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## Cold Case: Making the Case for Applied Modeling of Cold Hardiness in Seedling Production and Regeneration

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### Abstract

Climate change creates unprecedented challenges for seedling production and reforestation. Developing new tools is necessary to understand seedling physiology and phenology under novel environmental conditions. A process-oriented cold hardiness model that can accurately predict daily cold hardiness is a tool that can inform nursery cultural decisions, planting, and seed source selection, especially in cases of assisted migration. This model can provide daily estimates of cold hardiness status and biologically interpretable parameters that reveal population-specific characteristics with low error and high efficiency. This paper was presented at Growing Pains: Scaling up the Reforestation Pipeline—Joint Annual Meeting of the Western Forest and Conservation Nursery Association and the Forest Nursery Association of British Columbia (Portland, OR, September 19–21, 2023).

### Introduction

The future success of seedling production and reforestation faces many challenges. An overarching theme to these challenges is the impacts of climate change and modern forest management practices. These factors disrupt the natural cycles of plants that have evolved over millennia. One such cycle is plant phenology, the timing of recurring life events that are commonly associated with seasonal changes such as budburst in spring, flowering and fruiting

in summer, and leaf senescence in fall. Phenology has been observed and recorded for much of recent history, with cherry blossom records dating back to the 800s (Piao et al. 2019). Growing degree days (GDD) may be the first occurrence of phenological modeling, originating in the 1700s, and is still commonly used by growers, agronomists, entomologists, and pathologists (Piao et al. 2019). The concept of GDD can be thought of as a type of “thermal time” and is still applied to nursery crop production and reforestation (Bradford 2002, Ferguson et al. 2011, Kaya et al. 2021).

Tracking thermal time in GDD and chill hours is common in nurseries. These empirical methods are based on historical research and serve as a guide for growers. This practice has sufficed for many decades across many different production systems, but the future, under climate change, will demand a more thorough understanding of seedling phenology and physiological mechanisms to create tools capable of mitigating unprecedented challenges.

In addition to climate change, increasing seedling demand due to postwildfire reforestation efforts also creates challenges in seedling production and regeneration. On Federal land in the United States, forest loss to wildfires in recent decades has resulted in a backlog of reforestation demand. The 2021 Repairing Existing Public Land by Adding Necessary Trees (REPLANT) Act aims to reforest 1.2 billion trees in response to this backlog (Stabenow 2021). This heavy demand pressure for seedlings strains nursery production, challenges infrastructure capacity, and disrupts typical growing and planting practices, all of which create novel risks to seedling cold hardiness

(Fargione et al. 2021, Grossnickle and MacDonald 2021). In response to climate change, assisted migration (seed source movement) is likely to soon become the standard in reforestation. Though the intention is moving populations or species to new regions where they are better adapted, assisted migration creates the risk of maladaptation, or a mismatch between evolved traits and the local environment (Malmqvist et al. 2018). Understanding how populations will handle future heat and drought and how they will tolerate current environments, including cold weather extremes, will be important to prevent maladaptation and ensure reforestation success.

Cold hardiness is a phenological characteristic of plants that is driven in part by temperature and is thus susceptible to effects of climate change. Cold hardiness—the ability of a plant tissue to survive low temperature exposure—can be characterized into three phases during the dormant season of temperate woody plants (Bigras et al. 2001). First, acclimation occurs during fall into winter when plants gradually become cold hardier. Second, peak hardiness (or maximum hardiness) occurs during winter and is when plants show the greatest resistance to cold stress. Third, deacclimation occurs when plants rapidly and irreversibly lose cold hardiness and progress toward budburst and vegetative growth resumption. Though the phenology of cold hardiness and dormancy overlap, and both respond to temperature, they occur via separate mechanisms within plant tissues and follow different seasonal patterns.

Dormancy phenology also progresses through a series of stages driven by environmental conditions. In conifer seedlings, drought-induced dormancy may occur in summer or early fall. At this stage, the plant is in a state of ecodormancy, also called quiescence (Haase 2011), and dormancy can be released (i.e., growth can resume) if the environment becomes favorable. A species-specific combination of photoperiod and chilling temperatures contributes to the progression into endodormancy in the late fall and early winter, which cannot be released by environmental conditions directly but is controlled by internal physiology (Lang et al. 1987). This physiological dormancy must be released through the accumulation of chilling temperature exposure (i.e., a chilling requirement). When chilling requirements have been met, endodormancy progresses into ecodormancy during which forcing temperatures contribute to budburst and cold hardiness deacclimation (Bailey and Harrington 2006), which are highly correlated throughout late winter into spring (Aitken and Adams 1997).

