Modeling Dormant Bud Cold Hardiness and Budbreak in Twenty-Three *Vitis* Genotypes Reveals Variation by Region of Origin

John C. Ferguson,[1,2,3] Michelle M. Moyer,[1] Lynn J. Mills,[1]
Gerrit Hoogenboom,[2] and Markus Keller[1]*

Abstract: Cold injury is a key environmental challenge in many grape-producing regions, especially those at high latitudes. Although grapevines acclimate to cold temperatures in fall and deacclimate when warm temperatures return in spring, cold hardiness varies with species, cultivar, phenology, ambient weather, photoperiod, and plant organ, which hampers implementation of effective mitigation practices. Using long-term data sets of lethal temperatures and spring phenology for primary buds of *Vitis vinifera* and *Vitis labruscana*, we parameterized and evaluated a discrete-dynamic model that simulates cold hardiness from early fall through budbreak of 23 genotypes. The model uses mean daily temperature as the sole input variable to drive daily changes in hardiness. Genotype-specific parameters, such as initial and maximum hardiness, temperature thresholds, acclimation and deacclimation rates, and chilling and heating requirements, were optimized through an iterative process. The model predicted cold hardiness with $0.89 \leq r^2 \leq 0.99$, depending on genotype. Because it simulates hardiness at budbreak, the model can also be used to predict the time of budbreak. Optimized model parameters revealed a north/inland-south/coastal gradient for genotype origin in terms of initial and maximum cold hardiness, and time of budbreak. Budbreak occurred earlier in hardier genotypes, consistent with more rapid deacclimation of genotypes originating from colder climates, paradoxically making these genotypes more vulnerable to spring frost in warmer environments. The current model of grapevine bud cold hardiness has uses in both climate modeling and risk assessment.

Key words: budbreak, cold hardiness, differential thermal analysis, grapevine, model, phenology, *Vitis*

Cold hardiness (H_c), or the ability to tolerate freezing temperatures, is a major concern in many grapegrowing regions of the world where the ambient temperature can drop below freezing. Cold hardiness is a dynamic trait acquired in response to shortening photoperiod and declining temperature in late fall or early winter and varies with species, cultivar, phenology, ambient weather, and the plant organ of interest (Xin and Browse 2000, Gusta and Wisniewski 2013, Pagter and Arora 2013). Green, growing organs and tissues generally lack hardiness and may sustain injury at temperatures only slightly <0°C. Damage can occur even when the ambient air temperature remains >0°C if radiative cooling under clear sky conditions leads to subzero tissue temperatures. Conversely, plant tissues are most cold hardy during midwinter (i.e., the middle of the dormant season) when ambient temperatures are lowest. Depending on the aforementioned variables, grapevines (*Vitis* spp.) may survive temperatures ranging from approximately -10°C to less than -30°C during the dormant period (Fennell 2004, Mills et al. 2006, Keller 2010, Ferguson et al. 2011).

The transition between the growing and dormant seasons is associated with acclimation and deacclimation processes that alter the level of H_c (Keller 2010, Gusta and Wisniewski 2013, Pagter and Arora 2013). The genetic programs for dormancy and H_c are superimposed, and the transition from paradormancy to endodormancy is a prerequisite for the subsequent acquisition of full H_c (van der Schoot and Rinne 2011). Even in midwinter these processes respond to fluctuations in temperature that lead to short-term changes in H_c. This is especially noticeable when plants begin to deacclimate in response to unseasonal warm spells (Ferguson et al. 2011, Pagter and Arora 2013). Temperature-driven acclimation/deacclimation cycles continue until the changes leading up to budbreak render the deacclimation process irreversible. Furthermore, the dynamic nature of H_c is partially genetically determined; different species and cultivars may acquire varying levels of H_c as well as vary in their responses to changes in temperature.

[1]Department of Horticulture, Irrigated Agriculture Research and Extension Center, Washington State University, Prosser, WA 99350; [2]AgWeatherNet, Washington State University, Prosser, WA 99350; and [3]present address: 23244 Lower Terrace, Eagle River, AK 99577.

*Corresponding author (mkeller@wsu.edu)

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These aspects of H_c complicate production strategies and lead to spatial and temporal variation in crop production. A specific low temperature that is of no concern at one point during the dormant season could pose a threat at other times or could be problematic for some cultivars being grown at a specific site but not for other cultivars or other sites (Ferguson et al. 2011). This has important practical consequences. In regions where the risk of cold damage is high, good agricultural practices suggest developing vineyards in areas less prone to damaging cold temperature occurrence or cold-air pooling (Widrlechner et al. 2012). Cultivar selection can be used to match appropriate genotypes with varying degrees of H_c to different sites, but this requires detailed knowledge of the dynamic behavior of each cultivar in response to changing meteorological conditions. Understanding this dynamic behavior is also required to make informed decisions pertaining to the implementation of protective measures such as the use of wind machines or heaters. In addition, the choice of pruning practices may be influenced by the timing and severity of a damaging cold event (Keller and Mills 2007, Dami et al. 2012).

The dilemma faced in production viticulture is in knowing precisely at what time and location damaging temperatures may occur. To address this challenge, we developed a robust numerical H_c model for dormant primary buds of three diverse grape genotypes (Ferguson et al. 2011). This dynamic thermal-time model predicts bud hardiness using genotype-specific coefficients (e.g., minimum and maximum hardiness, acclimation and deacclimation rates, and ecodormancy boundary) with daily mean temperature as the single input variable. A key strength of such a model is that, given only temperature measurements, H_c prediction can be extended across entire regions, which is considerably more cost-effective than conducting frequent real-time H_c assessments at multiple locations.

Initial feedback from early adopters of this model showed several limitations, including the few genotypes that were parameterized and relatively poor predictive performance during late winter/early spring, when buds are deacclimating. The latter issue is critical given the extensive variation in local weather conditions, including unexpected frost events, during this period. In some instances, the model tended to predict unrealistic H_c values (-5 to -10°C) at a time when budbreak was observed in the field (Ferguson et al. 2011). The likely explanation for this anomaly is that the model was developed for dormant buds using data generated by differential thermal analysis (DTA). Such data are not readily obtained once buds approach budbreak and their water content rises. Moreover, bud sampling was terminated at varying times in some genotypes and some years to permit timely winter pruning, resulting in a relative paucity of available DTA data close to budbreak. Thus, the model can only extrapolate H_c to this time, a shortcoming that is addressed by using spring phenology data in the new model presented here.

The present study had two main objectives. The first was to develop model variants for a wide range of grape genotypes. These genotypes comprise cultivars of *Vitis vinifera* L., of diverse Eurasian origin and used mostly for wine production, and *Vitis labruscana* Bailey, of northeastern North American origin and mostly used for juice production. The second objective was to enhance the performance of the previous model during the period leading up to and during budbreak, a time for which limited DTA data are available. We limited our analysis to primary buds due to their role as the main source of yield potential for the subsequent growing season. All abbreviations and units of measurement used are defined in Supplemental Table 1.

Materials and Methods

Cold hardiness data. The H_c of endo- and ecodormant primary buds of up to 23 *Vitis* spp. genotypes has been routinely measured in our laboratory since 1988, using cane samples collected in the vineyards of the Irrigated Agriculture Research and Extension Center (IAREC) in Prosser, WA (lat. 46.3°N; long. 119.7°W; 260-365 m asl), and in the cultivar collection of Ste. Michelle Wine Estates, Paterson, WA (lat. 45.9°N; long. 119.6°W; 195 m asl). Data were collected as described for cultivars of *V. vinifera* and *V. labruscana* (Mills et al. 2006) (Table 1), using DTA that measures low-temperature exotherms (LTE) and high-temperature exotherms (HTE). An LTE corresponds to the (lethal) temperature at which supercooled intracellular water freezes in an organ. The H_c is expressed as LT_{50}, which is the lethal temperature for 50% of buds tested. Measurements of H_c typically started in the fall (near the time of harvest) and continued through the dormant period until either pruning limited plant material availability or rapid deacclimation prior to budbreak made the DTA method unreliable. The latter limitation arises from the fact that it is increasingly impossible to distinguish LTE from HTE in swelling buds, as their water content increases from <50% to >75% and they lose the ability to supercool (Lavee and May 1997, Fuller and Telli 1999, Fennell 2004). An HTE indicates the freezing of extracellular water, which occurs at higher temperatures and is usually not lethal, although it induces cellular dehydration (Xin and Browse 2000, Fennell 2004). Consequently, our H_c data sets start and end at differing times each year. Data for each genotype were collected at ~2-week intervals, but for some genotypes in some years DTA measurements were conducted daily or weekly. The genotypes assessed changed from year to year (Table 1), depending on availability or industry interest. The country of origin for each genotype was taken from the National Grape Registry (ngr.ucdavis.edu). In addition, the genotypes were assigned to five broad groups according to the environment of their original distribution (Table 1). Because the precise geographic origin of many *V. vinifera* cultivars is unknown, we applied a simple procedure that resulted in a gradient from mild (group 1) to cold (group 5) winters: south (groups 1 and 2) or north (groups 3 and 4) of the Alps, coastal (groups 1 and 3) or inland (groups 2 and 4). The *V. labruscana* cultivars were assigned to group 5.

