Title: Yield potential definition of the chilling requirement reveals likely underestimation of

the risk of climate change on winter chill accumulation

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Type of paper: Original research paper

Abstract

Evaluation of chilling requirements of cultivars of temperate fruit trees provides key

information to assess regional suitability, according to winter chill, for both industry expansion

and ongoing profitability as climate change progresses. Traditional methods for calculating

chilling requirements use climate controlled chambers and define chilling requirements using a

fixed bud burst percentage, usually close to 50% (CR-50%). However, this CR-50% definition

may estimate chilling requirements that lead to flowering percentages that are lower than

required for orchards to be commercially viable. We used sweet cherry to analyse the traditional

method for calculating chilling requirements (CR-50%) and compared the results with a more

restrictive method, where the chilling requirement was defined by a 90% bud break level (CR_m-

90%). For sweet cherry, this higher requirement of flowering success (90% as opposed to 50%) better represents grower production needs as a greater number of flowers lead to greater potential yield. To investigate the future risk of insufficient chill based on alternate calculations of the chilling requirement, climate projections of winter chill suitability across Europe were calculated using CR-50% and CR_m-90%. Regional suitability across the landscape was highly dependent on the method used to define chilling requirements and differences were found for both cold and mild winter areas. Our results suggest that bud break percentage levels used in the assessment of chilling requirements for sweet cherry influence production risks of current and future production areas. The use of traditional methods to determine chilling requirements can result in an underestimation of productivity chilling requirements for tree crops like sweet cherry which rely on a high conversion of flowers to mature fruit to obtain profitable yields. This underestimation may have negative consequences for the fruit industry as climate change advances with climate risk underestimated.

Keywords: *Prunus avium*, sweet cherry, flowering, temperature, phenology, projections

Introduction

Temperate deciduous fruit trees represent an important economic and food resource. Maintaining and expanding temperate fruit production is an industry priority and is likely to become more challenging under anthropogenic climate change. One aspect of tree physiology which will likely be influenced by climate change is sufficient accumulation of winter chilling (Luedeling et al. 2011). In temperate fruit trees, the timing of bud break and flowering is highly correlated with a proper release of endodormancy, or rest, which is controlled by the exposure to cold temperatures in winter (Saure 1985). During this rest period a certain exposure to cold temperatures, defined as the chilling requirement, must be satisfied prior to the bud being released from endodormancy (Lang et al. 1987). This period of rest prevents bud break in response to conditions suitable for growth conditions, such as a warm spell in winter, which would then expose sensitive tissues to subsequent damaging cold conditions. The consequences of insufficient chill accumulation have been extensively studied and include delayed, light, irregular and prolonged bud break and flowering (Samish 1953; Erez and Couvillon 1987; Erez 2000) as well as damage to bud development including deformed buds (Petri and Leite 2004; Viti et al. 2008). Within the context of climate change, these sub-optimal production outcomes may increase in frequency (Guy 2014). To predict such potential impacts to assist with orchard climate adaptation and guide breeding strategies, evaluation of cultivar specific chilling requirements (CR) is needed (Dennis 2003; Campoy et al. 2011; Chuine et al. 2016).

Precise determination of the CR is not possible under field conditions. As such, various experimental methods have been used to evaluate dormancy depth (Cook et al. 2017; Vitra et al. 2017), date of dormancy release (Dennis 2003; Dantec et al. 2014; Castède et al. 2014; Chmielewski and Götz 2016) and to assess the relationship between bud break and chilling and forcing temperatures (Harrington et al. 2010; Luedeling and Gassner 2012; Andreini et al. 2014; Laube et al. 2014). Forcing experiments using controlled climate chambers have been

commonly used to assess bud dormancy progression since the method was first proposed for the evaluation of CR in peach (Bennet 1949; Weinberger 1950) . This approach involves sampling tree cuttings through autumn and winter and evaluating bud break after they have been exposed to warm temperatures in a controlled climate chamber (Tabuenca 1967; Dennis 2003; Vitasse and Basler 2014). In implementing this methodology two main criteria have been used to determine CR: 1) percentage of floral or vegetative bud break within a given period of time in the chamber (e.g. 50% break after 10 days) and 2) the time required in the forcing chamber to reach a given stage of development (e.g. bud break) (Saure 1985; Dennis 2003). the first approach often determines CR as the chill accumulation in the field leading to 30-50% bud break after 7 to 10 days in the forcing chamber (Hauagge and Cummins 1991; Ruiz et al. 2007; Viti et al. 2010; Campoy et al. 2012; Castède et al. 2014). This criteria varies by study with for instance, CR being determined after the emergence of only 3-4 flowers in the forcing chamber (Chmielewski and Götz 2016; Götz et al. 2017).

