The problem and promise of
modeling plant leafout under warmer winters

E.M. Wolkovich[1], Justin Ngo[1], Victor van der Meersch[1], Jonathan Auerbach[2]

January 4, 2026

[1] Forest & Conservation Sciences, Faculty of Forestry, University of British Columbia, 2424 Main Mall, Vancouver, BC V6T 1Z4, Canada
[2] Department of Statistics, George Mason University, 4511 Patriot Circle, Fairfax, VA 22030, United States

Abstract

How warmer winters affect plant leafout has major implications for carbon storage and ecosystem stability. Recent evidence that the advance of spring leafout has slowed as anthropogenic climate change has increased has reignited a decades-old debate over winter 'chillling'—the concept that woody temperate plants require sufficient winter cool temperatures to budburst each spring. The problem with chilling is that it is largely used as a placeholder theory: it does not correspond with an observable event, is not falsifiable, and thus is of limited use for advancing scientific understanding. In this paper, we review how current research built on the concept of chilling combined with limited data has led to the proliferation of untestable models that are consistent with a wide range of forecasts and provide little insight into actual plant biology. We argue that the concept of chilling should be reevaluated like past theoretical constructs of limited scientific value, such as 'dormin' or 'ether,' to help accelerate our understanding of plant development. This can be done by leveraging new insights from molecular biology to build better models that fit to both experimental and observational data, and designing better experiments to more rigorously test new theory.

Plant leafout in the spring has shifted weeks earlier in many regions due to warming from anthropogenic climate change with consequences for a wide range of ecosystem services (Keenan *et al.*, 2014; Pörtner *et al.*, 2022). Which underlying processes drive this trend, however, is debated, as recent research suggests winter warming may slow or stall further advances (Fu *et al.*, 2015; Piao *et al.*, 2017). Such reports focus on a two-step model of leafout where plants first require cool winter temperatures, often called 'chilling,' before they can accumulate enough warm temperatures—'forcing'—to leafout each year. This model of chilling is only one of many models proposed since the concept was first introduced (Basler, 2016; Hufkens *et al.*, 2018). But, while forcing ends in an observable event such as leafout, the day plants achieve their chilling requirements coincides with no known measurable event.

Current models of chilling are consistent with a diverse suite of possible future leafout. Chilling

in the same location for the same plant under different models can easily forecast significantly increased or greatly reduced chilling and thus greatly advanced or slowed leafout (Guy, 2014; Chuine *et al.*, 2016). This variability often occurs within any one model of chilling, given different parameter values (Figure 1). Such extreme variability of spring phenology predicted from current models highlights fundamental gaps in our understanding. While decades of experimental evidence suggest that winter temperatures impact leafout (Charrier *et al.*, 2015; Baumgarten *et al.*, 2021) new research has highlighted major flaws in these models as currently applied, including multiple papers now suggesting estimates of 'chilling' could easily be artifacts of poor models or correlated observational climate data (Wolkovich *et al.*, 2021; Gao *et al.*, 2024).

Now appears an opportune time to address the problems in our concept of chilling in models of leafout. Because accurate forecasts of spring phenology are critical for carbon sequestration, many crops and a number of other services important to humans, there is widespread interest in improving chilling models (Luedeling *et al.*, 2015; Chuine *et al.*, 2016). At the same time, new results from molecular and cellular studies of dormancy are providing new insights into when and how chilling works (Pan *et al.*, 2023; Zhu *et al.*, 2021), which could rule in—or out—some of the myriad current models. Here, we review the theory of chilling, its origins and potential problems, as well as new opportunities for major advances and how shifting current practices could accelerate progress. We argue that revisiting the current concept of chilling—and its utility—could help build better models and design better experiments.

What is chilling?

How plants in temperature-limited systems avoid leafout during warm spells in the winter has long been debated by plant biologists (e.g., Lamb, 1948; Weinberger, 1950). Most work to date has focused on the idea that plants enter some form of dormancy in the fall, which is then released before warm temperatures in the spring begin. This idea hypothesizes that the slow accumulation of cool temperatures—or chilling—over the winter extends through periods of short warm spells in the winter and thus prevents leafout before spring. The term 'chilling' is now used across numerous fields in plant biology to refer to a process where dormant buds exposed to cool temperatures accelerate a phenological event that later occurs after warm temperatures.

Much of our fundamental understanding of chilling comes from studies on temperate woody fruit crops where chilling can be critical to yield. Peach trees planted into warmer climates well outside their range often have extremely low fruitset because most flower buds do not burst (Weinberger, 1950; Overcash & Campbell, 1955; Erez *et al.*, 1971). Initial studies of this phenomenon with related experiments—where cut ends of dormant branches (cuttings) exposed to cooler temperatures in chambers burst more fully and more quickly—underlies most of the models of chilling used today for crops and wild tree species (Weinberger, 1950; Ettinger *et al.*, 2020).

Focused on how chilling can accelerate events, researchers have calculated 'chilling' required for leafout of forest trees from cutting experiments similar to those used for peaches (reviewed in Ettinger *et al.*, 2020), ground observations of budburst (Luedeling *et al.*, 2009b), and satellite measures of greenup (Kaduk & Los, 2011). These estimates rely on phenological models that have become critical across a suite of fields, from climatology, where modeling how vegetation on the

land surface responds to anthropogenic climate change affects carbon storage, to crop biology, where estimated chill units guide growers in which specific cultivar to plant, and has led to the cross-disciplinary field of phenology (Schwartz, 1994; Cleland *et al.*, 2007; Chuine *et al.*, 2013).