Spring phenology data. Owing to the above limitations, H_c was approximated during the rapid deacclimation period leading up to and during budbreak, using phenological data obtained since 1988 in the same IAREC vineyards from

Table 1 Summary of raw data for development and evaluation of a genotype-specific model of grapevine bud cold hardiness (H_c).

		DTA-derived H_c data		Phenology-derived H_c data		Data for model optimization		Data for H_c model evaluation		Data for budbreak model evaluation	
Genotype[a]	**Origin**[b]	**Years**	N_d[c]	**Years**	N_p[c]	**Years**	N_o[c]	**Years**	N_{he}[c]	**Years**	N_{be}[c]
Barbera	Italy (2)	2006-2010	5	2006-2010	5	2006-2010	5	n/a	0	n/a	0
Cabernet franc	France (3)	2005-2008, 2011	5	1988-2005	18	2005-2007	3	2003, 2004, 2008, 2011	4	1989, 1991-2004	15
Cabernet Sauvignon	France (3)	1988-2011	24	1988-2005, 2011	19	1988-2001, 2004-2008	19	2002, 2003, 2009-2011	5	2002, 2003, 2011	3
Chardonnay	France (4)	1996-2011	16	1988-2005, 2011	19	1993-2001, 2004-2008	14	2002, 2003, 2009-2011	5	1989, 1991, 1992, 2002, 2003, 2011	6
Chenin blanc	France (4)	1988-1993, 2006-2008	9	1988-1994, 1996-2005	17	1988-1993	6	2003-2008	6	1994, 1996-2005	11
Concord	USA (5)	1988, 1989, 1992, 1997, 1999-2011	17	1991-2005, 2011	16	1988, 1989, 1991-2001, 2004-2008	18	2002, 2003, 2009-2011	5	2002, 2003, 2011	3
Dolcetto	Italy (2)	2006-2010	5	2006-2010	5	2006-2010	5	n/a	0	n/a	0
Gewürztraminer	Germany (4)	2005-2008, 2011	5	1988-2005	18	2001-2003, 2005-2007	6	2000, 2004, 2008, 2011	4	1989, 1991-2000, 2008	12
Grenache	Spain (1)	2006-2010	5	1991-2005	15	2003-2008	6	2002, 2010	2	1991-1994, 1997-2002	10
Lemberger	Austria (4)	2006-2008	3	1988-1994, 1996-2002	14	2000-2002, 2006-2008	6	n/a	0	1989-1994, 1996-1999	10
Malbec	France (3)	2004-2011	8	1988-1994, 1996-2002	14	1998-2000, 2004-2006	6	1994, 1996, 1997, 2001, 2002, 2007- 2011	10	1989, 1991-1994, 1996, 1997, 2001, 2002	9
Merlot	France (3)	1996-2011	16	1988-1994, 1996-2005, 2011	18	1992-1994, 1996-2001, 2004-2008	14	2002, 2003, 2009-2011	5	1989, 1991, 2002, 2003, 2011	5
Mourvèdre	Spain (1)	2005-2010	6	2006-2010	5	2005-2007, 2009	4	2008, 2010	2	2008, 2010	2
Nebbiolo	Italy (2)	2006-2010	5	2006-2010	5	2006-2010	5	n/a	0	n/a	0
Pinot gris	France(4)	2003-2010	8	1991-2005	15	1998, 1999, 2003-2007	7	1997, 2000-2002, 2008-2010	7	1991-1997, 2000-2002	10
Riesling	Germany (4)	1988-2011	24	1988-2005, 2011	19	1988-2001, 2004-2008	19	2002, 2003, 2009-2011	5	2002, 2003, 2011	3
Sangiovese	Italy (1)	2005-2010	6	2006-2010	5	2005-2007, 2009, 2010	5	2008	1	2008	1
Sauvignon blanc	France (4)	2006, 2009, 2010	3	1988-2005	18	2003-2006, 2009, 2010	6	n/a	0	1989-2002	14
Sémillon	France (3)	2006-2008	3	1988-2005	18	2003-2008	6	n/a	0	1988-2002	15
Sunbelt	USA (5)	2003-2010	8	1991-2005	15	1998, 1999, 2003-2007	7	2000-2002, 2008-2010	6	1991-1997, 2000-2002	10
Syrah	France (2)	1999-2011	13	2004-2009	6	1999-2001, 2004-2008	8	2002, 2003, 2009-2011	5	2009	1
Viognier	France (2)	1999-2010	12	2009	1	2002-2010	9	n/a	0	n/a	0
Zinfandel	Croatia (1)	2006-2010	5	1991-1994, 1996-2005	14	2003-2008	6	2001, 2002, 2009, 2010	4	1991-1994, 1996-2002	11

[a]Concord and Sunbelt are *V. labruscana* cultivars; all other genotypes are *V. vinifera*.

[b]Country derived from the US National Grape Registry (ngr.ucdavis.edu). Environment (group noted in parentheses): 1, coastal southern Europe; 2, inland southern Europe; 3, coastal northern Europe; 4, inland northern Europe; 5, northeastern North America.

[c]Abbreviations for number of years: N_d, with DTA measurements; N_p, with phenology observations; N_o, used for model optimization; N_{he}, used for H_c model evaluation; N_{be}, used for budbreak model evaluation.

which DTA data were collected (Table 1). The day of year (DOY) was recorded for woolly bud, budbreak, first leaf, second leaf, and fourth leaf separated from the shoot tip. Published data (Table 2) were used to infer H_c at each DOY for our phenological data. Because no cultivar-specific data are currently available, we used the same H_c across all cultivars within a species for a specific phenological stage. The *V. vinifera* values were derived from cv. Pinot noir (Gardea 1987) and the *V. labruscana* values from cv. Concord (Proebsting et al. 1978); these authors used similar protocols of freezing bud samples to a range of predetermined temperatures, then thawing the samples for ≥24 hr and visually evaluating tissue browning as a measure of cold damage. The phenology-derived H_c data were added to the DTA-derived H_c data to extend the data set beyond budbreak.

Model parameterization. The present H_c model was built on the discrete-dynamic model (Ferguson et al. 2011); that report describes and discusses the complete mathematical structure and underlying assumptions of the model presented herein. The model was coded and parameterized in SAS (ver. 9.2; SAS Institute, Cary, NC). The daily mean air temperature (T_{mean}) was used as the input variable that drives changes in acclimation and deacclimation to predict daily changes in H_c (ΔH_c). The ΔH_c was added to the previous day's H_c ($H_{c,i-1}$) to give the current day's H_c ($H_{c,i}$). The T_{mean} was estimated as the average of the minimum (T_{min}) and maximum (T_{max}) daily temperatures provided by the nearest (<10 km) Washington State University (WSU) AgWeatherNet (weather.wsu.edu) station for each vineyard site: the IAREC on-site station (lat. 46.3°N; long. 119.7°W; 265 m asl) and the Paterson station (lat. 45.9°N; long 119.5°W; 129 m asl). Although T_{mean} ignores possible diurnal acclimation/deacclimation cycles due to differences in T_{min} and T_{max}, it is the unit that corresponds to, and therefore is relevant for, the measured H_c data which were acquired at most daily. Moreover, photoperiod was not included as a driving variable, because the starting point (DOY 250) for the model was chosen for endodormant buds (see below). Though shorter photoperiods may induce bud dormancy in grapevines, low temperatures are required to acquire full H_c (Schnabel and Wample 1987, Fennell and Hoover 1991; M. Keller and L.J. Mills, authors' unpublished data, 2013). In addition to the introduction of spring phenology, the differences in H_c among genotypes were captured by genotype-specific parameters as described previously (Ferguson et al. 2011) with the following modifications (abbreviations in Supplemental Table 1).

Table 2 Published lethal temperatures (*LT*) used to infer grapevine bud cold hardiness (H_c) from spring phenology.

