because day length will remain the same and be the limiting factor.	
• Under warmer future conditions, diameter growth in coast Douglas-fir could continue up to 4 weeks into the fall at higher elevations and latitudes because, currently, temperature is the limiting factor at those sites.	
• Evidence from summer 2015 indicates that diameter growth may stop months earlier than usual if extreme heat waves occur when photoperiods are longest.	

night of hydration. Cumulatively, daily measurements taken during the growing season show a wavelike pattern of daily fluctuations that trend upward as the tree grows new layers of wood, permanently increasing the diameter of the stem. Then, at some point, growth halts, usually in the fall to give the new wood time to harden before winter. Dendrometers can capture the day diameter growth stops for the season.

This is the precise information that the team of scientists was looking for when they installed dendrometers on 113 trees at three study sites: a cool site near the local upper elevation limit for coast Douglas-fir; an intermediate site, in terms of elevation and temperature, at the core of the species’ range; and a warm site in an inland basin, near Medford, below the species’ local lower elevation limit.



A map showing range of coast Douglas-fir and location of study sites, and seed sources.



Connie Harrington

An electronic dendrometer fitted around a tree stem. The sensor recorded the stem’s diameter every 30 minutes, enabling researchers to determine when annual diameter growth stopped.

Purpose of PNW Science Findings

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

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Two Distinct Pathways

In general, we know that trees stop growing in the fall so that new tissue won't be damaged by frost or cold temperatures. But what are the mechanisms behind this, and how might the timing change as falls become warmer? And as extreme summer temperature patterns like those in 2015 become more common, what will this mean for future tree growth and wood production in the region?

Using the dendrometer data collected between 2010 and 2015, Ford was able to model the daily probability of growth cessation as a function of photoperiod and temperature. He had to first determine if the variables that predict when growth stops were cumulative or instantaneous. Cumulative variables, such as chilling hours for example, contribute to budburst so the researchers explored measures such as accumulated heat to see if these could predict when a tree would stop seasonal growth. "We tried those kinds of measures first for growth cessation, but it didn't really work out. So we tried instantaneous measures,

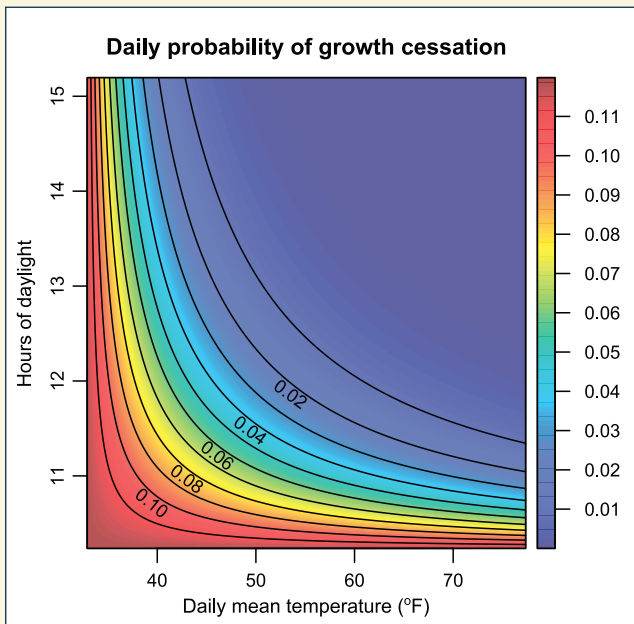
like photoperiod on the day growth stopped, or temperature on the day growth stopped, and that seemed to work pretty well," says Ford. "That was very interesting from a modeling point of view. It might reflect something about how plants respond; or it might be that we haven't figured out the best way to calculate the way cumulative effects are occurring."

Fall cessation is now the norm, but summer cessation may become more prevalent in the future.

The data revealed two distinct pathways that triggered growth cessation: a fall pathway and a summer pathway. Fall growth cessation occurred over 98 percent of the area and is associated with both low temperatures and short photoperiods. The less common pathway—summer cessation—occurred under long photoperiods and high temperatures.

