



Review

Climate change impacts on winter chill for temperate fruit and nut production: A review

Eike Luedeling*

World Agroforestry Centre, Nairobi, Kenya

ARTICLE INFO

Article history:

Received 2 May 2012
 Received in revised form 6 July 2012
 Accepted 9 July 2012

Keywords:

Adaptation
 Chilling Hours
 Chill Portions
 Climate analogues, Dynamic Model
 Tree dormancy

ABSTRACT

Temperate fruit and nut species require exposure to chilling conditions in winter to break dormancy and produce high yields. Adequate winter chill is an important site characteristic for commercial orchard operations, and quantifying chill is crucial for orchard management. Climate change may impact winter chill. With a view to adapting orchards to climate change, this review assesses the state of knowledge in modelling winter chill and the performance of various modelling approaches. It then goes on to present assessments of past and projected future changes in winter chill for fruit growing regions and discusses potential adaptation strategies. Some of the most common approaches to modelling chill, in particular the Chilling Hours approach, are very sensitive to temperature increases, and have also been found to perform poorly, especially in warm growing regions. The Dynamic Model offers a more complex but also more accurate alternative, and use of this model is recommended. Chill changes projected with the Dynamic Model are typically much less severe than those estimated with other models. Nevertheless, projections of future chill consistently indicate substantial losses for the warmest growing regions, while temperate regions will experience relatively little change, and cold regions may even see chill increases. Growers can adapt to lower chill by introducing low-chill cultivars, by influencing orchard microclimates and by applying rest-breaking chemicals. Given substantial knowledge gaps in tree dormancy, accurate models are still a long way off. Since timely adaptation is essential for growers of long-lived high-value perennials, alternative ways of adaptation planning are needed. Climate analogues, which are present-day manifestations of future projected climates, can be used for identifying and testing future-adapted species and cultivars. Horticultural researchers and practitioners should work towards the development and widespread adoption of better chill accumulation and dormancy models, for facilitating quantitatively appropriate adaptation planning.

© 2012 Elsevier B.V. Open access under [CC BY-NC-ND license](http://creativecommons.org/licenses/by-nc-nd/4.0/).

Contents

1. Introduction	219
2. Modelling winter chill	219
3. Equivalence of chill models	219
4. Performance of phenology models	220
5. Chill model comparisons	221
6. Climate change impacts on winter chill	222
7. Adaptation strategies	225
7.1. Better metrics	225
7.2. Low-chill cultivars	226
7.3. Dormancy avoidance	226
7.4. Microclimate manipulation	226
7.5. Chemical rest-breaking	226
8. Adaptation in the absence of thorough understanding	226
9. Concluding remarks	227
References	227

* Correspondence address: World Agroforestry Centre (ICRAF), United Nations Avenue, PO Box 30677-00100 Gigiri, Nairobi, Kenya. Tel.: +254 20 722 4120; fax: +254 20 722 4001.

E-mail address: e.luedeling@cgiar.org

1. Introduction

Fruit and nut trees that originate in cold-winter climates fall dormant in winter, enabling them to tolerate freezing temperatures in their native habitats (Vegis, 1964). During plant dormancy, visible growth is suspended (Samish, 1954) and all physiological processes are halted or slowed. They must be reactivated in spring for trees to produce leaves and flowers, and ultimately bear fruit (Samish, 1954). In order to avoid frost damage, it is crucial for trees to only resume growth when the cold season is over. For determining this moment, trees have evolved mechanisms to sense temperature, and they appear to be able to integrate over phases of cold and phases of warm temperatures (Vegis, 1964). In other words, they can sense ‘how long it has been how cold’ (chilling) and ‘how long it has been how warm’ (heat). Trees must fulfill their chilling and heat requirements in order to break dormancy (Samish, 1954; Vegis, 1964; Saure, 1985; Campoy et al., 2011b).

Both requirements are attuned to a certain climate regime. They must work together to ensure that dormancy is broken late enough to keep trees from starting to grow in winter. On the other hand, growth must be resumed early enough to allow trees to complete their annual reproductive cycles before the onset of the following winter season. Given these climatic requirements, productive cultivation of each tree cultivar is confined to a certain agroclimatic zone (Rumayor-Rodriguez, 1995), and choosing the right tree cultivar for a given climate regime is crucial for orchard productivity. Chilling requirements in particular are vital, especially where trees are grown in areas that are substantially warmer than their regions of origin (Chandler, 1942). This is true for a wide range of species, such as apples, pears, apricots, peaches, pomegranates, plums, walnuts, almonds and pistachios. Within each species, different cultivars have different chilling requirements (Guerrero et al., 2010), and identifying an appropriate cultivar is essential for anyone planting trees for commercial production.