	Genotype and *LT* (°C)			Phenology-inferred H_c used in model	
Phenological stage	Pinot noir (LT_{50})[a]	Concord (LT_{10})[b]	Concord (LT_{90})[b]	*Vitis vinifera*	*Vitis labruscana*[c]
Woolly bud	-3.4	-6.1	-12.2	-3.4	-9.2
Budbreak	-2.2	-3.9	-8.9	-2.2	-6.4
First leaf	-2.0	-2.8	-6.1	-2.0	-4.5
Second leaf	-1.7	-2.2	-5.6	-1.7	-3.9
Fourth leaf	-1.2	-2.2	-2.8	-1.2	-2.5

[a]Gardea (1987).
[b]Proebsting et al. (1978).
[c]Mean of Concord LT_{10} and LT_{90}.

First, we adapted the estimation of the initial hardiness ($H_{c,initial}$): that is, the H_c of endodormant buds in late summer or early fall after the shoots have formed brown periderm (only brown buds were sampled from shoots that were changing from green to brown) but before the subsequent, temperature-driven cold acclimation process in late fall and early winter (Pouget 1963, Schnabel and Wample 1987, Fennell 2004, Keller 2010). This was necessary because early H_c measurements were not routinely collected for many of the genotypes, since the original intent of these measurements was not the development of a model. Therefore, the $H_{c,initial}$ of *V. vinifera* cv. Cabernet Sauvignon, the genotype with the largest available data set (Table 1), was used to estimate the $H_{c,initial}$ of all other genotypes. The Cabernet Sauvignon $H_{c,initial}$ was computed as the mean H_c (n = 6) of the earliest (typically mid- to late September) yearly data available from the optimization data set (see below). Because H_c of different genotypes was often measured on different dates, Cabernet Sauvignon H_c was interpolated (SAS proc. Expand, step size = 1 day) between consecutive dates for which DTA measurements were available through the winter solstice (21 December, northern hemisphere). This termination date was chosen to include all measurements taken during the fall acclimation period; grapevines typically reach their most hardy condition or maximum H_c ($H_{c,max}$) by this date (Schnabel and Wample 1987, Ferguson et al. 2011). This procedure gave an estimated Cabernet Sauvignon H_c for each DOY for which a measured H_c of any other genotype was available. Using regression analysis (SAS proc. Reg), the linear relationship between H_c of Cabernet Sauvignon and that of each of the other genotypes was applied to extrapolate $H_{c,initial}$ of each genotype relative to the $H_{c,initial}$ of Cabernet Sauvignon (Table 3). This approach maintained the relative hardiness rankings among genotypes to start the model.

Second, we updated the least cold-hardy condition or minimum hardiness ($H_{c,min}$) allowable for the model. Previously we had used $H_{c,min}$ = -3°C across genotypes (Ferguson et al. 2011). The new $H_{c,min}$ was taken as the hardiness of green growing tissues (fourth leaf stage): -1.2°C for all *V. vinifera* cultivars and -2.5°C for *V. labruscana* cultivars (Table 2). The former value was derived from *V. vinifera* cv. Pinot noir (Gardea 1987) and the latter from *V. labruscana* cv. Concord (Proebsting et al. 1978); reliable data for other genotypes are currently unavailable.

Third, we altered the calculation of the asymptotic bounds applied during deacclimation (see eq. 6 in Ferguson et al. 2011) by adding an exponent theta (θ) to the logistic component ($c_{log,d}$) in Equation 1:

$$c_{log,d} = 1 - \left[\frac{H_{c,i-1} - H_{c,max}}{H_{c,min} - H_{c,max}}\right]^{\theta} \quad \text{Eq. 1}$$

($H_{c,i-1}$, H_c for day i-1; $H_{c,max}$, maximum H_c; $H_{c,min}$, minimum H_c). The theta-logistic equation is frequently used in ecology

and was originally introduced for models of population growth in systems with finite resources (Richards 1959, Nelder 1961, Gilpin and Ayala 1973). Our previous model had defaulted to $\theta = 1$ (Ferguson et al. 2011). Our rationale for this change was that allowing θ to vary by genotype would permit the model to better capture the accelerated deacclimation observed just before budbreak. Supplemental Figure 1 demonstrates the effect of different values for θ on simulated H_c as budbreak is approached.

Fourth, the chilling degree days (DD_c) required for dormancy release, captured in the ecodormancy boundary (EDB) that defines the transition of buds from endo- to ecodormancy, was calculated using a threshold temperature common to all genotypes ($T_{th,c} = 10°C$). This change from the genotype-specific T_{th} estimated in Ferguson et al. (2011) makes the fixed $T_{th,c}$ used for chilling requirements independent of the estimated T_{th} used for acclimation and deacclimation (Arora et al. 2003). This approach enables our estimated chilling requirements to be compared directly with published reports that commonly use $T_{th,c} = 10°C$ across grape genotypes (Pouget 1963, Dokoozlian 1999, García de Cortázar-Atauri et al. 2009).

Model optimization and evaluation. Whenever possible, the complete data set was separated into two categories: one set for model development and parameter optimization and another independent set for model evaluation (Table 1). For model development, we only parameterized genotypes for which ≥3 years of measured H_c data were available. Because the model will be used to predict future H_c, the last three available years of data for each genotype were included in the evaluation set (usually 2009–2010, 2010–2011, and 2011–2012). A damaging freeze occurred during the 2010–2011 dormant season, but since the model is to be used to predict such events, two additional seasons with freeze events (2002–2003, 2003–2004) were also included in the evaluation set. For genotypes with a limited number of years of available data, these rules were modified to include a subset of the above (Table 1). Both DTA and phenology observations were included, when feasible, in both the optimization and the evaluation data sets. Some genotypes were parameterized and the model fit evaluated internally (i.e., using the optimization data set), but due to limited data availability could not be given the more rigorous external (i.e., using the evaluation data set) evaluation.

Table 3 Initial cold hardiness ($H_{c,initial}$) estimated by linear regression analysis relative to *V. vinifera* cv. Cabernet Sauvignon. Cabernet Sauvignon $H_{c,initial}$ was calculated as the average from the earliest available data in late summer.

Genotype[a]	*n*	Intercept	Slope	r^2 [b]	$H_{c,initial}$ (°C)
Barbera	6	-0.49	0.94	0.94	-10.10
Cabernet franc	12	0.79	1.04	0.95	-9.91
Cabernet Sauvignon	179, 6[c]	0.00	1.00	1.00	-10.27
Chardonnay	136	-2.65	0.89	0.94	-11.81
Chenin blanc	22	-2.62	0.92	0.93	-12.07
Concord	53	-1.43	1.11	0.91	-12.84
Dolcetto	6	-1.11	0.87	0.98	-10.06
Gewürztraminer	13	-2.42	0.89	0.94	-11.59
Grenache	8	-0.27	0.95	0.96	-10.00
Lemberger	12	-4.37	0.84	0.95	-12.98
Malbec	17	-1.76	0.95	0.97	-11.51
Merlot	122	-0.66	0.94	0.92	-10.31
Mourvèdre	11	-0.77	0.85	0.88	-9.53
Nebbiolo	6	-1.25	0.96	0.97	-11.11
Pinot gris	18	-3.37	0.84	0.86	-12.04
Riesling	129	-3.22	0.91	0.91	-12.55
Sangiovese	11	-2.36	0.81	0.98	-10.67
Sauvignon blanc	4	-2.14	0.82	1.00	-10.59
Sémillon	11	-2.46	0.78	0.88	-10.43
Sunbelt	22	0.37	1.18	0.95	-11.79
Syrah	45	-1.31	0.87	0.93	-10.27
Viognier	23	-1.64	0.93	0.93	-11.15
Zinfandel	8	-0.42	0.97	0.91	-10.42

[a]Concord and Sunbelt are *V. labruscana* cultivars; all other genotypes are *V. vinifera*.
[b]All correlations significant at $p < 0.001$ except for Barbera ($p = 0.0013$).
[c]179 = number of C. Sauvignon observations available for regression; 6 = number of observations used to calculate C. Sauvignon $H_{c,initial}$.