Alongside these more macro-scale studies of chilling, molecular approaches have also examined chilling. Many studies have focused on vernalization—cool temperatures required for flowering (Kim *et al.*, 2009)—in *Arabidopsis thaliana*, with studies in woody species, especially *Populus* examining chilling before budbreak (Azeez *et al.*, 2021; Cai *et al.*, 2024). These studies generally use controlled temperatures to vary the hypothesized amount of chilling then examine molecular and cellular responses (e.g., Pan *et al.*, 2021; Azeez *et al.*, 2021; Cai *et al.*, 2024).

Today these studies have led to over 30 basic models where accumulated chilling releases plants from dormancy (Basler, 2016; Hufkens *et al.*, 2018). Though early debates considered whether plants were truly dormant or only growing slow ('dormancy' or 'rest' versus 'quiescence'; Considine & Considine, 2016), today most research assumes a model with two phases of dormancy: endodormany—where chilling occurs—and a period after but before the observed event, called ecodormancy (Figure 2). In most models, chilling can only be accumulated under certain temperatures—traditionally above zero but below 10°C—with certain temperatures being optimal for the most rapid accumulation of 'chill units,' where some unknown sum of chill units breaks endo-dormancy. Which temperatures are most effective at providing chilling is a common question addressed in experiments, with different experiments providing different answers (Vitasse *et al.*, 2013; Baumgarten *et al.*, 2021).

Variation in responses to 'chilling' across and within species yields hundreds of variants of the basic models (Basler, 2016; Hufkens *et al.*, 2018). Complexity comes from the hypothesized diversity of chilling temperature thresholds and sums across species and populations. Most assume different species require different sums of chill units, and may have different lower, upper and optimal chill temperatures. Within species, populations may require different sums of chill units, with populations in more mild climates—where warm interruptions in the winter are more common—requiring more chill units than those in areas with cold winters, where temperatures rarely rise above zero before spring (Campbell & Sugano, 1979; Leinonen, 1996).

The problem with chilling

An unobserved process

Chilling is a latent, unobserved process. Typically, 'chilling' describes the physiological phase (endo-dormancy) in which a plant experiences environmental temperatures that induce progress towards the next physiological phase (eco-dormancy) that ends in budburst (Figure 2). The problem is that the transition from endo- to eco-dormancy corresponds with no clearly measurable phenomenon, and thus the properties of each period cannot be determined from the observed budburst, even under experimental conditions in which the temperature can be manipulated. The parameters of a model governing this system are said to be underdetermined or unidentified.

For example, consider a simple model in which one would need to estimate the minimum and maximum temperatures that allow chilling to accumulate (two parameters) and the total sum of those temperature units needed to trigger a shift into the next physiological phase (often called,

'endo-dormancy break,' for one additional parameter). Models then need to estimate when plants start and stop accumulating (two more parameters). An experiment that raises temperatures and observes an earlier leafout could be explained by more rapid chilling accumulation leading to earlier endo-dormancy break, more rapid ecodormancy break, or an almost limitless mix of the two (Figure 1).

To address this, models often assign the start date of the endo-dormancy as known (e.g., starting 1 September in the northern hemisphere) and rely on assumptions to set the end date (Figure 1). A common and widely-used assumption, developed by early work on peaches, is that high and rapid budburst (leaf or flower) is evidence that chilling has been met (i.e. endo-dormancy has ended Erez & Lavee, 1971), but is rarely evaluated for other taxa or populations. This approach of assigning some unknown parameters as known has the benefit of avoiding adding more unknown model parameters, but has led researchers to be overly confident in a model of chilling where more is actually unobserved and unknown than acknowledged.

Hidden assumptions in complicated models

Hidden assumptions and numerous parameters can easily drive diverging models. Even if we assume that high and rapid percent budburst signals sufficient chilling, most models today include parameters that cannot be uniquely identified with current data, and explains why one model can often predict a huge variety of leafout possibilities (Figure 1). Researchers' tacit approach to these major issues likely has contributed to the expansion of models over the last few decades without any clear advances. While various models have added complexity via the shape of the optimal temperature range for chilling, allowing accumulated chilling to be reduced, shifting the start date of chilling, and/or allowing chilling and forcing to act at once (Luedeling *et al.*, 2009a; Gusewell *et al.*, 2017; Hänninen, 1990; Kramer, 1994), none of these have swept through the field.

As experiments and models have suggested a more complicated model of chilling, data have remained relatively uninformative to try to estimate all the complexities the models include. Further, recent models have often relied on even less data (Hänninen *et al.*, 2019). Many current methods use only observational data of the timing of leafout (or flowering) to attempt to estimate a model of chilling for different species or locations and project it forward to understand effects of anthropogenic climate change (Luedeling *et al.*, 2011, 2012; Gao *et al.*, 2024). Perhaps not surprisingly then, which model is deemed best varies strongly by method and approach (Caffarra *et al.*, 2011; Basler, 2016; Hufkens *et al.*, 2018), with no clear pattern.

Unclear aims

The flood of current models of budburst with similar levels of predictive accuracy is not necessarily a problem, depending on the aim. Many models of chilling are used for helping guide crop and tree planting—preventing planting too far outside the range of climates with sufficient chilling for a species, population, or cultivar. For this aim, models need to translate climate into relevant chilling and forcing values and define appropriate thresholds, but how exactly each model defines chilling and forcing is immaterial if the predictions are accurate enough. In such cases moving more towards machine learning models—which emphasize predictive accuracy often through black

box approaches—may provide improved models and more clearly acknowledge that the underlying process is obscure (Khodadadzadeh *et al.*, 2024). In contrast, if the aim is biological understanding, then the current number of highly contrasting but similarly predictive models suggests a problem.