Mismatched phenology (when plant response and environmental cues become asynchronous) can impact seedling success, especially in terms of growth and

hardiness. Temperature changes related to climate change have modified the timing and duration of phenological stages during dormancy, with reductions in chilling being the most important driver across temperate tree species (Ettinger et al. 2020). Accumulation of chilling temperatures is important to release endodormancy, control the efficacy of forcing temperatures for budburst, and regulate the rate of cold hardiness deacclimation (Bigras et al. 2001, Harrington and Gould 2015). Seasonality is predicted to change more in the future with longer summers and shorter winters, springs, and autumns. These changes will further disrupt dormancy phenology and reduce chilling accumulation (Wang et al. 2021). As budburst and shoot elongation occur, woody plants are the least cold hardy. Thus, a mismatch in the timing of budburst and seasonal climate can result in negative outcomes such as increased cold damage due to early deacclimation (Arora and Taulavuori 2016, Wisniewski et al. 2018) or delayed budburst due to lower exposure to chilling (Ettinger et al. 2020, Hsu et al. 2023). Climate change in the Pacific Northwest is anticipated to result in increases in precipitation as rain rather than snow (Mote et al. 2016). This change can affect seedling production systems. For example, the seedling lifting window will shift due to soil saturation, early warming, and late freezes, resulting in catastrophic damage to nursery crops or planted seedlings.

Empirical methods, like GDD, are likely to be inadequate in the future when environmental conditions fall outside of historical observations. However, models based on the understanding of biological processes can be more effective when applied to novel conditions, such as those caused by climate change (Cuddington et al. 2013). Fortunately, seedling production and reforestation efforts can be improved through implementing new technologies. New computing abilities and data collection techniques allow for the increased use of modeling tools in nursery production and reforestation practices (MacKenzie and Mahony 2021, Pasala and Pandey 2020).

This article describes a process-oriented cold hardiness model trained and tested with historical published Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) data. This example is meant to demonstrate how a model can be used for daily, real-time predictions of phenology status. This case uses cold hardiness in units of estimated lethal temperature to 50 percent of a population ( $LT_{50}$ ). Applied use of this model to provide predictions on a daily time scale can be useful in frost protection decision making and characterization of specific seed lots. Real-time knowledge of seed lot hardiness status can be used to inform decisions about culturing, lifting, storage requirements, planting timing, and planting site.

## Methods

Cold hardiness observational data were extracted from published literature. Criteria for data selection were the inclusion of multiple dates of cold hardiness observations for a seed source replicated over one or more dormancy seasons. Of the data sources reviewed, only one had multiple seasons of cold hardiness data for two seed sources (Timmis et al. 1994). Data were extracted from three additional data sources, which are described in a separate publication (Stuke et al. 2024). Data extraction from figures was performed with the ImageJ ‘Figure Calibration’ plugin (Miller 2011, Schneider et al. 2012). Cold hardiness from second-year bareroot Douglas-fir seedlings grown in Olympia, WA, was determined using artificial freeze tests and calculation of the  $LT_{50}$  based on visual damage expression (Timmis et al. 1994). Daily minimum and maximum temperatures for the closest weather station were acquired from climate data online (NOAA 2022) from October 1 through May 1 and included three dormancy seasons (starting in October 1974, 1976, and 1977). For the two seed sources tested (table 1), elevation was estimated based on the coordinates of the collection site (USGS 2022). Seed sources were identified as high and low elevation, and both were tested during all three full dormancy seasons.

**Table 1.** Modeling Data

| Seed source ID | No. of data points | Seed source lat. (°N) | Seed source long. (°W) | Seed source elevation (m) |
|----------------|--------------------|-----------------------|------------------------|---------------------------|
| High           | 29                 | 46.11                 | 122.54                 | 630 (2,067 ft)            |
| Low            | 24                 | 46.93                 | 123.81                 | 100 (328 ft)              |

The data set consists of 53 data points from 2 seed sources, both grown at the same nursery site in Olympia, WA, (46.9° N, 123.08° W) over a series of 3 dormancy seasons in the 1970s (1974–1975; 1976–1977; 1977–1978).