Climate change is likely to affect chilling (Schwartz, 1999; Baldocchi and Wong, 2008; Luedeling et al., 2011a). With global temperatures expected to rise by up to 6 °C by the end of the 21st century, compared to pre-industrial levels (IPCC, 2007), it is unlikely that this agroclimatic metric will remain stable (Else and Atkinson, 2010; Luedeling et al., 2011a). Advancing trends in bloom dates of many trees indicate that dormancy breaking processes are indeed changing, most likely in response to climate change (Guédon and Legave, 2008; Legave et al., 2009). This article reviews approaches to estimate winter chill, studies on the performance of different approaches and analyses of historic and projected future changes in winter chill. Finally, it assesses the state of knowledge about tree dormancy for adaptation to future changes and points out knowledge gaps that urgently need to be closed.

2. Modelling winter chill

Due to the importance of chill in fruit production, a number of efforts have been made to model this agroclimatic factor (summarized in Table 1). Samish (1954) and Vegis (1961) provide reviews of early scientific attempts to understand chill accumulation during the nineteenth and early twentieth centuries. Initially, temperatures below a certain threshold were considered to contribute to fulfillment of chilling requirements (Lammerts, 1941, 1945). The realization that freezing temperatures are not effective led to the development of the Chilling Hours Model (Bennett, 1949), also known as Weinberger Model (Weinberger, 1950), or Weinberger–Eggert Model (Valentini et al., 2001) or 0–7.2 °C Model (Darbyshire et al., 2011). In this model, temperatures between 0 and 7.2 °C are assumed to have a chilling effect, with each hour at temperatures between these thresholds contributing one Chilling

Hour. Chilling Hours are then summed throughout the dormant season.

The next significant advance in understanding the temperature response of trees during the chilling phase was the discovery that warm temperatures had a negative effect on chill accumulation (Overcash and Campbell, 1955). From this insight arose the Utah Model, which is characterized by differential weighting of temperature ranges, including negative weights for temperatures above 15.9 °C (Richardson et al., 1974). Variations of the Utah Model have been developed for a number of different regions, fruits and contexts (Gilreath and Buchanan, 1981; Shaltout and Unrath, 1983; Linvill, 1990; Anderson and Seeley, 1992; Linsley-Noakes and Allan, 1994; Warmund and Krumme, 2005). All these variations accumulate Chill Units over the course of the season. Campoy et al. (2011b) list several crop-specific chilling models in their comprehensive review on fruit tree dormancy.

The third modelling approach that is widely applied in practical horticulture is the so-called Dynamic Model (Fishman et al., 1987a, 1987b; Erez et al., 1990). This model is based on the assumption that chill accumulates as a result of a two-step process: in the first step, an intermediate chill product is produced in a process that is most efficient at low temperatures. This process is reversible, and the intermediate product can be destroyed by heat. Once it is exposed to moderate temperatures, however, the intermediate product can be transformed in an irreversible process into a Chill Portion. Chill Portions are accumulated, contributing to fulfillment of chilling requirements. This model is the only one among the common models that can explain the observed negative effect of high temperatures (Vegis, 1961; Thompson et al., 1975; Couvillon and Erez, 1985), the apparent limit to how much chill can be reversed (Erez et al., 1979), and the chill-enhancing effect of moderate temperatures when cycled with cool conditions (Erez and Couvillon, 1987). A major difference between the Dynamic Model and the earlier approaches is the importance given to the sequence of temperatures during the cold season. According to the Chilling Hours and Utah Models similar temperatures always have exactly the same effect, regardless of when they occur. In the Dynamic Model, several processes interact and the production of a Chill Portion is contingent on the existence of a certain quantity of the intermediate product. Similar temperatures at different times of the season can thus have very different effects on chill accumulation. Zhang and Taylor (2011) referred to this quality of the Dynamic Model as time-inhomogeneity, as opposed to the time-homogeneous nature of the other models.