If the aim is to understand the biological process that underlies the concept of chilling, then the specification of the model—what parameters it includes, and how well they can be estimated from the data—is important. In these cases, the model should represent the current biological understanding, and we would likely expect fewer models than the current proliferation. This aim also suggests comparing models through direct tests of how accurate they represent our understanding of plant biology, and not just their predictive accuracies across a range of climate regimes. Such models may also be predictively accurate, especially in cases beyond current climate regimes, but the primary goal is that they represent and help test plant biology. For this aim, new models are unlikely to be enough without new data and approaches that target the major problems facing models of chilling.

Overcoming the chilling problem

Richer, more informative data from molecular biology studies and other approaches (Fouché *et al.*, 2023; Walde *et al.*, 2024) hold the promise to shift chilling from an unobserved complex process to something we understand and can robustly forecast. Taking full advantage of this opportunity, however, would benefit from re-examining the concept our chilling across different disciplines to combine observational and experimental evidence, while providing the opportunity to question the future utility of 'chilling.'

Leverage new molecular insights

New molecular research provides hope that the transition from endo- to eco-dormancy is measurable. Molecular insights have long contributed to crop and forest tree models of chilling (Chuine & Regniere, 2017). Decades of work on vernalization have outlined the pathways—and genes—that lead to flowering only after winter's cool temperatures in biennial (herbaceous) populations of *Arabidopsis thaliana* (Figure 2, Wilczek *et al.*, 2009; Kim *et al.*, 2009). Research has linked some of these pathways to similar ones in woody species, and have also highlighted the sugar callose (1,3-β-D-glucan) as potentially pivotal for chilling (van der Schoot *et al.*, 2014; Pan *et al.*, 2021). Multiple studies across multiple species have now shown that (1) lower temperatures appear to degrade callose and (2) the release/loss of callose appears to re-start cell-to-cell communication before budburst (van der Schoot *et al.*, 2014). Taken together, these results suggest the loss of callose—generally degraded through 1,3-β-glucanases (a group of enzymes)—may be an indicator of endo-dormancy release, though other factors, such as phytohormones, also often change at the same time (Tylewicz *et al.*, 2018; Pan *et al.*, 2021), and may provide a similar observable signal of endo-dormancy release (Rinne *et al.*, 2018; André *et al.*, 2022).

If callose is a major controller of endo-dormancy and its release, chilling models could be limited to those that match the idea of callose degradation—meaning models that include a temperature range over which the enzyme is active (Figure 2). In contrast, models using simple temperature

thresholds (e.g., all hours below -5°C equally allow chilling) would appear less biologically accurate, as enzymes generally do not work over such a wide range of temperatures.

Other new molecular insights similarly suggest that such simplified temperature metrics used in many chilling models may not map to molecular realities. For example, new work on how slow growth itself may act a 'long-term thermosensor' (Zhao *et al.*, 2020) adds to an increasing number of molecular studies that suggest plants integrate long-term thermo-sensing in the winter alongside responses to short-term temperatures (Antoniou-Kourounioti *et al.*, 2021; Satake *et al.*, 2022). The best models of leafout may thus need to integrate across multiple timescales. While this could easily complicate models already burdened with complexity, new insights from molecular biology could rule out models by focusing on new experiments and modeling approaches.

Model experimental and observational data together

Research on chilling could accelerate by working across what today are three fairly separated silos: model building for crops and other forecasting needs (usually called process-based models), experiments at the branch or whole-plant level, and molecular research. Currently, crop biologists, phenological process-based modelers of forest trees, molecular biologists and hardiness modelers all develop unique and rarely compared models of dormancy and budburst (but see Kovaleski, 2022), highlighting a major problem, but also a major opportunity. Synthesizing and benchmarking models—and their underlying biological understanding of chilling—across the many research fields developing chilling models today would help identify models that are equivalent and/or perform especially poorly and could begin to discard some models.

Comparing models more directly would hopefully drive new approaches that estimate chilling by fitting experimental and observational data together in one model. This is rarely (if ever) done, in part because of how differently they may be observed, including the challenging diversity of environmental conditions across these two data types (for example, many experiments apply cold temperatures in the dark and include extreme temperature differences, while in observational data photoperiod shifts each day and temperatures are more similar) but also because of separate modeling approaches. Researchers rarely if ever fit process-based models to new empirical data; instead they use so-called 'statistical models' that often follow canonical treatment designs (e.g., ANOVA). Statistical models are usually far simpler, and make a suite of unstated assumptions that contradict the current understanding of chilling (see Figure 3). Many of the original studies that led to the concept of chilling, however, bridged across observational and experimental studies more often and leveraged datasets that created greater extremes in observational data—by focusing on crops planted well outside their natural range (e.g., peaches in Florida and Israel, Erez & Lavee, 1971; Richardson, 1974). These approaches did this in part by more explicitly mapping from biological processes to statistical models, making it easier to use the models to define new tests to challenge the biological theory.