These criteria may not adequately represent CR that are required for profitable fruit production, in particular for crops which require high conversion of floral buds to fruit (e.g. sweet cherry). These businesses rely on high and consistent bud break rates which set a high yield potential. Poor rates of floral and vegetative bud break, that is the proportion of floral and vegetative buds that truly open, can have a major impact on temperate fruit crop productivity (Erez 2000). For small fruits, such as sweet cherry, a large number of viable flowers is required to reach commercial productivity, with a maximum bloom level ideal. Therefore, setting a CR value which only leads to 30-50% bud break may underestimate the CR needed for commercial profitability. This in turn will misjudge the potential risk of climate change on cherry production.

In this work, one of the most commonly employed methods in temperate fruit trees to estimate CR (chilling accumulation in field that leads to 50% bud break after 10 days forcing) was used

for sweet cherry and was contrasted with a modified method that sets a higher bud break

percentage to better match requirements for high yield potential (90% bud break). We used CR

determined from both methods to create climate change projections of the potential risk of

insufficient chill accumulation for sweet cherry across Europe. This work emphasises the need

to evaluate CR in terms of the minimum requirement of chill for commercial viability to best

prepare industry and breeding programs for expansion and climate change.

Materials and methods

Bud break observations

We chose four sweet cherry cultivars for analysis encapsulating a presumed range in CR based

on flowering dates (Fig. 1). The trees used for the experiments were grown following

commercial orchard management in the fruit tree experimental orchards of the Institut National

de la Recherche Agronomique (INRA)-Bordeaux research centre, located in Bourran, in Lot-

et-Garonne (France, 44°19'N 0°24'E, 70m asl) and 60 km away in Toulenne, in Gironde

(France, 44°34'N 0°16'W, 8m asl). Cultivars 'Cristobalina' and 'Regina' were grown in

Bourran, 'Fertard' in Toulenne and 'Burlat' in both sites. Dates for beginning of flowering (5-

10% open flowers, BBCH 61; Fadón et al., 2015) and maturity (BBCH 89) were recorded for

the four cultivars between 2000 and 2017 in order to define the differences among cultivars.

For the experimental data, two or three branches bearing floral buds were randomly cut from

the two trees per cultivar and placed in a climate-controlled chamber under forcing conditions

(25°C, 16h light/8h dark) each fortnight between 1st September and 8th April (2015-2016 and

2016-2017 seasons), except for 'Cristobalina' which was sampled only in the 2015-2016

season.,. Every two or three days the total number of floral buds that reached bud break (BBCH

stage 53; Fadón et al. 2015) was recorded. Bud break percentage was calculated as the

percentage of flower buds at BBCH stage 53 in relation to the total number of floral buds on

the branches.

Fig. 1 Range of flowering (white boxes) and maturity (grey boxes) dates for the four studied cultivars (2000 – 2017)

Chill requirement estimation

Chill was calculated in chill portion (CP) using the Dynamic chill model (Fishman et al. 1987),

which has previously been found to be the best fitting chill model among several tested models

for a range of fruit tree species (Alburquerque et al. 2008; Luedeling et al. 2009b, 2013a;

Campoy et al. 2011; Guo et al. 2013).

To calculate CP hourly, we collected mean temperatures from local weather stations (years

2015-2017, INRA CLIMATIK, https://intranet.inra.fr/climatik, stations 47038002 and

33533002 for Bourran and Toulenne, respectively). CP were calculated using the original model

parameters provided in the R package chillR (Luedeling et al. 2013b; Luedeling 2018). Chill

was accumulated from October 1st until the sampling date.

To assess CR, we used two methods. Firstly, we applied the commonly used approach which

defines CR as the accumulated chill in the field which leads to 50% of the buds surpassing stage

BBCH 55 after 10 days in forcing conditions (CR-50%) (Ruiz et al. 2007; Alburquerque et al.

2008; Campoy et al. 2012; Sánchez-Pérez et al. 2012; Azizi Gannouni et al. 2017). Secondly,

we used a similar approach but with a longer period in forcing conditions (2-3 weeks) and a

higher bud break percentage, 90%, required to define CR (CR_m-90%).

Future climate data

For the analyses of future climate risk, we used two gridded datasets of temperatures in Europe.