In particular when including efforts outside the field of horticulture, numerous additional modelling approaches have been proposed, e.g. by Bidabé (1965), Cesaraccio et al. (2004), Chmielewski et al. (2011), Chuine et al. (1998), Linkosalo et al. (2010), Legave et al. (2008) and Hänninen and Kramer (2007). These models have not widely been applied on fruit and nut trees, and will therefore not be discussed further in this article. However, it may be worthwhile for horticultural modellers to examine these models for insights into how chilling models can be improved.

3. Equivalence of chill models

While all of the common horticultural models have been successful to a certain extent in guiding orchard management and cultivar selection, they are quite different and not all equally credible. For example, the sharp thresholds in the Chilling Hours Model and most versions of the Utah Model are unlikely to reflect biological reality. It should also be noted that most models are exclusively based on observations in the field, while systematic controlled-environment experiments seem to only have happened for the Dynamic Model. This is also the only one among the commonly used

Table 1
Overview of major chilling models and comparison with regard to the inclusion of major scientific insights into temperature effects on chill accumulation.

Model names and authors	Time step	Differential temperature weights	Continuous weights	Chill negation by heat	Limit to chill negation	Enhancement by moderate temps.	Two-phase chilling
Chilling Hours Model (Bennett, 1949; Weinberger, 1950)	h	–	–	–	–	–	–
Utah Model (Chill Units; Richardson et al., 1974)	h	+	–	–	–	–	–
Variations of the Utah Model							
North Carolina Model (Shaltout and Unrath, 1983)	h	+	–	+	–	–	–
Anderson and Seeley, 1992	h	+	+	+	–	–	–
Positive Utah Model (Linsley-Noakes and Allan, 1994)	h	+	–	+	+	–	–
Modified Utah Model (Linville, 1990)	h	+	+	+	–	–	–
Regional models in Georgia and Florida	m	–	–	–	–	–	–
Chmielewski et al. (2011)	d	–	–	–	–	–	–
Legave et al. (2008)	d	±	±	–	–	–	–
Cesaraccio et al. (2004)	d	+	+	–	–	–	–
“non-horticultural” dormancy models (e.g. Chuine and Cour (1999), Linkosalo et al. (2008))	d	±	±	±	–	–	–
Dynamic Model (Chill Portions; Fishman et al. (1987a, 1987b))	h	+	+	+	+	+	+

+ indicates that the respective characteristic is included in the model; – indicates that it is not included; ± means that different versions exist, with only some including the characteristic.

Model characteristics are temperature step (h = hourly, d = daily, m = monthly), differential weighting of different temperature ranges, continuous (as opposed to step-wise) distribution of weights, negation of earlier chill by high temperatures, a limit to how much chill can be negated, enhancement of earlier chill by moderate temperatures and an assumed two-step process of chill accumulation.

The authors given in the table are not necessarily the model developers.

models that can be called ‘process-based’ (as opposed to purely empirical), even though the development of the model was based on hypothetical processes (Fishman et al., 1987a, 1987b), rather than on processes with a sound scientific basis.

In the context of climate change projections, it is concerning that different models produce different results. Luedeling et al. (2009d, 2010) analysed the response of four common chilling models to climate change projected for several sites in California. For warming projected by three general circulation models for the A2 greenhouse gas emissions scenario, losses projected by the Chilling Hours Model were up to 2.5 times, and by the Utah Model 1.5 times as severe as losses projected by the Dynamic and the Positive Utah Models, when expressed relative to a 1950 baseline. Choice of the model was thus the most important determinant of projection results, casting serious doubts on the suitability of at least some of the models for climate change projection. Even for historically observed winter chill, estimates with different models are not proportional. On average over six weather stations in California, Luedeling et al. (2009e) showed that over a period of 57 years, ratios between winter chill estimated with different models were strongly variable, ranging for example between 8 and 18 for the ratio of Chilling Hours to Chill Portions. Assuming that one of these models is ‘correct’, chilling estimates by a grower using the wrong model could thus be off by a factor of more than 2, in extreme years. Similar patterns were found for ratios between all four tested models. In the same context, the authors also explored the ratio between the same metrics for an environment, in which a constant temperature of 6 °C is maintained. Such treatments are occasionally used as artificial chilling treatment (Vergara and Pérez, 2010). The corresponding Chilling Hours to Chill Portions ratio was greater than 20 and thus outside the range of ratios observed in the field. Luedeling et al. (2009e) used these considerations to argue that chilling requirements determined under controlled constant temperature conditions are unlikely to be applicable to orchard conditions.