Experiments bridging across methods may have the greatest opportunity to provide data that would truly challenge current models of chilling. Testing models across large environmental gradients in the field is one of the best ways to find out where models work—and where they fail. For example, molecular biologists tested vernalization models by through comparing predicted to observed

flowering times in a common garden study across Europe (Wilczek *et al.*, 2009), and supported the temperature-dependent growth model by testing its predictions of what happens when growth is altered but temperature is held constant (Zhao *et al.*, 2020). Similar examples for challenging other models of chilling date back over 40 years to when many of the models used today were developed (Richardson, 1974; Chuine *et al.*, 2016; Ettinger *et al.*, 2020), but could take place now. Models of chilling can make predictions under lower field chilling then test them using individuals planted beyond the range (either planting those individuals now or identifying such cases in forestry provenance trials or similar). Process-based modelers could also challenge their models more through more dramatic variation in biology, via experiments that include genetic mutants or similar variants.

Is the concept of 'chilling' necessary for scientific progress?

Results from new molecular experiments designed to identify novel ways to directly observe and measure chilling could upend the current concept of 'chilling.' As increasing evidence suggests the concept aligns with multiple shifts at the cellular and molecular level (Figure 2), researchers across disciplines will need to consider how to continue using the term 'chilling.' One approach is to try to align previous and current definitions through new studies, for example, by testing for callose loss (Yu *et al.*, 2024) alongside previous-used markers of dormancy shifts—including the often-used bioassay of high and rapid budburst at higher temperatures (indicating endo-dormancy release), and additional methods, such as weighing flower buds (Chuine *et al.*, 2016) or tracing water reactivation into cells (Faust *et al.*, 1991; Kalcsits *et al.*, 2009; Walde *et al.*, 2024). Another approach is to work towards new terms that more clearly align with new measurements and insights.

Because chilling is an unobserved process, it may link eventually to one measurable compound or regulator (similar to florigen or auxin) or to a more complicated biology, making the term less useful (Aksenova *et al.*, 2006). Current results suggests the latter, and already the term 'chilling' is used to mean different things. For example, while we focus here on the term as an accumulation process during an unobserved physiological phase (endo-dormancy), many experiments currently use the term 'chilling' to refer to a treatment where researchers do not know the physiological phase (for example, cuttings or buds from woody plants are often chilled at 5°C for 6 weeks in the dark in a 'chilling' treatment, then transferred to warming 'forcing' conditions, Flynn & Wolkovich, 2018; Ettinger *et al.*, 2020).

Diverging definitions suggest that the best path for 'chilling' may be to follow that of other terms modern plant biologists may not remember, such as dormin or anthesin (hypothesized compounds to induce dormancy and floral anthesis, respectively, Aksenova *et al.*, 2006; Dörffling, 2015), and let the term fade into obsolescence. Models for forecasting and new experiments at the branch and whole plant level would then focus on modeling and measuring genes, regulators, hormones and other compounds that emerged from a history of research on 'chilling,' but use other terms and concepts. Chill unit estimates for widely planted forest trees and specific varieties of crops would likely hold on longer. They too, however, may shift to new estimates or units based on better measures, especially as increasing anthropogenic climate change makes getting the mechanistic biology of plant development right for human adaptation more important.

1 References

Aksenova, N., Milyaeva, E. & Romanov, G. (2006) Florigen goes molecular: seventy years of the hormonal theory of flowering regulation. *Russian Journal of Plant Physiology* **53**, 401–406.

André, D., Zambrano, J.A., Zhang, B., Lee, K.C., Rühl, M., Marcon, A. & Nilsson, O. (2022) Populus svl acts in leaves to modulate the timing of growth cessation and bud set. *Frontiers in Plant Science* **13**, 823019.

Antoniou-Kourounioti, R.L., Zhao, Y., Dean, C. & Howard, M. (2021) Feeling every bit of winter–distributed temperature sensitivity in vernalization. *Frontiers in Plant Science* **12**, 628726.

Azeez, A., Zhao, Y.C., Singh, R.K., Yordanov, Y.S., Dash, M., Miskolczi, P., Stojkovič, K., Strauss, S.H., Bhalerao, R.P. & Busov, V.B. (2021) Early bud-break 1 and early bud-break 3 control resumption of poplar growth after winter dormancy. *Nature communications* **12**, 1123.

Basler, D. (2016) Evaluating phenological models for the prediction of leaf-out dates in six temperate tree species across central europe. *Agricultural and Forest Meteorology* **217**, 10–21.

Baumgarten, F., Zohner, C.M., Gessler, A. & Vitasse, Y. (2021) Chilled to be forced: the best dose to wake up buds from winter dormancy. *New Phytologist* **230**, 1366–1377.

Caffarra, A., Donnelly, A. & Chuine, I. (2011) Modelling the timing of *Betula pubescens* budburst. II. Integrating complex effects of photoperiod into process-based models. *Climate Research* **46**, 159–170.

Cai, F., Jin, X., Tian, Y., Huang, Z., Wang, X., Zhang, Y., Sun, Y. & Shao, C. (2024) Molecular regulation of bud dormancy in perennial plants. *Plant Growth Regulation* **102**, 1–11.

Campbell, R.K. & Sugano, A.I. (1979) Genecology of bud-burst phenology in Douglas-fir - response to flushing temperature and chilling. *Botanical Gazette* **140**, 223–231.

Charrier, G., Ngao, J., Saudreau, M. & Ameglio, T. (2015) Effects of environmental factors and management practices on microclimate, winter physiology, and frost resistance in trees. *Frontiers in Plant Science* **6**.