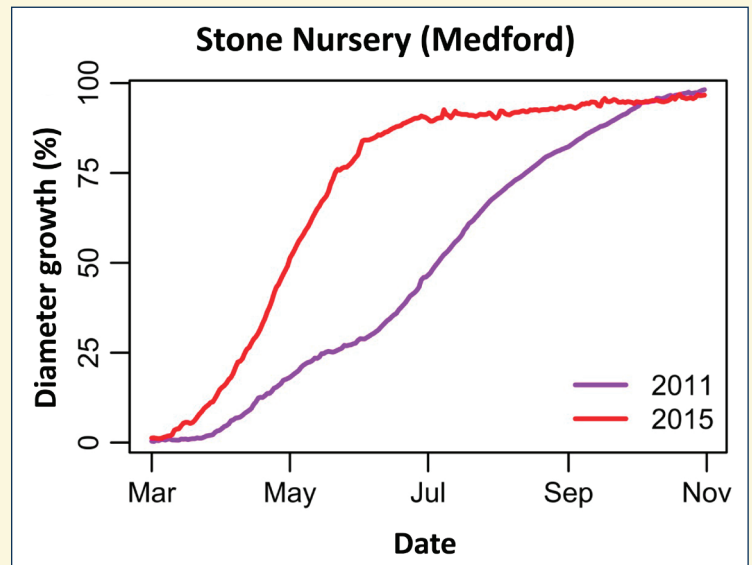
For either pathway to trigger the cessation of tree growth, it appears both temperature and photoperiod conditions must be met. For instance, when some sites reached 104 °F during the long photoperiods of early summer, this triggered the summer cessation pathway and diameter growth stopped. When similar high temperatures occurred later in the summer, the shorter photoperiods seemed to help mediate the high temperature so that trees kept growing.

"Our summer cessation model is based on a small amount of data, so we want to be careful about drawing conclusions," says Ford. "But on the other hand, the reason that dataset is small is that it's such a rare event so it provides important insight, potentially, into how plants will respond to a novel climate that's just not present in the region right now." All the trees, representing three genotypes of Douglas-fir, that stopped growing in July 2015 resumed growth the following spring. This early cessation of growth has been documented once before at a study on balsam fir in Canada.

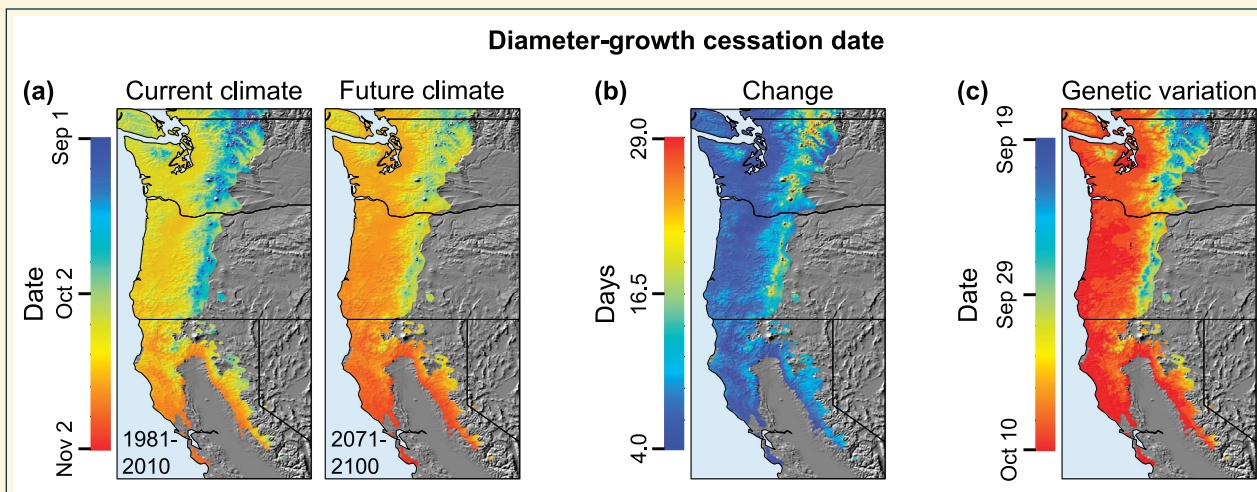


Cool temperatures or short photoperiods can trigger cessation (generally the red zone). Trees from seed sources experiencing frequent frosts ceased growth earlier.

Adapted from Ford et al. 2017



Two seasons of dendrometer data from a study site near Medford, Oregon. In 2011, the trees stopped growing in November, likely cued by low temperatures and fewer hours of daylight. In 2015, 9 of 12 trees at the same study site stopped growing in early July, a possible response to high temperatures that coincided with long photoperiods.