These were regionally downscaled climate datasets for historical and projected temperature

made available by EURO-CORDEX (http://www.euro-cordex.net; Jacob et al., 2014). This

dataset used the SMHI-RCA4 regional change model (50 km resolution, EUR-44) with

projection data from the climate models MOHC-HadGEM2-ES and NOAA-GFDL-GFDL-

ESM2M. Two scenarios (RCP 4.5 and RCP 8.5) were assessed for each climate model. We

corrected the differences for the temperatures between EURO-CORDEX projections and

recorded data using the European observation (E-OBS) gridded temperature dataset with 0.25°

resolution (v.14; Haylock et al., 2008). For the bias correction, we calculated the average

anomaly grid as the mean temperature difference between the E-OBS and regional climate

model datasets for 1978-2005. Gridded annual chill accumulation values were then calculated

for the datasets (E-OBS, MOHC-HadGEM2_ES and NOAA-GFDL-GFDL-ESM2M), after

adding the anomaly grid to the RCM datasets.

Hourly temperatures were generated for the three climate datasets using the R package chillR

(Luedeling 2018) which uses a sine curve and a logarithmic function for day-time and night-

time temperatures, respectively. Chill was then accumulated between October 1st and March

31st.

Safe winter chill (SWC; Luedeling et al., 2009b) was used to estimate future production risk in

Europe based on winter chilling conditions for each cultivar and for the two CR estimated using

the two methods. SWC is the amount of winter chill that can be reliably expected in 90% of all

years, or the 10th percentile of the dataset. Here this corresponds to the data within each of the

time periods analysed (1975-2005, 2026-2050, 2075-2100). This metric is meaningful to fruit

producers, because failure to meet chilling requirements in more than 10% of years is likely to

render production uneconomical (Luedeling et al. 2009a).

Fig. 2 Floral bud break percentage for the four cultivars with various field chill accumulation values (in chill portions). Note that no results for 'Cristobalina' were recorded for chill accumulation greater than 69 CP as bud burst had begun in the field.

Results

Bud break percentage based on chill accumulation

Evaluation of bud break response to accumulated chill in the field prior to cuttings revealed that

low - but not nil - bud break percentages were observed for branches that had been sampled in

the early season (mid-November; Fig. 2). These results suggest that early ('Cristobalina') and

mid-flowering ('Burlat') cultivars could slightly respond (i.e. less than 5% bud burst) to forcing

temperatures after accumulating only 13 CP. The rate of bud break percentage increased as

more chill was accumulated in the field. Using 'Burlat' as an example, bud break percentage

increase markedly faster for branches that accumulated at least 90 CP than for branches sampled

earlier during chill accumulation (e.g. 32 CP). The maximum bud break percentage, illustrated

by the plateau for each line, (Fig. 2) also increased with more chill accumulation. These results

indicate that the amount of accumulated chill primarily drives bud break percentages as the

buds were all exposed the same amount of time to forcing temperatures (Fig. 2).

The response of bud break percentage to accumulated chill notably differ between cultivars.

For example, the early flowering cultivar 'Cristobalina' (i.e. low-chill cultivar) was found to

have higher bud break potential (45% bud break) after low levels of accumulated chill (32 CP)

whereas the late flowering (i.e. high-chill cultivar) cultivar 'Regina' only reached 14.5% bud

break after accumulating 32 CP. For the late flowering cultivars to meet the equivalent 45%

bud break, 53 CP and 65 CP were needed for 'Regina' and 'Fertard', respectively. We also

observed this pattern for the capacity to reach high bud break percentage. After accumulating

40 CP, 'Cristobalina' and 'Burlat' reached 100% and 84% bud break, respectively, whereas the

late flowering cultivars ('Regina' and 'Fertard') only reached 28% and 16% bud break,

respectively (Fig. 3, Fig. S1).

Fig. 3 Bud break data used to calculate CR-50% and CR$_m$-90%. Upper panel: bud break percentage after 10 days under forcing conditions; lower panel: maximal bud break percentage reached under forcing conditions. Horizontal dotted lines represent the 50% and 90% thresholds for CR-50% and CR$_m$-90% respectively. Black and grey lines represent data for cultivars grown in Bourran and Toulenne, respectively. Solid lines are for 2015-2016 data while dashed lines are for 2016-2017 data

Chilling requirement estimation

Chilling requirement values calculated using the common approach (CR-50%) were highly

variable between years (Fig. 3, Table 1). The CR range calculated using a 90% bud break

threshold (CR$_m$-90%) were less variable.

Taking the average chill accumulation to reach 50% and 90% bud break, CR for each cultivar

were estimated (Table 1). CR differs with cultivar and by the method used to evaluate it but the

CR estimated by CR$_m$-90% are all higher than CR-50%.

Table 1 Chill requirement values (CP) between the four cultivars and the method used to calculate CR. Bold values are the mean CR recorded.