Chuine, I., Bonhomme, M., Legave, J.M., de Cortazar-Atauri, I.G., Charrier, G., Lacointe, A. & Ameglio, T. (2016) Can phenological models predict tree phenology accurately in the future? the unrevealed hurdle of endodormancy break. *Global Change Biology* **22**, 3444–3460.

Chuine, I., Garcia de Cortazar Atauri, I., Hanninen, H. & Kramer, K. (2013) *Plant development models*, pp. 275–293. Kluwer, Dordrecht, the Netherlands.

Chuine, I. & Regniere, J. (2017) Process-based models of phenology for plants and animals. *Annual Review of Ecology, Evolution, and Systematics* **48**, 159–182.

Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A. & Schwartz, M.D. (2007) Shifting plant phenology in response to global change. *Trends in Ecology & Evolution* **22**, 357–365.

Considine, M.J. & Considine, J.A. (2016) On the language and physiology of dormancy and quiescence in plants. *Journal of Experimental Botany* **67**, 3189–3203.

Dörffling, K. (2015) The discovery of abscisic acid: a retrospect. *Journal of Plant Growth Regulation* **34**, 795–808.

Erez, A. & Lavee, S. (1971) Effect of climatic conditions on dormancy development of peach buds. i. temperature. *Journal of the American Society for Horticultural Science* .

Erez, A., Lavee, S. & Samish, R.M. (1971) Improved methods for breaking rest in the peach and other deciduous fruit species. .

Ettinger, A.K., Chamberlain, C.J., Morales-Castilla, I., Buonaiuto, D.M., Flynn, D.F.B., Savas, T., Samaha, J.A. & Wolkovich, E.M. (2020) Winter temperatures predominate in spring phenological responses to warming. *Nature Climate Change* **10**, 1137–U119.

Faust, M., Liu, D., Millard, M.M. & Stutte, G. (1991) Bound versus free water in dormant apple buds—a theory for endodormancy. *HortScience* **26**, 887–890.

Flynn, D.F.B. & Wolkovich, E.M. (2018) Temperature and photoperiod drive spring phenology across all species in a temperate forest community. *New Phytologist* **29**, 1135–1492.

Fouché, M., Bonnet, H., Bonnet, D.M. & Wenden, B. (2023) Transport capacity is uncoupled with endodormancy breaking in sweet cherry buds: physiological and molecular insights. *Frontiers in Plant Science* **14**, 1240642.

Fu, Y.S.H., Zhao, H.F., Piao, S.L., Peaucelle, M., Peng, S.S., Zhou, G.Y., Ciais, P., Huang, M.T., Menzel, A., Uelas, J.P., Song, Y., Vitasse, Y., Zeng, Z.Z. & Janssens, I.A. (2015) Declining global warming effects on the phenology of spring leaf unfolding. *Nature* **526**, 104–107.

Gao, X., Richardson, A.D., Friedl, M.A., Moon, M. & Gray, J.M. (2024) Thermal forcing versus chilling? misspecification of temperature controls in spring phenology models. *Global Ecology and Biogeography* **33**, e13932, e13932 GEB-2024-0136.R2.

Gusewell, S., Furrer, R., Gehrig, R. & Pietragalla, B. (2017) Changes in temperature sensitivity of spring phenology with recent climate warming in switzerland are related to shifts of the preseason. *Global Change Biology* **23**, 5189–5202.

Guy, R.D. (2014) The early bud gets to warm. *New Phytologist* **202**, 7–9.

Hänninen, H. (1990) *Modelling bud dormancy release in trees from cool and temperate regions.* 213.

Hänninen, H., Kramer, K., Tanino, K., Zhang, R., Wu, J. & Fu, Y.H. (2019) Experiments are necessary in process-based tree phenology modelling. *Trends in Plant Science* **24**, 199–209.

Hufkens, K., Basler, D., Milliman, T., Melaas, E.K. & Richardson, A.D. (2018) An integrated phenology modelling framework in r. *Methods in Ecology and Evolution* **9**, 1276–1285.

Kaduk, J.D. & Los, S.O. (2011) Predicting the time of green up in temperate and boreal biomes. *Climatic Change* **107**, 277–304.

Kalcsits, L., Kendall, E., Silim, S. & Tanino, K. (2009) Magnetic resonance microimaging indicates water diffusion correlates with dormancy induction in cultured hybrid poplar (populus spp.) buds. *Tree Physiology* **29**, 1269–1277.

Keenan, T.F., Gray, J., Friedl, M.A., Toomey, M., Bohrer, G., Hollinger, D.Y., Munger, J.W., O'Keefe, J., Schmid, H.P., Wing, I.S. *et al.* (2014) Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nature Climate Change* **4**, 598–604.

Khodadadzadeh, M., Kalverla, P. & Zurita-Milla, R. (2024) Harmonizing machine learning based phenological modeling: A unified workflow for comparative analyses. *IGARSS 2024 - 2024 IEEE International Geoscience and Remote Sensing Symposium*, pp. 5333–5336.

Kim, D.H., Doyle, M.R., Sung, S. & Amasino, R.M. (2009) Vernalization: winter and the timing of flowering in plants. *Annual Review of Cell and Developmental* **25**, 277–299.

Kovaleski, A. (2022) Woody species do not differ in dormancy progression: differences in time to budbreak due to forcing and cold hardiness. *Proceedings of the National Academy of Sciences* **119**, e2112250119.

Kramer, K. (1994) Selelecting a model to predict the onset of growth of *Fagus sylvatica*. *Journal of Applied Ecology* **31**, 172–181.