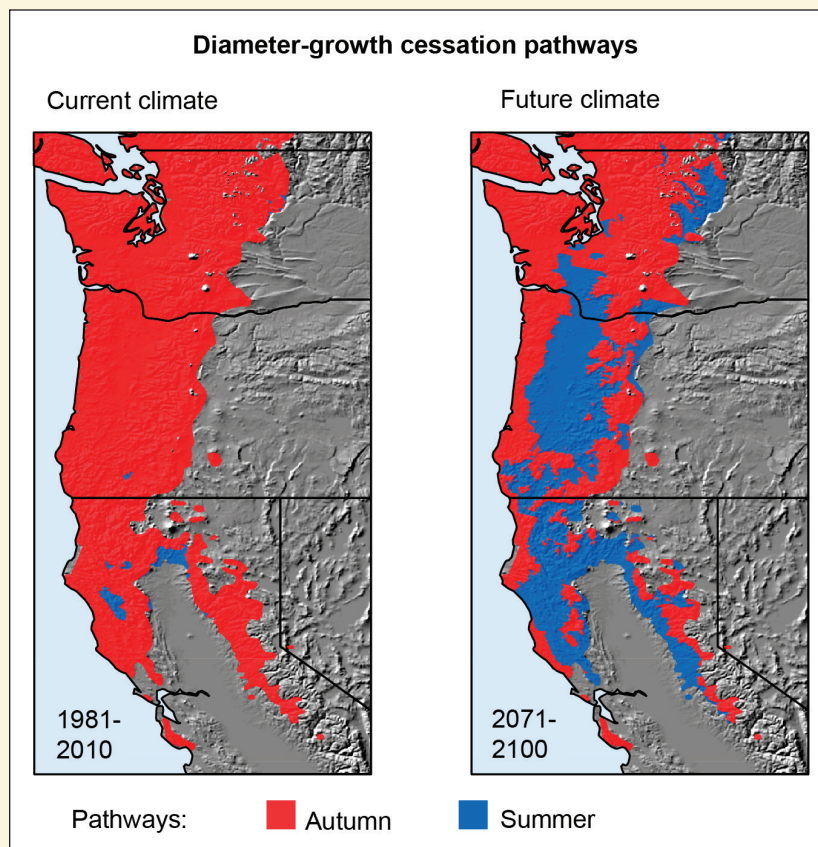
The expected date of diameter-growth cessation (under the fall cessation pathway) depends on the environment where the tree is grown and the climate of the seed source. Cessation is projected to occur later in the year by 2100.

Projecting When Future Growing Seasons Will End

With these two cessation pathways identified, the researchers then modeled how fall cessation may change under future climate scenarios that assume increasing greenhouse gas emissions (RCP8.5). Over much of the study area, little change is projected by the end the century. In the cooler portions of the Douglas-fir range, however, diameter growth may extend 2 to 4 weeks later into the fall by 2100.

“Depending on where you are in the range, either photoperiod or temperature becomes more important,” Harrington explains. “At lower latitudes in northern California or southern Oregon, photoperiod is really important because the temperature is still relatively warm in the fall, but the photoperiod is declining. Further north in the range or at higher elevations, the photoperiod isn’t declining very rapidly, but the temperature is.”

Recognizing that their summer growth-cessation observations were an anomaly of sorts, the researchers modeled those data separately. They determined that under the current climate, summer cessation potentially occurs over about 2 percent of the range of coast Douglas-fir. By 2100, summer growth cessation may occur over 30 percent of the range if extreme heat waves become more frequent and occur in late June and early July during the longest photoperiods. Summer growth cessation is most likely to become prevalent in areas that already experience summer temperatures that may be near the threshold of diameter-growth cessation during long photoperiods. “This could be really limiting for the warm end of the range,” says St. Clair.



Currently, about 3 percent of coast Douglas-fir likely stop growing in the summer when high temperatures coincide with long photoperiods (the blue area on the map). By 2100, more than 30 percent of the range is projected to stop diameter growth in the summer.

Different populations of Douglas-fir have adapted to their local conditions. As local temperature regimes change, gene flow among populations may facilitate adaptation to the changed conditions. This may happen naturally, or by intentionally replanting with seed sources from a warmer site to a cooler site to enable stands to be better suited to future

warmer conditions. The intentional transfer of seed sources to be adapted to future conditions has been called assisted migration. For populations of Douglas-fir currently growing at the warmest sites, which already exhibit the strongest disposition toward late cessation, there are few other populations that could be a source for gene flow to promote even later

Adapted from Ford et al. 2017

cessation. So while shifts in growth phenology will likely promote climate change resilience in the cooler parts of the Douglas-fir range, these shifts might reduce resilience in the warmer parts if natural gene flow is from cooler sites.