## Modeling

The model used in this project was modified from a grape (*Vitis* spp.) cold hardiness extension testing program (Ferguson et al. 2011, 2014). This model was selected because it is used for real-time predictions of cold hardiness for dozens of grape cultivars and only requires daily minimum and maximum temperature as the input variables. The model has reliably predicted grape bud cold hardiness across many cultivars over many years (Ferguson et al. 2014). Though grapes and conifers differ in many ways, the model has several applicable

features for many species, such as the use of daily average temperature for cold hardiness prediction, testing with many years of climate data from a broad geographic range, biologically interpretable parameters, inclusion of chilling and forcing temperature accumulation requirements, and parameters specific to the acclimation and deacclimation periods of cold hardiness phenology. These aspects make the model a strong candidate for use in tree seedling operational decisions.

This cold hardiness model uses a set of biologically interpretable parameters for each seed source tested (table 2). Parameters specific to each seed source are determined using an automated model calibration process built into Cropbox: a declarative crop modeling framework (Yun and Kim 2023). To prevent overfitting, 70 percent of data points from each seed lot were randomly selected as a training dataset (used for calibration) and the remaining 30 percent were used as a testing dataset for model validation.

The general operation of the model is that chilling units are accumulated until the chilling requirement is met. Thereafter, forcing units are accumulated until the upper limit of cold hardiness is met or the end of the modeling

**Table 2.** Parameters and variables used in the cold hardiness model

| Symbol      | Description                            | Range                       |
|-------------|--|-----------------------------|
| $DD_c$      | Chilling degree-days                   |                             |
| $DD_f$      | Forcing degree-days                    |                             |
| $H_c$       | Cold hardiness                         | -40 to 0 °C (-40 to 32 °F)  |
| $H_{c, ll}$ | Lower limit cold hardiness temperature | -25 to -15 °C (-13 to 5 °F) |
| $H_{c, ul}$ | Upper limit cold hardiness temperature | -5 to 0 °C (23 to 32 °F)    |
| $H_{c, 0}$  | Initial cold hardiness value           | -7 to 0 °C (19.4 to 32 °F)  |
| $T_{th, a}$ | Threshold temperature of acclimation   | 0 to 10 °C (32 to 50 °F)    |
| $T_{th, d}$ | Threshold temperature of deacclimation | 0 to 15 °C (32 to 50 °F)    |
| $k_a$       | Acclimation rate                       | 0 to 1                      |
| $k_d$       | Deacclimation rate                     | 0 to 1                      |
| $R_f$       | Forcing requirement                    | 100 to 500 $DD_f$           |
| $R_c$       | Chilling requirement                   | -500 to -100 $DD_c$         |

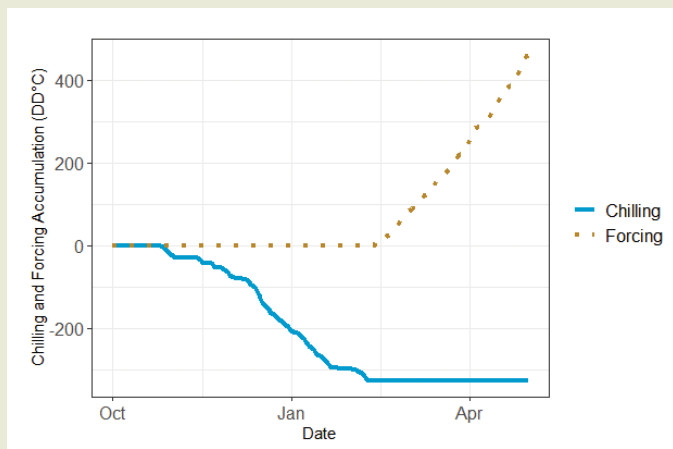
Adapted from Ferguson et al. (2011, 2014). Manually input range limits, based on biological assumptions, are included for model parameters.

period is reached, whichever occurs first (figure 1). A series of equations determines the daily change in cold hardiness based on daily temperature inputs (figure 2), which can estimate  $LT_{50}$  daily. Model performance was determined using goodness of fit metrics, which compare model predictions with observed  $LT_{50}$  values. The model's equations and assumptions are published in Stuke et al. (2024).

## Results

The parameters used in the model (table 2) result in different responses for the different seed lots produced at the same time and location. Estimates for the high- and low-elevation seed lots have some notable differences (table 3). The parameters have easily interpretable meanings and can reveal characteristics about how different populations respond to certain climate conditions. For example, the high seed lot had a lower temperature threshold for deacclimation and a lower chilling requirement compared with the low seed lot (table 3). This difference suggests that the high seed lot is very sensitive to warming and may be more vulnerable to early deacclimation, which may create issues when producing this seed lot in warmer regions or in cases of early warming, especially if late frost occurs.