	CR-50%	CR$_m$-90%
'Cristobalina'	**29** CP	**42** CP
'Burlat'	77, 86, 89, 91 CP (**86 CP**)	94, 99, 106 CP (**92 CP**)
'Regina'	82, 85, 90 CP (**86 CP**)	94, 104 CP (**99 CP**)
'Fertard'	96, 105 CP (**101 CP**)	104, 112 CP (**108 CP**)

Future risk due to insufficient chill

Estimation of the risk of insufficient chill accumulation across Europe based on the two

methods to determine CR (Table 1) exposed areas potentially unsuitable for the cultivation of

each sweet cherry cultivar (Figs 4, 5, S2 and S3). We focused on MOHC-HadGEM2-ES, rcp8.5,

projecting the highest increase in temperatures (most pessimistic; Fig. 4) and NOAA-GFDL-

GFDL-ESM2M, rcp4.5, projecting the lowest increase in temperatures (optimistic; Fig. 5).

Areas defined in Figures 4 and 5 reveal that for the four cultivars, the regions at risk of not

meeting CR increase substantially by 2075-2100 using both estimations of CR (CR-50% and

CR$_m$-90%). The area at risk is larger for CR$_m$-90% than for CR-50% for both scenarios. Areas

coloured in pink, show the areas that meet CR according to CR-50% but not according to CR$_m$-

90% (Figs 4 and 5). Therefore, these pink areas show the difference of estimated risk of

insufficient chill depending on the method used to define CR. The difference in risk based on

CR methodology is particularly evident for the high-chill cultivar 'Regina'. Under both climate

scenarios, a large area of Europe will not meet CR_m-90% whereas using CR-50% a much

smaller area of risk was found (Figs 4 and 5).

Fig. 4 Maps of Europe showing where safe winter chill (10th percentile) will not meet chilling requirements as estimated by forcing experiments (CR-50%; red areas) and by optimal bud break rate (CR_m-90%; pink and red areas) for the four cultivars. Blue indicates CR will be met for both CR values. Thresholds for the chilling requirements calculated in Table1 were used. Scenario MOHC-HadGEM2-ES, rcp8.5, projects the highest increase in temperatures (most pessimistic)

Fig. 5 Maps of Europe showing where safe winter chill (10th percentile) will not meet chilling requirements as estimated by forcing experiments (CR-50%; red areas) and by optimal bud break rate (CRm-90%; pink and red areas) for the four cultivars. Blue indicates CR will be met for both CR values. Thresholds for the chilling requirements calculated in Table1 were used. Scenario NOAA-GFDL-GFDL-ESM2M, rcp4.5, projects the lowest increase in temperatures (most optimistic)

Discussion

Bud break percentage in response to chill accumulation

We evaluated bud break responses to various levels of chill accumulation in the field using forcing experiments on cultivars with contrasting chill requirements. The rate of bud break gradually increased with accumulated chill in the field, thus confirming that chill primarily drives the capacity of the buds to burst. Greater chill accumulation increased the maximum bud break percentage but with a different maximum response between cultivars (Fig. 3). Overall, the results indicate that the amount of accumulated chill can substantially limit the percentage of bud break even under optimal growth conditions (Fig. S1). This is especially true for the early flowering cultivar 'Cristobalina' which shows a very strict control of bud break percentage by the amount of chill accumulated with limited effect of heat accumulation (Fig. 4; Fig. S1). In addition, according to our data, there is a limit to the effect of heat on the bud break percentage. When bud break percentages were considered as a response to chill and heat accumulation (Fig. S1), results suggest that for a given chill accumulation bud break might never reach 100%. For example, bud break percentage in 'Regina' fails to reach 60% if chill accumulation is under 60 CP regardless of the level of heat accumulated. This provides a clear chill requirement limit on maximum bud break percentage.

The interaction of chilling with heat requirements and bud break was also shown in different temperate *Rosaceae*: cherry (Measham et al. 2017), peach (Couvillon and Erez 1985; Okie and Blackburn 2011), sour cherry (Felker and Robitaille 1985), apple (Powell 1986) and pear (Spiegel-Roy and Halston 1979); and in a notable group of forest species (Laube et al. 2014). This interaction has been associated to a 'residual effect of dormancy' (Erez 2000), a parameter indicating the distance to optimal chilling, and therefore, productivity (Okie and Blackburn 2011). This term is used when crops show symptoms of insufficient chilling (e.g. light bud break or fruit set and uneven foliation) even after satisfaction of their CR, usually corresponding

to CR-30% or CR-50% (Campoy et al. 2011). Therefore, increasing the required bud break

percentage when assessing CR will provide a more reliable measure of CR which should

minimise productivity problems associated with the 'residual effect of dormancy' for new

growing areas and improve commercial viability. Other studies that have calculated CR for

species that set yield potential based on flower numbers (e.g. almond; Egea et al. 2003), may

also consider recalculation of CR based on a commercial bud break requirement to assist with

current and future industry planning.