St. Clair emphasizes the importance of seed sources when planting Douglas-fir under current environmental conditions, while keeping in mind conditions 50 years from now: “Populations differ with respect to adaptive traits, and that can affect the long-term productivity and adaptation of stands,” he explains.

When Trees Take a Summer Break

The most obvious implication for a tree that stops growing as much as 3 months earlier than normal is slower overall growth. For anyone who grows and sells trees, it will take longer to have merchantable timber for harvest.

Early growth cessation may also reduce drought resistance in the tree and ultimately its long-term survival. Trees produce two kinds of wood: earlywood and latewood, visible as the light and dark patterns of tree rings. Earlywood has larger cells than latewood, which makes a difference in the tree’s hydraulic system. Earlywood transports most of the water within the tree when moisture stress is low in the spring and early summer. Under stress, however, the water column in the larger cells breaks more easily. This leads to air bubbles in the water column, which, while not as deadly as an air bubble in a human’s vein, is still not good for the tree because that part of the water transport system is no longer working. A narrower water column is easier to maintain, so water movement through the smaller latewood cells becomes more important during drier periods.

When a tree stops growing earlier in the season, however, it has had less time to produce latewood and thus may be unable to transport water effectively when stressed for moisture. This may be the mechanism behind branch dieback, or even delayed mortality. Harrington

LAND MANAGEMENT IMPLICATIONS

- Over the cooler portions of the coast Douglas-fir range, the expected date of diameter-growth cessation could shift 4 to 29 days later into the fall by 2100 for trees following the fall cessation pathway.
- Under the current climate, summer cessation potentially occurs over 2 percent of the range of the coast Douglas-fir. Under a high-emissions climate change scenario, diameter growth could cease in summer over 30 percent of the range by the end of the century owing to the likely occurrence of heat waves earlier in the growing season.
- Early cessation of diameter growth will reduce wood production, particularly the production of latewood, which is more drought resistant than earlywood. Reducing drought resistance is likely to reduce tree survival over the long term.

speculates that when a tree dies after surviving several consecutive years of drought, it simply may have not had enough latewood cells to deliver water to the tree crown even if drought conditions no longer exist.

Harrington is continuing to investigate the physiological mechanisms associated with summer growth cessation. “We know that there’s a cessation of mitosis—cell division—when temperatures get up to or above 40 °C [104 °F]. We know that the cambium, the part

A tree that stops growing early in the season may be more susceptible to future moisture stress.

of the tree where cell division is happening, is controlled by factors in the leaves; so the cambium itself is not responding to the environment, it’s the leaves that are responding and producing different hormones that are then transported to the cambium,” says Harrington. “My hypothesis is that these heat-shock proteins are produced in the leaf when it’s very hot and are transported to the cambium and tell the tree not to grow.”

Intrigued by the study’s findings, industrial timber producer Weyerhaeuser Company has contributed study sites and expertise to further research. Edgar Fuchs, a regeneration scientist with Weyerhaeuser, is working closely with Harrington during this second phase.

“We are interested in future scenarios that can impinge on yield,” says Fuchs. “This seemed like a great opportunity to combine with Connie to address common interests that are going to be affecting us, and may even be affecting us currently.”

“The work the U.S. Forest Service is doing is important to understand potential growth loss opportunities for us as a commercial entity and to determine a mitigation strategy deployable across our landscapes,” Fuchs explains. “This work informs our strategies and what our response might be going forward. It has implications for our tree improvement group, enabling them to understand where some of the genetic sources we hold might be deployed if we see landscape-level shifts in climate.”

“What we call the beginning is often the end. And to make an end is to make a beginning. The end is where we start from.”

–T.S. Eliot

Further Reading

Ford, K.R.; Harrington, C.A.; St. Clair, J.B. 2017. Photoperiod cues and patterns of genetic variation limit phenological responses to climate change in warm parts of the species’ range: modeling diameter-growth cessation in coast Douglas-fir. *Global Change Biology*. 23(8): 3348–3362. <https://www.fs.usda.gov/treesearch/pubs/54549>

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