The two seed sources primarily differed in the shoulder seasons (fall and spring), with the low seed source acclimating and deacclimating later than the high seed source (figure 3). The model fits the general pattern of cold hardiness observational data, but in the 1976–1977 and 1977–1978 dormancy seasons, peak cold hardiness estimates did not achieve low enough  $LT_{50}$  values. This

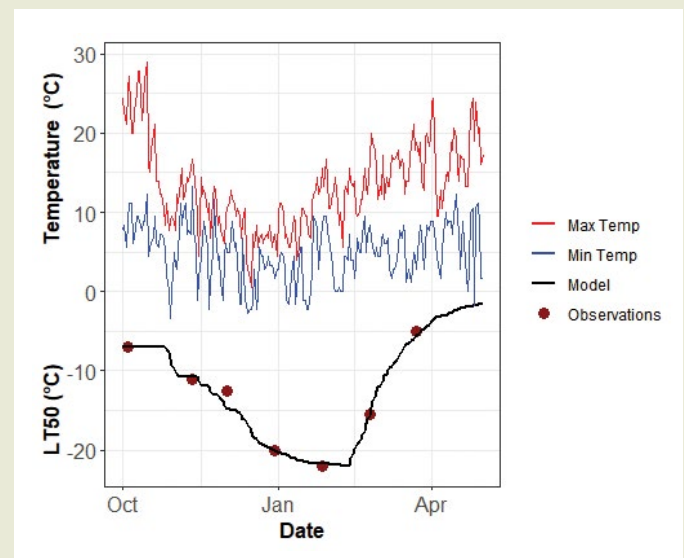


**Figure 1.** The model described in this paper operates by accumulating chilling during acclimation and forcing during deacclimation after a chilling requirement is met.

**Table 3.** Parameter estimates for high and low seed sources

| Parameter  | High                       | Low                        |
|------------|----------------------------|----------------------------|
| $T_{th,a}$ | 7.3 °C (45 °F)             | 7.9 °C (46 °F)             |
| $T_{th,d}$ | <b>0.07 °C (32 °F)</b>     | <b>1.3 °C (34 °F)</b>      |
| $R_c$      | <b>-338 DD<sub>c</sub></b> | <b>-788 DD<sub>c</sub></b> |
| $R_f$      | 173 DD <sub>f</sub>        | 422 DD <sub>f</sub>        |
| $H_{c,ll}$ | -24 °C (-11 °F)            | -24 °C (-11 °F)            |
| $H_{c,ul}$ | -0.6 °C (33 °F)            | -3.8 °C (25 °F)            |
| $H_{c,o}$  | -5.6 °C (22 °F)            | -4.7 °C (24 °F)            |
| $k_a$      | 0.7                        | 0.5                        |
| $k_d$      | 0.09                       | 0.1                        |

Parameter estimates from Timmis et al. (1994) indicate phenological differences in the high and low seed sources. Biologically meaningful differences are bolded and include chilling requirement ( $R_c$ ) and the temperature threshold for deacclimation ( $T_{th,d}$ ). Parameters were determined during model training using 70 percent of datapoints for each seed source. Parameter definitions are listed in table 2. Chilling degree days are given in negative values.

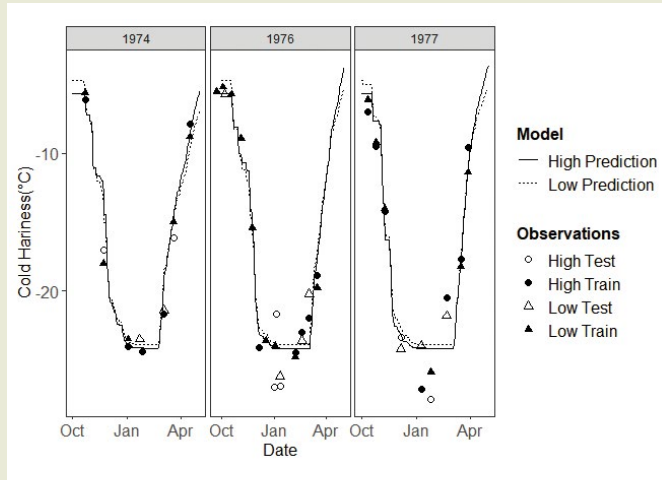


**Figure 2.** The model used here functions on daily temperature inputs and produces estimates of cold hardiness, which can be specific to populations based on parameter values selected during the model training process. The model operates on a daily time interval, so that estimates of cold hardiness can be updated after weather data from the previous day are available. This input method also allows the opportunity for predictions of future cold hardiness by using historical averages to project weather patterns.