The model was optimized and evaluated in SAS. We used stepwise iterative methods as described previously (Ferguson et al. 2011) to select the combination of model parameters that gave the best fit to the measured values in the optimization data set. A total of 1,653,750 parameter combinations, taken from an eight-dimensional hyperspace, were tested by stepwise selection for each genotype (Supplemental Table 2). This method identified the set of parameters that minimized the root mean square error (*RMSE*) between predicted and observed H_c as suggested by Willmott (1982). The internal validity (Caffarra and Eccel 2010) was tested by Pearson correlation analysis (SAS, proc. Reg) of predicted versus observed H_c and by calculation of the *RMSE*, using the optimization data set (see Table 1). The optimized parameters were then used to evaluate the performance of the individual genotype model variants externally, using the evaluation data set. Tests for external model evaluation included correlation analysis as well as calculation of the *RMSE*. Model accuracy was tested by calculating the mean error, or bias (*B*), of predicted versus observed H_c. Associations between pairs of optimized model parameters were explored using correlation analysis. In addition, effects of genotype origin on model parameters were tested using one-way ANOVA and correlation analysis.

Model use to predict budbreak. As described above, H_c was inferred from observed spring phenology to extend the temporal scope of our data set beyond budbreak. This novel approach allowed us to also explore the H_c model for its potential use as a budbreak model. For this purpose budbreak was defined as the stage at which 50% of the bud population in the observation vineyards showed green tips. When H_c approaches temperatures only slightly below 0°C, deacclimation becomes irreversible and budbreak is imminent (Fennell 2004, Kalberer et al. 2006). To test the present model's ability to predict budbreak, we assumed that the predicted budbreak date corresponded to the DOY for which the model first predicted $H_c \geq -2.2°C$ for *V. vinifera* cultivars and $H_c \geq -6.4°C$ for *V. labruscana* cultivars (Table 2). The *RMSE* and

B were calculated, and correlation analysis (SAS, proc. Reg) was conducted to compare predicted versus observed DOYs of budbreak, using the phenology data in Table 1.

Results

The optimized model parameters revealed considerable phenotypic variation among the 23 *Vitis* spp. genotypes evaluated in this study. The genotypes differed in their $H_{c,initial}$ in early fall and $H_{c,max}$ in midwinter, T_{th} during eco- and endodormancy, acclimation and deacclimation rates (k_a and k_d), and EDB (Table 4), as well as in spring phenology (Table 5). For example, while their $H_{c,initial}$, k_a, and k_d varied, the two *V. labruscana* cultivars had significantly lower θ and better $H_{c,max}$ ($p < 0.001$) than the *V. vinifera* cultivars (Table 4). However, the greater midwinter hardiness of *V. labruscana* was coupled with an earlier budbreak than in most *V. vinifera* cultivars (Table 5). These data also confirmed the reputation of Riesling as one of the hardiest *V. vinifera* cultivars, whereas Mourvèdre was the least hardy genotype in our study. Across all genotypes, the estimated $H_{c,initial}$ varied from -9.5°C in Mourvèdre to -13.0°C in Lemberger, whereas $H_{c,max}$ varied from -21.9°C in Sangiovese to -29.5°C in Concord (Table 4). One-way ANOVA showed a significant effect of geographic origin on $H_{c,initial}$ ($p < 0.001$), $H_{c,max}$ ($p < 0.001$), θ ($p = 0.038$), and budbreak DOY ($p = 0.005$). Correlation analysis confirmed these results; origin group number was negatively correlated with $H_{c,initial}$, $H_{c,max}$, and budbreak DOY (Figure 1), indicating a north/inland-south/coastal gradient for genotype origin of decreasing hardiness and later budbreak.

Across the 23 genotypes $H_{c,initial}$ was positively correlated with $H_{c,max}$ (Figure 2A). The $T_{th,endo}$ correlated positively with $k_{d,endo}$ ($r = 0.56$, $p = 0.006$) and negatively with $k_{a,endo}$ ($r = -0.90$, $p < 0.001$), while $T_{th,eco}$ correlated positively with $k_{d,eco}$ ($r = 0.81$, $p < 0.001$). Budbreak DOY was positively correlated with $H_{c,initial}$ (Figure 2B) and $H_{c,max}$ (Figure 2C), which indicates that hardier genotypes tend to begin spring growth earlier than less hardy genotypes when grown in the same environment. Omitting the two *V. labruscana* cultivars from the correlation analysis did not change the nature or significance of these associations. Multiple regression analysis showed that the genotype-specific H_c model parameters (Table 4) accounted for 87% ($p = 0.002$) of the variation in budbreak DOY (Table 5) among genotypes; $H_{c,initial}$, θ, EDB, $T_{th,eco}$, and $k_{d,eco}$ together accounted for 81% ($p < 0.001$) of this variation.

The model reliably predicted the typical course of cold acclimation of primary buds of different grapevine cultivars in fall, their midwinter hardiness, and the overall deacclimation pattern in spring (Figure 3). Integrating spring phenology to extend the H_c data set markedly improved the model fit during the irreversible deacclimation phase leading up to budbreak (Figure 4) compared with the earlier model (Ferguson et al.

Table 4 Model parameters used to simulate primary bud cold hardiness (H_c) of 21 *V. vinifera* cultivars and two *V. labruscana* cultivars. Parameters were optimized in a stepwise process to minimize the *RMSE* between observed and predicted H_c from the optimization data set. (Abbreviations listed in Supplemental Table 1.)

Genotype[a]	$T_{th,endo}$ (°C)	$T_{th,eco}$ (°C)	$k_{a,endo}$	$k_{d,endo}$	$k_{a,eco}$	$k_{d,eco}$	$H_{c,initial}$ (°C)	$H_{c,max}$ (°C)	$H_{c,min}$ (°C)	θ	EDB (°C)	n	r^2 [b]	*RMSE*
Barbera	15.0	3.0	0.06	0.10	0.02	0.08	-10.1	-23.5	-1.2	7	-700	67	0.98	1.4
Cabernet franc	13.0	4.0	0.12	0.04	0.10	0.10	-9.9	-25.4	-1.2	7	-500	30	0.97	1.3
Cabernet Sauvignon	13.0	5.0	0.12	0.08	0.10	0.10	-10.3	-25.1	-1.2	7	-700	510	0.96	1.5
Chardonnay	14.0	3.0	0.10	0.10	0.02	0.08	-11.8	-25.7	-1.2	7	-600	421	0.97	1.4
Chenin blanc	14.0	4.0	0.10	0.04	0.02	0.10	-12.1	-24.1	-1.2	7	-700	75	0.99	1.1
Concord	13.0	3.0	0.12	0.02	0.10	0.10	-12.8	-29.5	-2.5	3	-600	196	0.97	1.7
Dolcetto	12.0	4.0	0.16	0.10	0.10	0.12	-10.1	-23.2	-1.2	3	-600	44	0.99	0.8
Gewürztraminer	13.0	6.0	0.12	0.06	0.02	0.18	-11.6	-24.9	-1.2	5	-400	50	0.97	1.7
Grenache	12.0	3.0	0.16	0.02	0.10	0.06	-10.0	-22.7	-1.2	5	-500	37	0.98	1.3
Lemberger	13.0	5.0	0.10	0.02	0.10	0.18	-13.0	-25.6	-1.2	7	-800	40	0.98	1.5
Malbec	14.0	4.0	0.10	0.06	0.08	0.08	-11.5	-25.1	-1.2	7	-400	68	0.96	1.9
Merlot	13.0	5.0	0.10	0.04	0.02	0.10	-10.3	-25.0	-1.2	7	-500	372	0.96	1.6
Mourvèdre	13.0	6.0	0.12	0.08	0.06	0.14	-9.5	-22.1	-1.2	5	-600	45	0.97	1.4
Nebbiolo	11.0	3.0	0.16	0.02	0.02	0.10	-11.1	-24.4	-1.2	3	-700	62	0.98	1.3
Pinot gris	13.0	6.0	0.12	0.02	0.02	0.20	-12.0	-24.1	-1.2	3	-400	77	0.97	1.6
Riesling	12.0	5.0	0.14	0.02	0.10	0.12	-12.6	-26.1	-1.2	7	-700	373	0.97	1.6
Sangiovese	11.0	3.0	0.14	0.02	0.02	0.06	-10.7	-21.9	-1.2	7	-700	62	0.95	1.7
Sauvignon blanc	14.0	5.0	0.08	0.06	0.10	0.12	-10.6	-24.9	-1.2	7	-300	93	0.98	1.4
Sémillon	13.0	7.0	0.10	0.08	0.02	0.20	-10.4	-22.4	-1.2	5	-300	43	0.98	1.3
Sunbelt	14.0	3.0	0.10	0.06	0.10	0.12	-11.8	-29.1	-2.5	1.5	-400	42	0.96	1.8
Syrah	14.0	4.0	0.08	0.06	0.04	0.08	-10.3	-24.2	-1.2	7	-700	141	0.95	1.5
Viognier	14.0	5.0	0.10	0.08	0.10	0.10	-11.2	-24.0	-1.2	7	-300	93	0.91	1.6
Zinfandel	12.0	3.0	0.16	0.02	0.10	0.06	-10.4	-24.4	-1.2	7	-500	40	0.99	1.1
Combined												2981	0.97	1.5

[a]Concord and Sunbelt are *V. labruscana* cultivars; all other genotypes are *V. vinifera*.
[b]All correlations between observed and predicted H_c significant at $p < 0.001$.