Chilling requirement calculation

The chill accumulation necessary to reach 90% (CR_m-90%) of flower bud break was found to

be higher than the chilling requirements estimated with the common forcing method (CR-50%)

as shown in Table 1. This reflects that the traditional assessment of chilling requirements may

underestimate the CR needed to reach commercial productivity in sweet cherry. It would not

be advisable to choose CR-100% (100% bud break in the controlled environments) as a small

percentage (i.e. 10%) allows for a buffer for minor physiological problems or accidental bud

drop during the manipulation of plant material on growth chambers.

The potential underestimation of CR due to experimental design may be trivial for temperate

areas characterised by cold winters, where chill accumulation in the field normally exceeds the

CR of all cultivars with both CR-50% and CR_m-90% easily achieved. For locations with more

marginal chill accumulation, assessments of suitability based on CR-50% instead of CR_m-90%

will likely have a more significant impact. The underestimation of CR could lead to

unexpectedly higher frequency and severity of productivity problems due to insufficient

chilling fulfilment. This will be particularly applicable to low-chill cultivars that are grown in

mild winter climates which are usually oriented to the profitable early-market (Egea et al. 2010).

Values for both CR-50% and CR_m-90% were highly variable between years and sites, although

less variable for CR_m-90%. Similar variability was been reported for sweet cherry in Australia

(Measham et al. 2017) and apricot in Spain and South Africa (Campoy et al. 2012). This

variability in CR estimation should be appreciated when considering production risk. One

potential source of variability in recorded CR is the chill model that we used in the analysis.

Indeed, the Dynamic model, used here to quantify chilling, was developed for Mediterranean

regions, and therefore may not be suitable for colder climates. However, past studies have

shown that, regardless of the climatic conditions, the Dynamic model is currently the most

accurate model to use for predicting chill requirements (Luedeling et al. 2011; Luedeling 2012).

Further investigation will be necessary to evaluate the accuracy of the model to ensure the

robustness of our analysis and predictions. This line of enquiry would similarly benefit other

assessments of CR in small fruit temperate species such as sweet cherry (Alburquerque et al.

2008) or almond (Egea et al. 2003) and projections of winter chill (Luedeling et al. 2011). It

would also be valuable to better understand the source of plasticity in bud responses to cold in

order to improve chill models for contrasted climatic conditions.

Future production risk due to insufficient chill

The projections of chill accumulation provide new evidence of climate change risks for the

cultivation of sweet cherry across Europe. Risk of insufficient chill accumulation increased with

the chilling requirement of the cultivar and the method used to calculate it (CR-50% or CR_m-

90%). In the Mediterranean basin (a marginal chill area), only extra-low chill cultivars, such as

'Cristobalina', were found suitable across the 21st century. However, for high-chill cultivars,

suitable areas were restricted and almost the whole of the continental Europe recorded risk,

especially using the CR_m-90% estimation (Figs. 4 and 5). These results highlighting CR

underestimation compounded by warming winters provide a warning message concerning the

sustainability of sweet cherry production in Europe and provide a case for breeders to develop

cultivars adapted to the upcoming climatic conditions. This is especially pertinent for species

for which no low-chill cultivars have been bred so far, such as sweet cherry and apricot.

Adaptation options other than new cultivars or new growing regions are currently available to

growers. In particular, dormancy breaking agents can be used to compensate for insufficient

chilling (Erez 2000). Greater understanding of these agents' ability to compensate for

insufficient chill under climate change is required to understand if these provide an enduring

adaptation strategy. Reliance on these products may not be a sustainable option with regulations

in recent years restricting product allowable (e.g. Dormex®).

These projections were made using two GCMs. Ideally, a full ensemble of models would be

used to assess potential impact (e.g. CMIP 5; Taylor et al. 2012)). Here, we used two models

among the limited set available with data for this assessment (projections with daily temperature

data). For the purposes of this assessment, this was sufficient to illustrate changes in risk based

on CR definitions and a greater set of scenarios may be used to further explore the risk analysis.

Furthermore, this analysis used gridded temperature data that may not always be representative

of microclimates within orchards and as such, thus these risk projection results should be

considered a guide only.

Climate change: a shift in growing areas and cultivars.

For the most pessimistic climate scenario (Fig. 4), the projections show notable risk for chill

fulfilment of high chill cultivars in areas currently considered as sufficiently cold, i.e. Greece,

Italy, France and British Isles. This highlights that high chill cultivars will need to be replaced

with lower chill cultivars. However, these cultivar replacements need to be considered within

the wider agri-climate setting. For example, cultivars with lower chill requirements tend to be

characterised by earlier flowering dates, especially under warming spring temperatures and may

therefore be at higher risk of early-season frost damage (Bigler and Bugmann 2018; Vitasse et

al. 2018). Selection of appropriate cultivars therefore require a wider risk assessment to avoid

maladaptation.