Lamb, R.C. (1948) Effect of temperatures above and below freezing on the breaking of rest in the Latham raspberry. *Proceedings of the American Society for Horticultural Science*, vol. 51, pp. 313–315, AMER SOC HORTICULTURAL SCIENCE 113 S WEST ST, STE 200, ALEXANDRIA, VA 22314 . . . .

Leinonen, I. (1996) Dependence of dormancy release on temperature in different origins of pinus sylvestris and betula pendula seedlings. *Scandinavian Journal of Forest Research* **11**, 122–128.

Luedeling, E., Blanke, M. & Gebauer, J. (2012) Chilling challenges in a warming world. *II International Symposium on Horticulture in Europe 1099*, pp. 901–907.

Luedeling, E., Blanke, M. & Gebauer, J. (2015) *Chilling Challenges in a Warming World*, vol. 1099 of *Acta Horticulturae*, pp. 901–907.

Luedeling, E., Girvetz, E.H., Semenov, M.A. & Brown, P.H. (2011) Climate change affects winter chill for temperate fruit and nut trees. *Plos One* **6**.

Luedeling, E., Zhang, M.H. & Girvetz, E.H. (2009a) Climatic changes lead to declining winter chill for fruit and nut trees in California during 1950-2099. *Plos One* **4**.

Luedeling, E., Zhang, M.H., McGranahan, G. & Leslie, C. (2009b) Validation of winter chill models using historic records of walnut phenology. *Agricultural and Forest Meteorology* **149**, 1854–1864.

Overcash, J. & Campbell, J. (1955) The effects of intermittent warm and cold periods on breaking the rest period of peach leaf buds. .

Pan, W., Li, J., Du, Y., Zhao, Y., Xin, Y., Wang, S., Liu, C., Lin, Z., Fang, S., Yang, Y. *et al.* (2023) Epigenetic silencing of callose synthase by vil1 promotes bud-growth transition in lily bulbs. *Nature Plants* **9**, 1451–1467.

Pan, W., Liang, J., Sui, J., Li, J., Liu, C., Xin, Y., Zhang, Y., Wang, S., Zhao, Y., Zhang, J. *et al.* (2021) Aba and bud dormancy in perennials: current knowledge and future perspective. *Genes* **12**, 1635.

Piao, S.L., Liu, Z., Wang, T., Peng, S.S., Ciais, P., Huang, M.T., Ahlstrom, A., Burkhart, J.F., Chevallier, F., Janssens, I.A., Jeong, S.J., Lin, X., Mao, J.F., Miller, J., Mohammat, A., Myneni, R.B., Penuelas, J., Shi, X.Y., Stohl, A., Yao, Y.T., Zhu, Z.C. & Tans, P.P. (2017) Weakening temperature control on the interannual variations of spring carbon uptake across northern lands. *Nature Climate Change* **7**, 359–+.

Pörtner, H.O., Roberts, D.C., Tignor, M., Poloczanska, E.S., Mintenbeck, K., Alegría, A., Craig, M., Langsdorf, S., Löschke, S., Möller, V., Okem, A. & Rama, B. (2022) *Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press.

Richardson, E. (1974) A model for estimating the completion of rest for 'Redhaven' and 'Elberta' peach trees. *HortScience* **9**, 331–332.

Rinne, P.L.H., Paul, L.K. & van der Schoot, C. (2018) Decoupling photo- and thermoperiod by projected climate change perturbs bud development, dormancy establishment and vernalization in the model tree populus. *BMC Plant Biology* **18**.

Satake, A., Nagahama, A. & Sasaki, E. (2022) A cross-scale approach to unravel the molecular basis of plant phenology in temperate and tropical climates. *New Phytologist* **233**, 2340–2353.

Schwartz, M.D. (1994) Monitoring global change with phenology – the case of the spring green wave. *International Journal of Biometeorology* **38**, 18–22.

Tylewicz, S., Petterle, A., Marttila, S., Miskolczi, P., Azeez, A., Singh, R.K., Immanen, J., Mähler, N., Hvidsten, T.R., Eklund, D.M. *et al.* (2018) Photoperiodic control of seasonal growth is mediated by aba acting on cell-cell communication. *Science* **360**, 212–215.

van der Schoot, C., Paul, L.K. & Rinne, P.L.H. (2014) The embryonic shoot: a lifeline through winter. *Journal of Experimental Botany* **65**, 1699–1712.

Vitasse, Y., Hoch, G., Randin, C.F., Lenz, A., Kollas, C., Scheepens, J.F. & Koerner, C. (2013) Elevational adaptation and plasticity in seedling phenology of temperate deciduous tree species. *Oecologia* **171**, 663–678.

Walde, M.G., Wenden, B., Chuine, I., Gessler, A., Saurer, M. & Vitasse, Y. (2024) Stable water isotopes reveal the onset of bud dormancy in temperate trees, whereas water content is a better proxy for dormancy release. *Tree Physiology* **44**, tpae028.

Walde, M.G., Wu, Z., Fox, T., Baumgarten, F., Fu, Y.H., Wang, S. & Vitasse, Y. (2022) Higher spring phenological sensitivity to forcing temperatures of asian compared to european tree species under low and high pre-chilling conditions. *Frontiers in Forests and Global Change* **5**, 1063127.

Weinberger, J.H. (1950) Chilling requirements of peach varieties. *Proceedings of the American Society for Horticultural Science* **56**, 122–128.