2011). Across the 23 genotypes, the optimized model parameters predicted the measured LT_{50} values within the optimization data set with an overall $r^2 = 0.97$ and $RMSE = 1.5$°C. This internal validity test showed that $r^2 \geq 0.91$ for all genotypes, while *RMSE* varied from 0.8°C for Dolcetto to 1.9°C for Malbec (Table 4). The external model evaluation, using the evaluation data set, showed that the error was somewhat higher than that found for the optimization data set, both for the overall *RMSE* (2.0°C; Supplemental Table 3) and for the individual genotypes (Figure 5). In this analysis, the lowest *RMSE* was found for Mourvèdre (1.2°C) and the highest for Concord (2.6°C). Correlation analysis demonstrated that the variation in predicted H_c accounted for 89% (Syrah) to 99% (Cabernet franc) of the variation in observed H_c in the independent evaluation data set (Figure 5). Overall model accuracy was high ($B = 0.2$°C); among the 16 genotypes for which at least one year of data were available to conduct an external evaluation, *B* varied from -0.5°C (Syrah and Sunbelt) to 1.0°C (Cabernet Sauvignon) (Supplemental Table 3). Despite this bias, the model accurately predicted Cabernet Sauvignon buds to be sufficiently acclimated to withstand the unseasonable freeze event (-17.3°C) that occurred at this location in late November 2010 (Figure 6). Although sampling of Cabernet Sauvignon buds for DTA ceased in early February 2011 because these vines were pruned, Figure 6 also illustrates the model's ability to simulate the differences in spring deacclimation between a genotype with early budbreak (Chardonnay) and one with late budbreak (Cabernet Sauvignon; Table 5).

The November 2010 cold event resulted in varying degrees of bud injury in vineyards across Washington's south-central region. Variation in H_c among genotypes (Table 4) was clearly an influencing factor, as some *V. vinifera* cultivars sustained severe damage, while others escaped with minimal or no damage in the same vineyard location. The model effectively captured these differences, predicting damage for some but not other cultivars at many locations. Site location also had an influence on the extent of damage within a cultivar; differences in bud injury due to this cold event occurred between vineyards planted to the same cultivar. This disparity could have been caused either by variation in H_c or by variation in T_{min} between these locations. Thus, we compared two contrasting *V. vinifera* cv. Merlot vineyards, one near Alderdale, WA, with almost 100% of the primary buds killed, and another near Paterson, WA, with no reported bud damage. Running the model using temperature data from AgWeatherNet stations (Alderdale: lat. 45.9°N; long. 119.9°W; 187 m asl; Paterson: lat. 45.9°N; long. 119.5°W; 129 m asl) located near each vineyard demonstrated that cold acclimation of Merlot buds was similar at the two locations, leading to a predicted H_c of -19.9°C in Alderdale and -19.8°C in Paterson (Figure 7). The main difference, however, was related to the T_{min} experienced during the freeze event: $T_{min} = -21.1$°C in Alderdale,

Table 5 Model evaluation statistics for the comparison of observed with predicted budbreak dates from the evaluation data set when the cold hardiness model is repurposed to model day of budbreak (DOY 1 = 1 January; note that the model uses DOY 366 = 1 January).

	Mean budbreak DOY (± SE)				Budbreak model evaluation				
Genotype[a]	***n***	**Observed**	**Predicted**	***RMSE***[b]	***n***	***r*²**	***p***	***RMSE***[c]	***B***
Barbera	5	113 ± 1.7	111 ± 4.7	8.4	0	na	na	na	na
Cabernet franc	16	109 ± 2.2	108 ± 1.9	2.0	15	0.30	0.034	8.0	-1.5
Cabernet Sauvignon	19	117 ± 1.1	118 ± 1.6	6.5	3	0.96	0.135	3.9	-3.7
Chardonnay	18	109 ± 1.3	108 ± 1.7	5.7	6	0.37	0.197	8.7	-3.3
Chenin blanc	17	108 ± 1.3	107 ± 1.8	4.8	12	0.36	0.041	5.4	-1.0
Concord	16	106 ± 1.3	103 ± 2.1	7.4	3	0.69	0.378	9.3	-8.3
Dolcetto	5	116 ± 2.6	117 ± 3.8	4.2	0	na	na	na	na
Gewürztraminer	16	110 ± 1.7	106 ± 2.2	8.7	12	0.29	0.070	8.3	-3.3
Grenache	13	117 ± 1.4	119 ± 2.1	7.0	10	0.41	0.047	7.1	3.1
Lemberger	13	107 ± 1.7	103 ± 2.0	4.2	10	0.49	0.025	7.0	-4.6
Malbec	13	110 ± 1.9	115 ± 2.3	8.3	9	0.65	0.009	6.6	4.2
Merlot	17	117 ± 1.3	115 ± 1.8	5.6	5	0.27	0.372	8.3	-6.6
Mourvèdre	5	122 ± 2.8	122 ± 4.1	6.2	2	1.00	na	5.0	3.0
Nebbiolo	4	113 ± 2.6	121 ± 3.0	9.0	0	na	na	na	na
Pinot gris	15	114 ± 1.8	109 ± 2.1	7.4	10	0.36	0.065	10.1	-7.3
Riesling	19	112 ± 1.1	113 ± 1.4	4.3	3	1.00	0.028	1.9	-1.7
Sangiovese	4	114 ± 1.8	125 ± 3.0	12.0	1	na	na	13.0	13.0
Sauvignon blanc	17	110 ± 1.4	108 ± 2.0	9.3	14	0.46	0.008	6.0	-1.3
Sémillon	18	112 ± 1.4	108 ± 1.9	7.5	15	0.52	0.003	6.1	-2.6
Sunbelt	15	106 ± 1.2	105 ± 2.2	5.9	10	0.49	0.024	7.1	-1.2
Syrah	6	117 ± 2.0	119 ± 3.6	8.8	1	na	na	0.0	0.0
Viognier	1	109	112	3.0	0	na	na	na	na
Zinfandel	14	114 ± 1.9	119 ± 2.0	5.5	11	0.53	0.011	7.6	5.2
Combined	286	112 ± 0.4	111 ± 0.6	6.7	152	0.45	<0.001	7.3	-1.0

[a]Concord and Sunbelt are *V. labruscana* cultivars; all other genotypes are *V. vinifera*.
[b]Optimization data set.
[c]Evaluation data set.

whereas T_{min} = -14.0°C in Paterson where free air drainage prevented cold air pooling. Absolute damage levels were not quantified in this study, but were estimated by observations reported by growers of the percentage budbreak in spring and the extent of retraining and replanting in the subsequent 2011 growing season.

The model not only identified a loss in H_c due to unseasonably warm temperatures, but also was sensitive enough to simulate slightly different H_c values for relatively minor differences in average temperatures over longer periods (Figure 7). For instance, the sudden increase of T_{mean} up to 11.9°C in Alderdale and 10.6°C in Paterson during four days in mid-January was associated with an almost immediate deacclimation response in both locations. Moreover, the average T_{mean} was 0.3°C higher in Alderdale than in Paterson between mid-January and early March, whereas T_{mean} was 0.3°C lower in Alderdale than in Paterson from early March through April. These small differences were sufficient to reverse the relative level of predicted H_c between the two locations over these two periods.

Because the model was designed to predict H_c at budbreak, we tested its ability to be used as a budbreak model. There was significant variation among genotypes in the time of observed and predicted budbreak (Table 5). The average observed difference between the earliest genotypes (Concord and Sunbelt) and the latest genotype (Mourvèdre) was 16 days, and the model predicted this difference at 19 days.