Interestingly, new areas suitable for cultivars with relatively high chill requirements appear in

North-Eastern Europe by the end the century. This result stems from experiments which

indicated temperatures below 0 to -2°C are not effective for chill accumulation as they might

inhibit all cellular functions and this low temperature restriction has been included in most

models of chil (e.g. (Richardson et al. 1974; Fishman et al. 1987; Hänninen 1990).

Consequently, current climatic conditions that are too cold to satisfy chill requirements,

according to current understanding of chill accumulation, will improve in suitability for chill

accumulation and illustrates new production areas suitable for fruit tree cultivation. Again, other

agri-climate risks (e.g. frost risk, water availability) need to be evaluated prior to establishing

new growing regions.

Overall, this paper reveals that the method used to assess chilling requirements does have an

important impact on assessments of the regional and cultivar suitability of sweet cherry. To

more broadly understand the risk warming will pose to crops that need a high bloom load for

profitability we propose the evaluation of chilling requirements using higher percentages of bud

break (around 90%) over a longer period under forcing conditions. This approach should be

undertaken to assess chilling requirements for the evaluation of new cultivars. These findings

can help inform selections made by breeders to develop climate adapted cultivars and for

growers to better understand current and future production risk in current and new growing

areas.

Acknowledgements

The authors would like to acknowledge the E-OBS dataset from the EU-FP6 project

ENSEMBLES (http://ensembles-eu.metoffice.com) and the data providers in the ECA&D

project (http://www.ecad.eu). JAC was supported by CEP Innovation and Aquitaine Region (AQUIPRU project 2014-1R201022971). The authors warmly thank Teresa Barreneche, Hélène Christmann, Jacques Joly, Lydie Fouilhaux, Noémie Vimont and Rémi Beauvieux for collecting the branches and collaborating on the phenotyping. The authors thank the INRA's '*Prunus* Genetic Resources Center' for preserving and managing the sweet cherry collections and the Fruit Experimental Unit of INRA-Bordeaux (UEA) for growing the trees and managing the orchards. Finally, many thanks to Alexis Berg for his help on the analysis of climatic projection data.

References

Alburquerque N, García-Montiel F, Carrillo A, Burgos L (2008) Chilling and heat requirements of sweet cherry cultivars and the relationship between altitude and the probability of satisfying the chill requirements. Environ Exp Bot 64:162–170. doi: 10.1016/j.envexpbot.2008.01.003

Andreini L, de Cortázar-Atauri IG, Chuine I, et al (2014) Understanding dormancy release in apricot flower buds (*Prunus armeniaca* L.) using several process-based phenological models. Agric For Meteorol 184:210–219. doi: 10.1016/j.agrformet.2013.10.005

Azizi Gannouni T, Campoy JA, Quero-García J, et al (2017) Dormancy related traits and adaptation of sweet cherry in Northern Africa: A case of study in two Tunisian areas. Sci Hortic (Amsterdam) 219:272–279. doi: 10.1016/j.scienta.2017.03.013

Bennet J (1949) Temperature and bud rest period. Calif Agric 3:9–12

Bigler C, Bugmann H (2018) Climate-induced shifts in leaf unfolding and frost risk of European trees and shrubs. Sci Rep 8:1–10. doi: 10.1038/s41598-018-27893-1

Campoy JA., Ruiz D, Egea J (2011) Dormancy in temperate fruit trees in a global warming context: A review. Sci Hortic (Amsterdam) 130:357–372. doi: 10.1016/j.scienta.2011.07.011

Campoy JA, Ruiz D, Allderman L, et al (2012) The fulfilment of chilling requirements and the adaptation of apricot (*Prunus armeniaca* L.) in warm winter climates: An approach in Murcia (Spain) and the Western Cape (South Africa). Eur J Agron 37:43–55. doi: 10.1016/j.eja.2011.10.004

Castède S, Campoy JA, Quero-García J, et al (2014) Genetic determinism of phenological traits highly affected by climate change in *Prunus avium*: flowering date dissected into chilling and heat requirements. New Phytol 202:703–15. doi: 10.1111/nph.12658

Chmielewski FM, Götz KP (2016) Performance of models for the beginning of sweet cherry blossom under current and changed climate conditions. Agric For Meteorol 218–219:85–91. doi: 10.1016/j.agrformet.2015.11.022

Chuine I, Bonhomme M, Legave JM, et al (2016) Can phenological models predict tree phenology accurately in the future? The unrevealed hurdle of endodormancy break. Glob Chang Biol 22:3444–3460. doi: 10.1111/gcb.13383