result may be attributed to a minimum limit of  $-25\text{ }^{\circ}\text{C}$  ( $-13\text{ }^{\circ}\text{F}$ ) assigned to  $H_{c,II}$  parameter fitting, which should be a consideration for adjustment in future model runs (Stuke et al. 2024).

Model residuals (figure 4) and goodness of fit statistics (table 4) demonstrate quantitatively how the model performed. For this dataset, the model had a good fit, with a slightly better fit for the low seed source than for the high



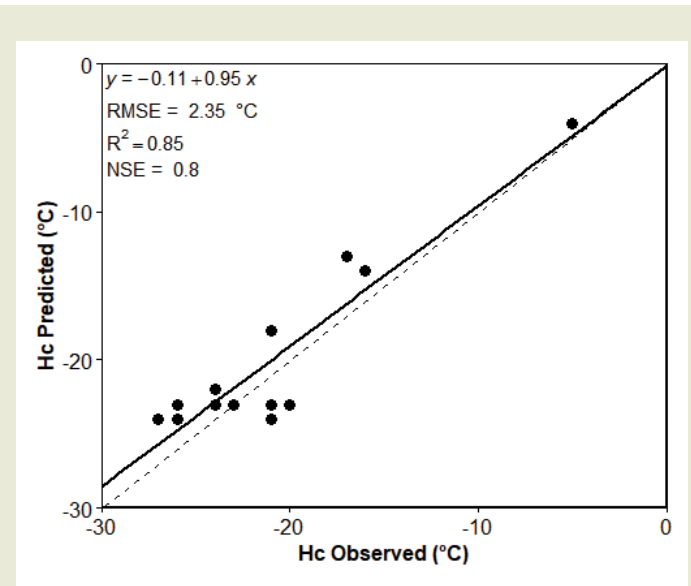
**Figure 3.** Model fits are shown here by lines, and observed cold hardiness is indicated by points. The difference between an observation and the modeled value at any timestep indicates a model residual, which can be used to calculate error. Training data are used for model calibration and testing data are used for model evaluation. Training data included 70 percent of data points and testing data included the remaining 30 percent. This separation reduces bias and the likelihood of overfitting.

seed source. This difference may be due to the low seed source having more data points, which may have improved the model calibration process. The regression of residuals shows that the model performed very close to the 1:1 line (figure 4) with a slope of 0.95, where a slope of 1.0 and complete overlap with the 1:1 line would indicate a perfect fit. Root-mean-square error (RMSE, the average difference between the model’s predicted values and the actual values) ranges from 2.03 to 2.7  $^{\circ}\text{C}$  ( $35.66$  to  $36.86\text{ }^{\circ}\text{F}$ ), which demonstrates how accurate the model is on average. Modifying the parameter range for the lower limit of cold hardiness to include the low temperature  $LT_{50}$  in 1976 and 1977 may reduce the RMSE, since these are the largest error sources in the model fit.

**Table 4.** Model validation statistics for high and low seed sources

| Statistic | High | Low  | Combined |
|-----------|------|------|----------|
| MAE       | 2.43 | 1.67 | 2.0      |
| RMSE      | 2.7  | 2.03 | 2.35     |
| d         | 0.91 | 0.97 | 0.95     |
| n         | 7    | 9    | 16       |

Model validation statistics summarizing goodness of fit using model residuals for the Timmis et al. (1994) data demonstrate good model fits for both seed sources but a better fit for the low seed source. Seed sources were modeled separately, and statistics are provided for each seed source, including mean absolute error (MAE; the average of the absolute values of model residuals), root-mean-square error (RMSE; the magnitude of error), index of agreement (d; an indicator of model efficiency on a scale of -1 to 1), and number of data points (n) for each seed source.



**Figure 4.** The relationship between observed and predicted cold hardiness values shows low error, indicating good model performance. Points show model residuals (observed and predicted value for each data point). Dotted lines show a 1:1 relationship between observations and predictions and the solid line shows the linear regression between observations and predictions. The linear regression equation, root-mean-square error (RMSE),  $R^2$  (the coefficient of determination), and Nash–Sutcliffe model efficiency (NSE) for each scenario are listed in the plot. Only datapoints from the testing subset are shown (30 percent of all datapoints).