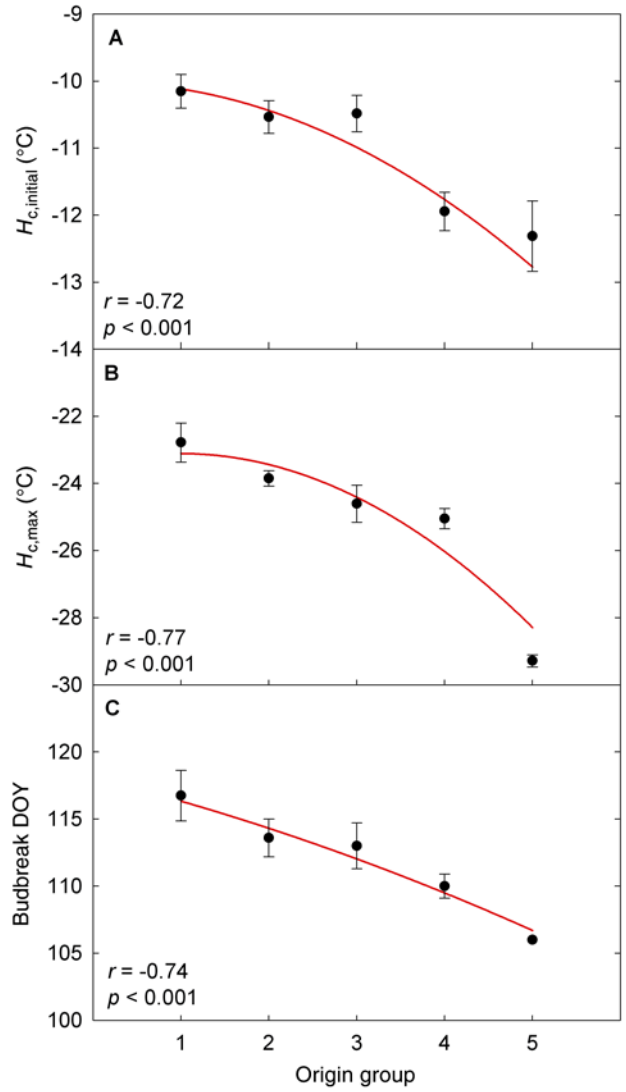

Figure 1 Association between grapevine genotype origin and initial bud hardiness ($H_{c,initial}$) in early fall (**A**), maximum bud hardiness ($H_{c,max}$) in midwinter (**B**), and date of budbreak in spring (**C**). Origin groups: 1, coastal southern Europe; 2, inland southern Europe; 3, coastal northern Europe; 4, inland northern Europe; 5, northeastern North America. Values are means ± SE, but *r* was calculated from raw data rather than means (all $p < 0.001$).

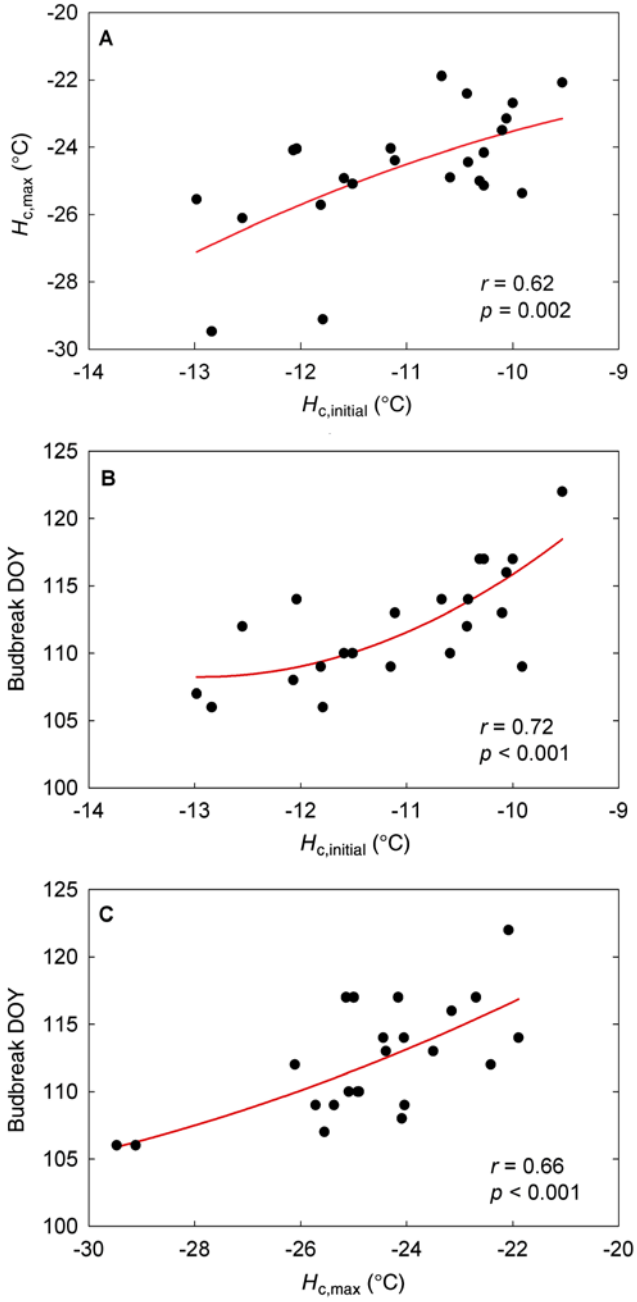

Figure 2 Association between genotype-specific model parameters, with grapevine genotypes represented by individual symbols: initial bud hardiness ($H_{c,initial}$) in early fall and maximum bud hardiness ($H_{c,max}$) in midwinter (**A**), $H_{c,initial}$ and date of budbreak (**B**), and $H_{c,max}$ and date of budbreak (**C**).

Phenology was not assessed for all genotypes in all years; consequently the absolute ranking shown in Table 5 is only approximate. Within the optimization data set, the overall *RMSE* for the comparison between the observed budbreak DOYs and those predicted by the H_c model was 6.7 days. The *RMSE* for individual genotypes ranged from 2.0 days (Cabernet franc) to 12.0 days (Sangiovese). Using the values from the evaluation data set, the overall *RMSE* was 7.3 days, and the *RMSE* for different genotypes varied from 0 days for Syrah to 13.0 days for Sangiovese. The external test for model accuracy found B = -1.0 day across all genotypes, but B varied from -8.3 days (Concord) to 13.0 days (Sangiovese). Across all genotypes, the model explained 45% of the variation in budbreak DOY, and significant correlations between observed and predicted budbreak DOY were found for about half of all genotypes tested (Table 5).

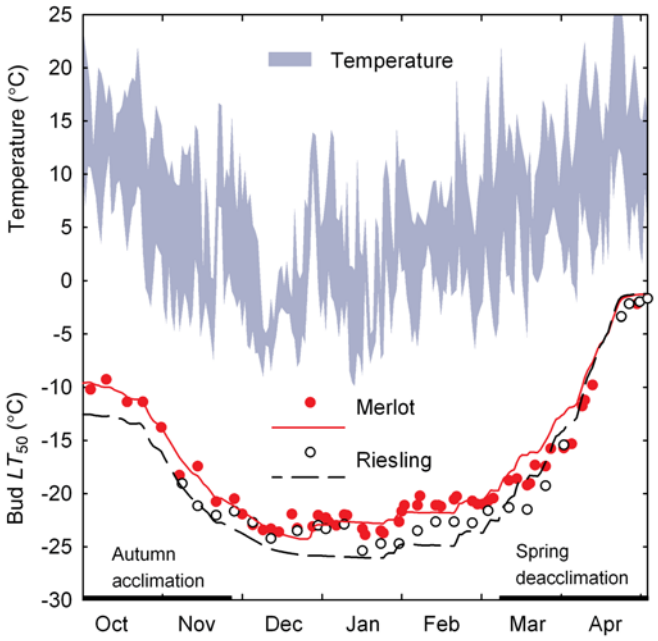

Figure 3 Daily maximum and minimum temperatures and predicted (lines) and observed (symbols) bud hardiness (LT_{50}) of *V. vinifera* cvs. Merlot and Riesling during the 2011–2012 dormant season.