Wilczek, A.M., Roe, J.L., Knapp, M.C., Cooper, M.D., Lopez-Gallego, C., Martin, L.J., Muir, C.D., Sim, S., Walker, A., Anderson, J., Egan, J.F., Moyers, B.T., Petipas, R., Giakountis, A., Charbit, E., Coupland, G., Welch, S.M. & Schmitt, J. (2009) Effects of genetic perturbation on seasonal life history plasticity. *Science* **323**, 930–934.

Wolkovich, E.M., Auerbach, J., Chamberlain, C.J., Buonaiuto, D.M., Ettinger, A.K., Morales-Castilla, I. & Gelman, A. (2021) A simple explanation for declining temperature sensitivity with warming. *Global Change Biology* **27**, 4947–4949.

Yu, S., Wenden, B., Ferguson, L. & Tian, L. (2024) Building climate resilient deciduous tree crops by deciphering winter dormancy.

Zhao, Y., Antoniou-Kourounioti, R.L., Calder, G., Dean, C. & Howard, M. (2020) Temperature-dependent growth contributes to long-term cold sensing. *Nature* **583**, 825–829.

Zhu, P., Lister, C. & Dean, C. (2021) Cold-induced arabidopsis frigida nuclear condensates for flc repression. *Nature* **599**, 657–661.
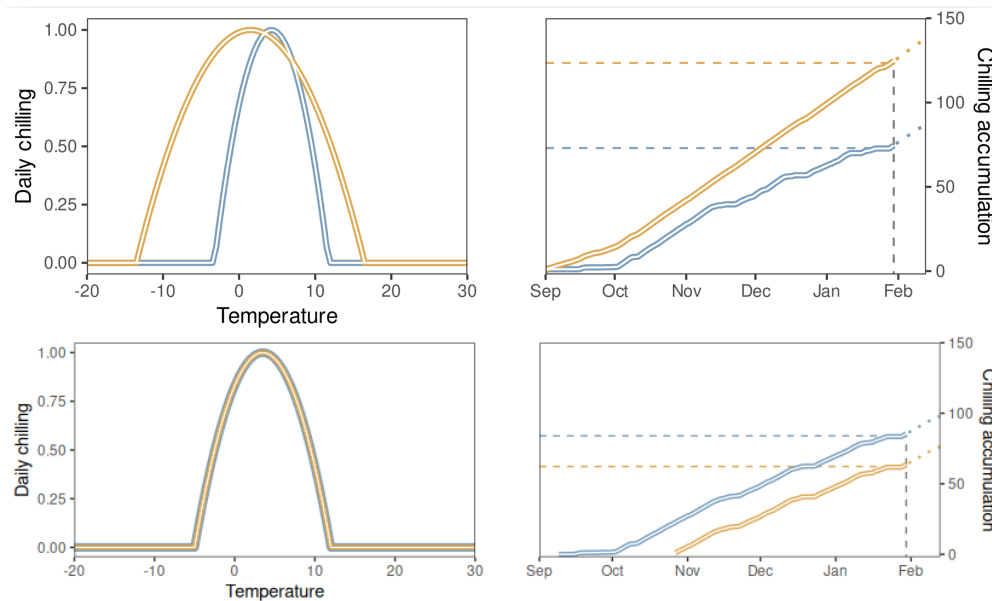
2 Figures