Cook NC, Calitz FJ, Allderman LA, et al (2017) Diverse patterns in dormancy progression of

apple buds under variable winter conditions. Sci Hortic 226:307–315. doi: 10.1016/j.scienta.2017.08.028

Couvillon GA, Erez A (1985) Influence of prolonged exposure to chilling temperatures on bud break and heat requirement for bloom of several fruit species. J Am Soc hort Sci 110:47–50

Dantec CF, Vitasse Y, Bonhomme M, et al (2014) Chilling and heat requirements for leaf unfolding in European beech and sessile oak populations at the southern limit of their distribution range. Int J Biometeorol 58:1853–1864. doi: 10.1007/s00484-014-0787-7

Dennis F (2003) Problems in standardizing methods for evaluating the chilling requirements for the breaking of dormancy in buds of woody plants. Hort Sci 38:347–350

Egea J, Ortega E, Martinez-Gomez P, Dicenta F (2003) Chilling and heat requirements of almond cultivars for flowering. Environ Exp Bot 50:79–85

Egea J, Rubio M, Campoy JA, et al (2010) "Mirlo Blanco", "Mirlo anaranjado", and "Mirlo Rojo": Three new very early-season apricots for the fresh market. HortScience 45:1893–1894

Erez A (2000) Bud Dormancy; Phenomenon, Problems and Solutions in the Tropics and Subtropics. In: Temperate Fruit Crops in Warm Climates. pp 17–48

Erez A, Couvillon GA (1987) Characterization of the moderate temperature effect on peach bud rest. J Am Soc hort Sci 112:677–680

Fadón E, Herrero M, Rodrigo J (2015) Flower development in sweet cherry framed in the BBCH scale. Sci Hortic (Amsterdam) 192:141–147. doi: 10.1016/j.scienta.2015.05.027

Felker FC, Robitaille HA (1985) Chilling accumulation and rest of sour cherry flower buds. J Am Soc Hortic Sci 110:227–232

Fishman S, Erez A, Couvillon GA (1987) The temperature dependence of dormancy breaking in plants: Mathematical analysis of a two-step model involving a cooperative transition. J Theor Biol 124:473–483. doi: 10.1016/S0022-5193(87)80221-7

Götz KP, Chmielewski FM, Gödeke K, et al (2017) Assessment of amino acids during winter rest and ontogenetic development in sweet cherry buds (*Prunus avium* L.). Sci Hortic (Amsterdam) 222:102–110. doi: 10.1016/j.scienta.2017.05.001

Guo L, Dai J, Ranjitkar S, et al (2013) Response of chestnut phenology in China to climate variation and change. Agric For Meteorol 180:164–172. doi: 10.1016/j.agrformet.2013.06.004

Guy R (2014) The early bud gets to warm. New Phytol 202:7–9. doi: 10.1111/nph.12728

Hänninen H (1990) Modelling bud dormancy release in trees from cool and temperate regions. Acta For. Fenn. 213:1–47

Harrington CA., Gould PJ, St.Clair JB (2010) Modeling the effects of winter environment on dormancy release of Douglas-fir. For Ecol Manage 259:798–808. doi: 10.1016/j.foreco.2009.06.018

Hauagge R, Cummins JN (1991) Seasonal variation in intensity of bud dormancy in apple cultivars and related *Malus* species. J Am Soc Hortic Sci 116:107–115

Haylock MR, Hofstra N, Klein Tank AMG, et al (2008) A European daily high-resolution gridded data set of surface temperature and precipitation for 1950-2006. J Geophys Res Atmos 113:D20119. doi: 10.1029/2008JD010201

Jacob D, Petersen J, Eggert B, et al (2014) EURO-CORDEX: New high-resolution climate

change projections for European impact research. Reg Environ Chang 14:563–578. doi:
10.1007/s10113-013-0499-2

Lang G, Early J, Martin G, Darnell R (1987) Endo-, para-, and ecodormancy: physiological
terminology and classification for dormancy research. Hort Sci 22:371–377

Laube J, Sparks TH, Estrella N, et al (2014) Chilling outweighs photoperiod in preventing
precocious spring development. Glob Chang Biol 20:170–82. doi: 10.1111/gcb.12360

Luedeling E (2018) chillR: Statistical Methods for Phenology Analysis in Temperate Fruit
Trees. R package version 0.70.6

Luedeling E (2012) Climate change impacts on winter chill for temperate fruit and nut
production: A review. Sci Hortic 144:218–229. doi: 10.1016/j.scienta.2012.07.011

Luedeling E, Gassner A (2012) Partial Least Squares Regression for analyzing walnut
phenology in California. Agric For Meteorol 158–159:43–52. doi:
10.1016/j.agrformet.2011.10.020