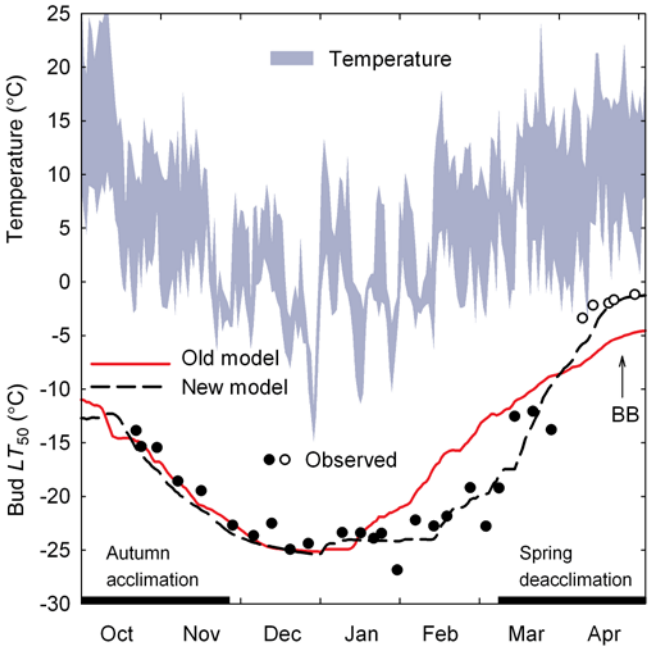

Figure 4 Comparison of the new cold hardiness model with integrated spring phenology with the old model (Ferguson et al. 2011). Daily maximum and minimum temperatures, and predicted (lines) and observed (symbols) cold hardiness (LT_{50}) of *V. vinifera* cv. Chardonnay primary buds during the 1996–1997 dormant season. Closed symbols represent DTA-derived data, open symbols represent phenology-derived data, BB indicates time of budbreak.

Discussion

Our long-term (≤24 years) data sets of both seasonal H_c measurements and spring phenology observations on field-grown grapevines enabled us to develop and evaluate discrete-dynamic model variants for primary bud hardiness of 23 genotypes, derived from two *Vitis* species, for the entire dormant season and extending through to budbreak. The integration of spring phenology and addition of the theta-logistic markedly improved model performance during the increasingly irreversible deacclimation phase leading up to budbreak compared with the published H_c model (Ferguson et al. 2011). Testing the performance of this comprehensive model under the actual situation of an unseasonable freeze event that occurred in November 2010 clearly demonstrated its robustness and sensitivity. Not only was the model able to differentiate genotypes that sustained bud injury from genotypes that were less susceptible, but it also predicted differences in damage levels between vineyard sites that were confirmed by observed differences in subsequent budbreak.

The stepwise optimization procedure, using more than 1.6 million iterations, for the model parameters uncovered considerable differences among genotypes and thus provided unique insights into their phenotypic behavior with respect to H_c during fall acclimation and spring deacclimation, as well as in midwinter. In the context of global climate change, the variation in k_a and k_d among genotypes is of particular interest. Variation in the propensity to deacclimate under unseasonably warm temperatures and in the ability to reacclimate when temperatures decline again determines bud survival for a given genotype as much as does its $H_{c,max}$ in midwinter. Differences in H_c dynamics among plant genotypes (both among species and among ecotypes or cultivars) may be explained by the evolution of acclimation and deacclimation responses that ensure survival of plants adapted to a particular geographic region (and hence climate) without limiting their competitiveness (Browse and Xin 2001). Thus, the better $H_{c,max}$ of the two *V. labruscana* cultivars compared with *V. vinifera* could be expected given the northeastern United States origin of the *V. labrusca* L. ancestors of the former (Keller 2010). Indeed, our results demonstrated that these genotypes fell in line with but extended the H_c gradient found for *V. vinifera* cultivars, which correlated with their presumed geographic origin.

The optimized model parameters showed that the cultivars originating from north-central Europe tended to start with a lower (more negative) $H_{c,initial}$ and to achieve better $H_{c,max}$, but they also had a tendency toward earlier budbreak than

their coastal or southern European counterparts. Riesling, of continental German provenance, was the hardiest *V. vinifera* cultivar in our study, whereas Mourvèdre (syn. Monastrell), originating from Mediterranean Spain, was the least hardy genotype. This finding agrees well with the idea that many *V. vinifera* cultivars may have been selected in their local environment before they were vegetatively propagated and that many of these local cultivars are genetically related to one another (Levadoux 1956, Myles et al. 2011).

Although bud temperature is the main determinant of the time of budbreak for a particular genotype (Keller and Tarara 2010), differences in budbreak timing among *Vitis* genotypes are well known (Kovács et al. 2003, García de Cortázar-Atauri et al. 2009, Nendel 2010). However, it is not immediately intuitive that winter-hardy genotypes should begin to grow before the less hardy genotypes when grown in the same location. One possible explanation is that there may have been little selection pressure for plants adapted to cold winter temperatures to maintain hardiness once spring approaches (Pagter and Arora 2013). Because environments with cold winters also typically have short growing seasons, the ability to begin spring growth rapidly under favorable and low-risk conditions presumably enables such genotypes to maximize seasonal resource acquisition and hence seed maturation. Given that the chilling requirement is often measured as the period of low temperature that is necessary to permit 100% of the buds to break (Cooke et al. 2012), genotypes that require less chilling to release dormancy may deacclimate earlier than, and therefore break bud before, genotypes that require more chilling. This idea is supported by the results

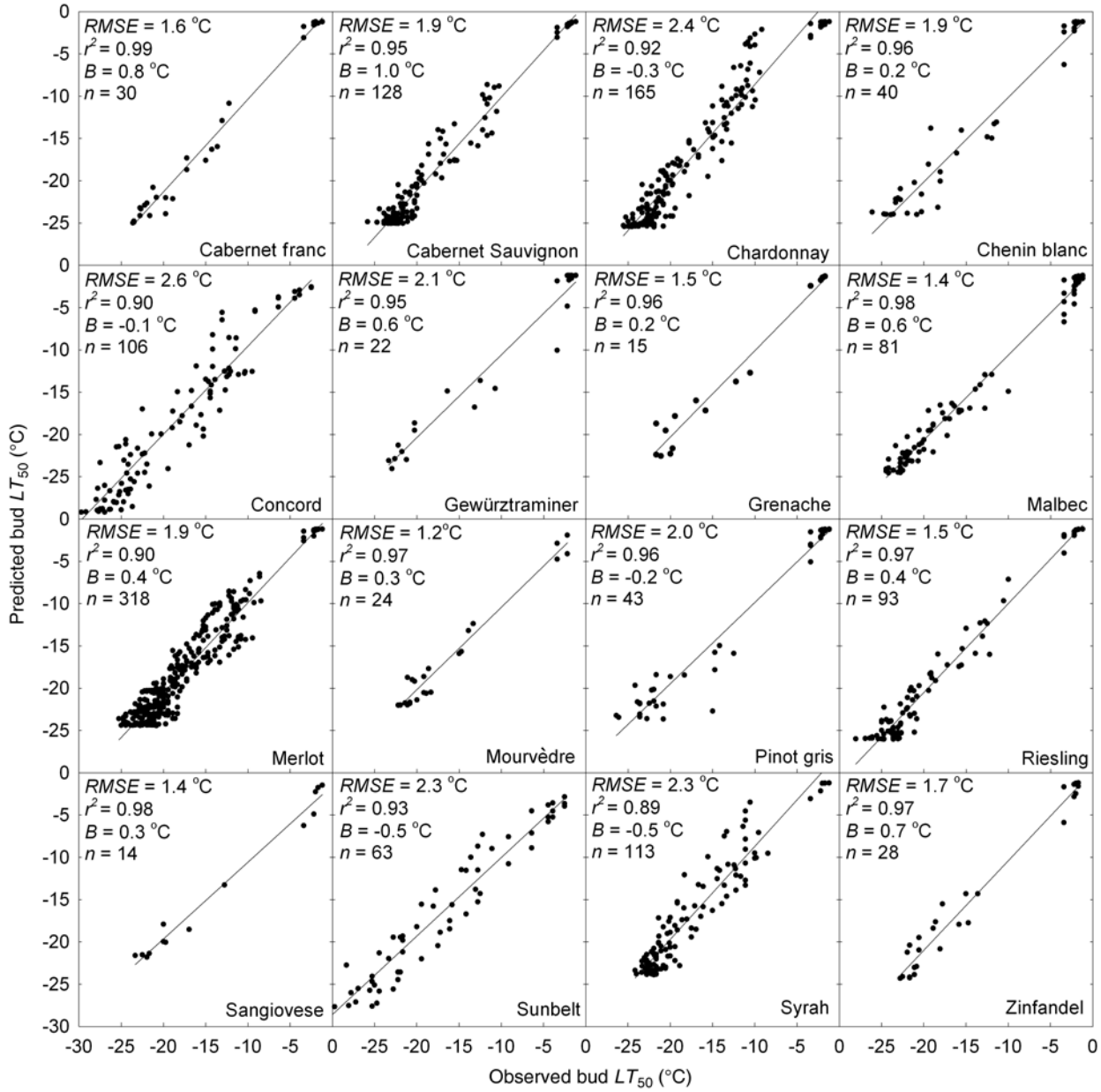

Figure 5 Comparison between observed bud hardiness (LT_{50}) and that predicted by genotype-specific model variants for the 16 grapevine genotypes for which an evaluation data set was available. Concord and Sunbelt are *V. labruscana* cultivars, all other genotypes are *V. vinifera*.

from multiple regression analysis in our study, which showed that $H_{c,initial}$, EDB, θ, $T_{th,eco}$, and $k_{d,eco}$ together explained >80% of the variation in date of budbreak among genotypes. Thus, genotypes originating from regions with cold winters will tend to begin spring growth earlier than genotypes from regions with mild winters when these genotypes are grown in the same environment, paradoxically making the former more vulnerable to spring frost in warmer environments (Kovács et al. 2003). These results suggest that the traits that determine H_c, dormancy, and budbreak timing may be at least partly linked, which has implications for breeding and for crop performance in a changing climate.