Figure 1: A major problem with current models of chilling is that they cannot uniquely estimate the most important aspects of chilling. We show here a simple example of a chilling model with three parameters—the minimum temperature for chilling, the maximum temperature, and the accumulation needed—shows that there are multiple solutions. Considering just two of these possible solutions highlights how the temperature range trade-offs with the accumulation: if the temperature range is wide (lower minimum, higher maximum) then the accumulation required will be higher, while if the range is smaller, then the accumulation needed is lower. The full suite of possible solutions is effectively endless (and the trade-off between range and accumulation is not linear, as it depends on the full width of the range, but also its placement relative to 0). Further, this model is not actually one of only three parameters as two additional parameters were set as known (start day of accumulation was set at 1 September, and the endodormancy break date at 30 January) so that the model could even be fit using common algorithms. This reality is present in every model of chilling, but rarely discussed and often not even mentioned.
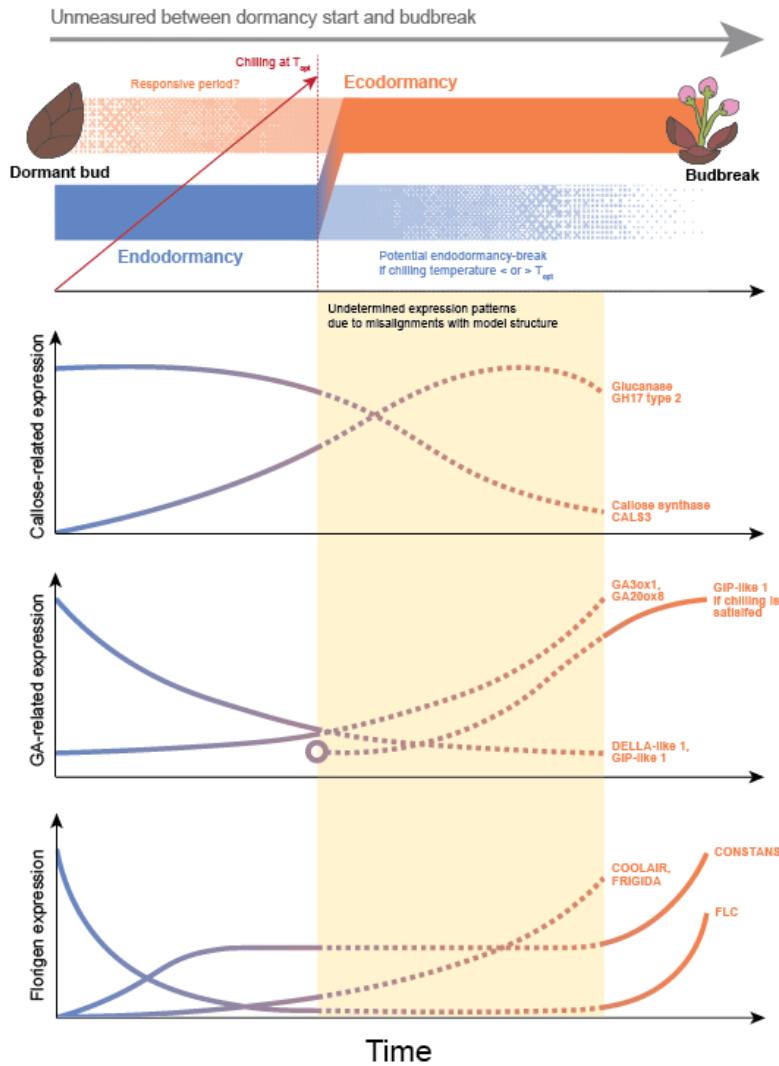
Figure 2: Aligning phenological models and molecular findings. Current phenological models of budbreak (top panel) assume two underlying states that lead to the observed process of budbreak: (1) endodormancy during which plants accumulate sufficient chilling to break endodormancy and transition to (2) ecodormancy, a period during which plants accumulate sufficient 'forcing' (warm temperatures) to break bud (flower or leaf). Over 30 variants of this model exist, including those where the phases are sequential (darker shading) or occur in parallel (dark and light shading). Molecular work suggests callose (second panel), alongside Gibberellic acid (GA, third panel) and florigen related genes may all underlie these hypothesized phases.
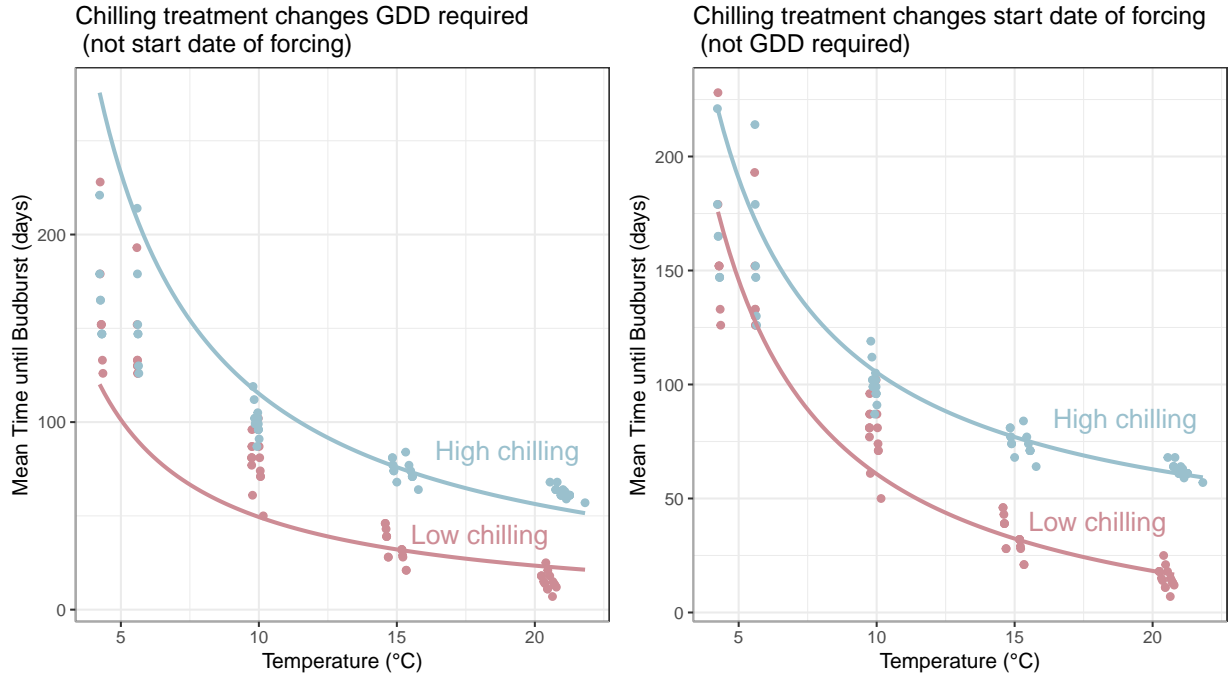
Figure 3: Many experiments studying chilling alter 'chilling' and 'forcing' by varying the duration that cool temperatures are applied ('chilling') following by different warm temperatures ('forcing') then fit simple linear models (e.g., most fit ANOVA models, with main effects of 'chilling' and 'forcing' treatments and their interaction—'chilling' × 'forcing'—to find a sub-additive effect of the two) that do not match the current biological understanding of chilling. Fitting models that match the proposed accumulation process is possible, however, as we show here using data from Walde *et al.* (2022) for *Quercus robur*, and considering two alternative biologies: (left) cool ('chilling') and warm treatments (*x* axis) interact, such that longer cool temperatures mean more warm temperatures are required for leafout, versus (left) longer cool temperatures change the start date of the accumulation of warm ('forcing') temperatures.