## Discussion

Knowing the daily estimated cold hardiness for seedlings in production can be valuable in determining minimum requirements for frost protection. Though it is a critical component of cold damage prevention in the nursery, irrigation-based frost protection of bareroot and outdoor grown container stock can have many disadvantages. Irrigation-based frost protection works by applying water to seedlings during cold weather events to provide insulation in the form of ice and warming by latent heat through the exothermic reaction that occurs when water freezes (Rose and Haase 1996). The physical weight of ice can cause mechanical damage to seedlings, reducing overall yield. Application of irrigation can oversaturate soils creating standing water and exclude equipment from accessing bareroot seedlings, thereby delaying lifting (figure 5). Lifting can also be delayed in container crops that are frost protected if blocks remain frozen. Nutrients can be lost through leaching of soil or soilless media and directly from foliage. Irrigation equipment can be damaged if pipes freeze during frost protection (figure 5). Additionally, frost protection can reduce chilling accumulation if seedling temperature is not kept below the threshold of physiologically active chilling temperatures. Though knowing cold hardiness status is key to making frost protection decisions, accurate temperature monitoring and site-specific weather predictions across nursery zones are critical.

In addition to the daily estimated  $LT_{50}$ , the calibrated model can be used to characterize and rank different plant populations by their sensitivity to specific weather conditions. For example, a comparison between chilling requirements and deacclimation rates can be used to determine which populations are more likely to deacclimate earlier during warming events (table 3). This knowledge can be used to prioritize interventions and select appropriate populations for reforestation, especially in cases of assisted migration. Knowing the status of chilling requirement in relation to accumulated chilling can also be

helpful in determining if additional storage is required to artificially induce hardening (Omi et al. 1991).

This model currently runs on calendar date and does not include a photoperiod component. For Douglas-fir seedlings that do not experience photoperiod manipulation (i.e., blackout or artificial lighting), natural daylength is minimally impactful on cold hardiness acclimation and deacclimation (Stuke et al. 2024). For nursery operations using blackout to induce budset, consideration of when to start the modeling period is important. The rapid change of photoperiod that blackout induces can trigger a stress response in seedlings that alters natural phenology and may have unique cellular and physiological consequences (Wallin et al. 2017). The impact of blackout on cold hardiness phenology is an area that requires more research to adequately model.

Seedling production and reforestation is critical to establishing forests that will grow into the future. Fargione et al. (2021) estimated that the economics to establish 26 million hectares (64.25 million acres) in the contiguous United States vary widely but could be \$33 billion or higher during the next 15 years, depending on planting targets and capacities (Fargione et al. 2021). The REPLANT Act further demonstrates investment in reforestation through the allocation of \$123 million in Federal funds annually (Stabenow 2021). If phenological issues affect seedling survival on even a fraction of reforested acreage, large costs will occur. The impact of cold damage on seedlings is likely underestimated because of the delay in expression of visual damage. Cold damage



**Figure 5.** Ice accumulates over bareroot seedlings due to irrigation-based frost protection (left). Though this practice is necessary to protect vulnerable seedlings, it can have many negative impacts as well, such as ice formation on irrigation equipment (right). Accurate estimation of cold hardiness can help in frost protection decision making. Photos courtesy of Washington Department of Natural Resources, Webster Nursery, Olympia, WA.

decreases seedling quality and increases disease even in nonlethal cases (Reich and Kamp 1993).

As the demands of reforestation and assisted migration place extra pressure on seedling production systems and forest regeneration, and climate change creates atypical weather patterns and extremes, understanding and predicting seedling responses to unprecedented seasonal conditions will be more important than ever. This model integrates seedling phenology and physiology in a seedling production context to guide future planting and population selection for reforestation.

## Conclusion

Though the model described in this article is not yet ready for nursery and reforestation operations without parameterization for specific populations, it provides the foundation for a tool that can be further developed with additional data. Modern modeling resources cannot replace intuitive and experienced growers and foresters, but they can be leveraged to assist in decision making and risk prevention. These tools will be critical for nursery production and forest regeneration as novel difficulties and unprecedented weather extremes increase in frequency due to climate change. Building strong collaborations among nurseries, foresters, and researchers will be crucial to overcome future demands and challenges.

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