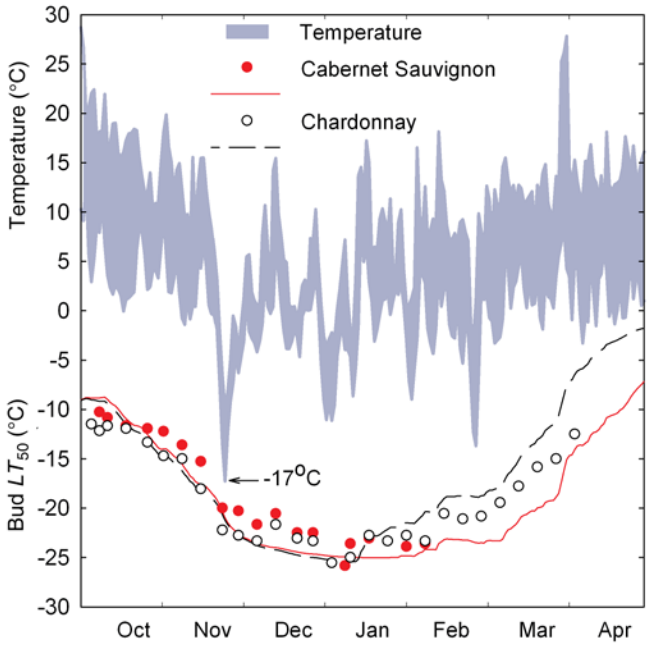

Figure 6 Daily maximum and minimum temperatures and predicted (lines) and observed (symbols) bud hardiness (LT_{50}) of *V. vinifera* cvs. Cabernet Sauvignon and Chardonnay during the 2010–2011 dormant season.

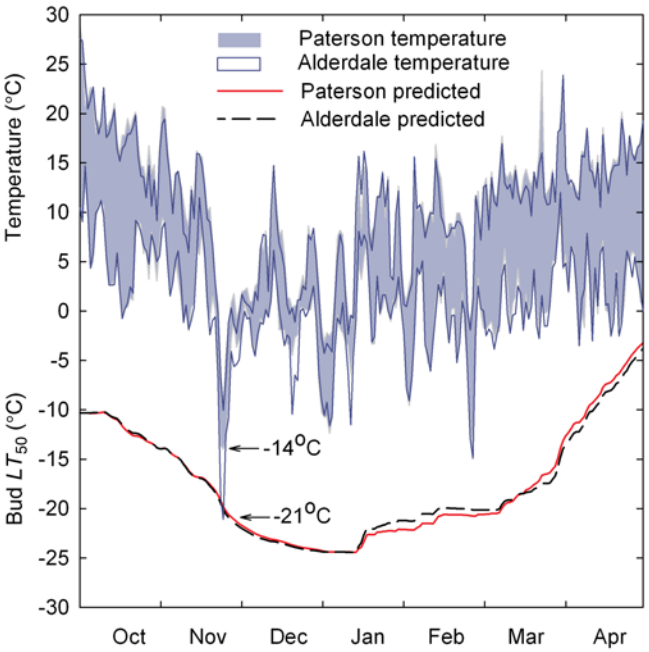

Figure 7 Daily maximum and minimum temperatures and predicted (lines) bud hardiness (LT_{50}) of *V. vinifera* cv. Merlot at two vineyard locations (Alderdale and Paterson, WA) during the 2010–2011 dormant season. In the absence of observed LT_{50} values, the model correctly predicted bud damage in Alderdale (T_{min} = -21.1°C) and no damage in Paterson (T_{min} = -14.0°C) during the same freeze event in November 2010.

The ability of our model to predict budbreak seems relatively poor, partly because the model was primarily optimized to simulate H_c. Optimization aimed to minimize the error over the entire dormant season, not specifically the error at budbreak as would be typical for budbreak models. Nevertheless, the overall *RMSE* (7 days) for observed versus predicted budbreak DOY compares favorably with the range of *RMSEs* (8 to 21 days) found in a recent comparison of existing budbreak models for 10 *V. vinifera* cultivars (García de Cortázar-Atauri et al. 2009). Similarly, a budbreak model for two *V. vinifera* cultivars that used multiyear data from 13 sites across northern Europe found a standard error of 4.5 days (Nendel 2010). The time of budbreak can also be impacted by viticulture practices and site factors (Williams et al. 1985, Friend and Trought 2007), as well as soil water content (M. Keller, unpublished data, 2013). Cultural practices were consistent between genotypes and years in the present study, but soil water content may have varied owing to low winter precipitation in this region (Davenport et al. 2008).

Our previous model (Ferguson et al. 2011) used a common, genotype-specific T_{th} for calculating both changes in H_c and chilling requirements to release dormancy. Although this approach may seem reasonable from a biological perspective, it made comparisons with other published chilling requirements problematic, since no other studies have used genotype-specific T_{th} for chilling calculations. Research on chilling requirements for grapevines has focused on summation at set temperatures common to all genotypes investigated (García de Cortázar-Atauri et al. 2009, Nendel 2010) and has not been complex enough to infer genotype-specific chilling temperature thresholds. Therefore, although in reality $T_{th,c}$ may be unique for each genotype, the current model uses a fixed $T_{th,c}$ = 10°C to calculate chilling for all genotypes while retaining the genotype-specific $T_{th,endo}$ and $T_{th,eco}$ to calculate changes in H_c. In other words, the model forces all genotypes to accumulate chilling degree days below 10°C while permitting each genotype to have its own temperature threshold that divides acclimation from deacclimation temperatures. The latter, moreover, is different before ($T_{th,endo}$) and after ($T_{th,eco}$) the EDB, that is, before and after dormancy has been released.

The present model was developed with temperature and LT_{50} data from only two locations. One might argue that the long-term nature of the optimization data set for some genotypes (up to 19 years) and the inherent variation in temperature patterns among these years should result in optimized parameters that permit application of the H_c model, as well as of its implications with respect to climate variability, to other, disparate regions. However, because this model was developed for a climate in which chilling requirements for grapevines are generally met, the purely mathematical parameterization may inadvertently overestimate actual chilling requirements.

Running the model in a region with considerably warmer winters might lead to the prediction of very slow deacclimation in spring, because the model would incorrectly estimate that the chilling requirement is not met and hence that buds remain endodormant. Such a scenario would overestimate H_c during the period leading up to budbreak in a warm climate or during an unusually warm winter. While this issue could be solved by reparameterizing the model using data from climates with mild winters, H_c data from such regions are not currently available because research in those regions has traditionally focused on chilling requirements (e.g., Dokoozlian 1999) rather than H_c. Nonetheless, our study demonstrates that the introduction of spring phenology data to infer H_c greatly alleviates this shortcoming.

Conclusion

A robust, quantitative model that simulates daily changes in primary bud H_c during endo- and ecodormancy and during budbreak for 23 diverse *Vitis* genotypes was developed. The model also predicts time of budbreak for these genotypes. A Microsoft Excel version of this model can be accessed through http://wine.wsu.edu/research-extension/weather/cold-hardiness. The only input data required to run the model is mean daily temperature, which is easily recorded by affordable weather stations and should make this model easy to use and widely accessible. The model should be useful in climate change modeling to predict cold acclimation and deacclimation responses of different genotypes under variable climate change scenarios. It may also be used as a risk-management tool for site selection in regions with unknown grapegrowing potential and for vineyard management in regions where cold damage is common. We are currently implementing the H_c model on AgWeatherNet (weather.wsu.edu). Using temperature data from each of the network's over 140 automated weather stations, the model automatically provides local and daily simulated H_c values for the grape cultivars reported in this study. Coupled with a weather forecasting service, the model may be used as an early warning system for impending and potentially damaging cold-temperature events. Supplemented with additional, static information on how to respond to cold damage, this forms a decision support system for risk assessment and damage mitigation in grapes.

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