Luedeling E, Girvetz EH, Semenov MA, Brown PH (2011) Climate change affects winter chill
for temperate fruit and nut trees. PLoS One 6:. doi: 10.1371/journal.pone.0020155

Luedeling E, Guo L, Dai J, et al (2013a) Differential responses of trees to temperature variation
during the chilling and forcing phases. Agric For Meteorol 181:33–42. doi:
10.1016/j.agrformet.2013.06.018

Luedeling E, Kunz A, Blanke MM (2013b) Identification of chilling and heat requirements of
cherry trees-a statistical approach. Int J Biometeorol 57:679–89. doi: 10.1007/s00484-012-
0594-y

Luedeling E, Zhang M, Girvetz EH (2009a) Climatic changes lead to declining winter chill for
fruit and nut trees in California during 1950-2099. PLoS One 4:. doi:
10.1371/journal.pone.0006166

Luedeling E, Zhang M, Luedeling V, Girvetz EH (2009b) Sensitivity of winter chill models for
fruit and nut trees to climatic changes expected in California's Central Valley. Agric
Ecosyst Environ 133:23–31. doi: 10.1016/j.agee.2009.04.016

Measham PF, Darbyshire R, Turpin SR, Murphy-White S (2017) Complexity in chill
calculations: A case study in cherries. Sci Hortic 216:134–140. doi:
10.1016/j.scienta.2017.01.006

Okie WR, Blackburn B (2011) Increasing chilling reduces heat requirement for floral budbreak
in peach. HortScience 46:245–252

Petri JL, Leite GB (2004) Consequences of Insufficient Winter Chilling on Apple Tree Bud-
break. Acta Hortic 662:53–60

Powell LE (1986) The chilling requirement in apple and its role in regulating time of flowering
in spring in cold-winter climates. Acta Hortic 179:1–11

Richardson E, Seeley SD, Walker D (1974) A model for estimating the completion of rest for
Redhaven and Elberta peach trees. Hort Sci 9:331–332

Ruiz D, Campoy JA, Egea J (2007) Chilling and heat requirements of apricot cultivars for
flowering. Environ Exp Bot 61:254–263. doi: 10.1016/j.envexpbot.2007.06.008

Samish RM (1953) Dormancy in woody plants. Annu Rev Plant Physiol 5:183–204. doi:
10.1146/annurev.pp.05.060154.001151

Sánchez-Pérez R, Dicenta F, Martínez-Gómez P (2012) Inheritance of chilling and heat
requirements for flowering in almond and QTL analysis. Tree Genet Genomes 8:379–389.

doi: 10.1007/s11295-011-0448-5

Saure M (1985) Dormancy release in deciduous fruit trees. Hortic Rev (Am Soc Hortic Sci) 7:239–299

Spiegel-Roy P, Halston FH (1979) Chilling and Post-Dormant Heat Requirement as Selection Criteria for Late-Flowering Pears. J Hortic Sci 54:115–120

Tabuenca M (1967) Necesidades de frio invernal de variedades deciruelo. An Aula Dei 8:383–391

Taylor KE, Stouffer RJ, Meehl GA (2012) An overview of CMIP5 and the experiment design. Bull Am Meteorol Soc 93:485–498. doi: 10.1175/BAMS-D-11-00094.1

Vitasse Y, Basler D (2014) Is the use of cuttings a good proxy to explore phenological responses of temperate forests in warming and photoperiod experiments? Tree Physiol 34:174–83. doi: 10.1093/treephys/tpt116

Vitasse Y, Schneider L, Rixen C, et al (2018) Increase in the risk of exposure of forest and fruit trees to spring frosts at higher elevations in Switzerland over the last four decades. Agric For Meteorol 248:60–69. doi: 10.1016/j.agrformet.2017.09.005

Viti R, Andreini L, Ruiz D, et al (2010) Effect of climatic conditions on the overcoming of dormancy in apricot flower buds in two Mediterranean areas: Murcia (Spain) and Tuscany (Italy). Sci Hortic 124:217–224. doi: 10.1016/j.scienta.2010.01.001

Viti R, Bartolini S, Andreini L (2008) Apricot Flower Bud Development : Main Biological , Physiological and Environmental Aspects Related to the Appearance of Anomalies. Int J Plant Dev Biol 2:25–34

Vitra A, Lenz A, Vitasse Y (2017) Frost hardening and dehardening potential in temperate trees from winter to budburst. New Phytol 216:113–123. doi: 10.1111/nph.14698

Weinberger J (1950) Chilling requirements of peach varieties. Proc Am Soc Hortic Sci 56:122–128