Variation in ratios between chilling metrics across the world is also substantial. Luedeling and Brown (2011) showed that the

ratio of Chilling Hours to Chill Portions varied between 0 and 34, Utah Chill Units to Chill Portions between –155 and 25 and the ratio of Utah Chill Units to Chilling Hours between –10 and +5. While these are the extreme ends of the spectrum, ratios were substantially different between major growing regions, to a large degree responding to mean annual temperature. This temperature dependence confirms that models may react quite differently to warming. The heterogeneity of ratios between metrics also implies that at least most of the models are not fit for global use and do not describe the chilling process in a way that can be generally applied across time, space or climate. Luedeling and Brown’s (2011) global maps of chill metric ratios provide an opportunity to convert chilling requirements determined with one model to units of another model. Due to the different structures and different ranges of effective temperatures used in the different models, however, the extent to which such conversions are possible is limited, in particular in warm growing regions.

4. Performance of phenology models

Chilling models alone cannot explain bloom dates, but in some studies, they have been combined with forcing (heat) models to predict bloom and leafing phases. Applying statistically derived chilling and heat requirements sequentially, Luedeling et al. (2009e) tried to reconstruct bloom dates of walnuts in California, using 1297 observed phenological dates. For four different chilling models (Chilling Hours Model, Utah Model, Positive Utah Model and Dynamic Model), predicted dates were between 5.4 and 7.2 days off observed dates, with standard deviations of these errors between 5.2 and 6.2 days. Considering that the mean range of phenological dates within the dataset, across cultivars and growth stages, was only 32 days, with a standard deviation of 7.2 days, the accuracy of predictions was fairly low.

Chmielewski et al. (2011) compared the performance of 5 phenology models for reproducing apple blossom dates in Germany. The authors used data for about half of 5630 phenological stations in Germany, each of which had between 1 and

45 years of data, for calibrating their models. The remainder of the dataset was used for validation. The model that performed best was the approach by Chuine et al. (1998), in which most attention was paid to the forcing function, while chilling was dealt with by simply classifying days into chilling and non-chilling days. Root mean square errors according to this model ranged from 3.05 to 6.88 days across growing regions, with an average of 4.40 days. Again, these estimates must be evaluated in the context of overall variation in the dataset. The standard deviation of blossoming of the cultivar Boskoop in Esteburg seems to be on the order of 8.5 days, with overall range of bloom dates around 35 days (reconstructed from a figure in the paper). With bloom variation in this range, model accuracy thus cannot be considered very high. The authors rightly concede that error estimates were 'within a range which is usually acceptable for this kind of model' (Chmielewski et al., 2011), hinting at the difficulty of producing accurate phenology models.

Legave et al. (2008) tested the performance of a number of chilling/forcing model combinations for explaining apple bloom in France and Belgium, selecting three models for further analysis. After adjusting parameters for all models in an automated procedure based on phenology recordings from France, they validated models using 23 years of bloom data from Gembloux in Belgium. Root mean square errors estimated from absolute errors given in the paper ranged between 3.1 and 5.5 days. According to data extracted from a figure in the paper, the standard deviation of bloom dates in Angers, the station with the most complete record (annual observations between 1963 and 2006), was on the order of 8 days. Again, the model leaves a large part of the variation in the bloom dataset unexplained.

While the above-mentioned studies used relatively large datasets for validating models, shorter datasets have also been used. For example, Anderson et al. (1986) validated a sequential chilling/forcing model, in which an adjusted version of the Utah Model was used for chill accumulation, based on between 2 and 5 observed phenological dates for sour cherry in Utah and Michigan.

Mean errors of predictions were only between 2.2 and 4 days, but the small sample size makes it difficult to evaluate the results. In this particular study, it is also not clear how the chilling and forcing requirements were determined, and whether or not the calibration dataset included those dates used for validation.

In summary, most studies that have evaluated the performance of combined chilling/forcing models have found that some model combinations are able to predict bloom dates to within a few days of actual bloom dates. However, since variation in observed bloom dates is not very large, all model combinations have left a large part of this variation unexplained. The occurrence of this situation even when models were calibrated with large observed datasets casts some doubts on the mathematical structure of the models and the assumptions underlying the different modelling approaches. All approaches published to date are almost entirely based on empirical observations rather than on thorough understanding of tree physiology. Some models still performed reasonably well in reproducing observed bloom patterns, but their suitability for climate change projections must be questioned. Empirical models are only valid for the range of conditions, from which observations were used to develop the models. Climate change scenarios are almost by definition not included within this range. This lack of calibration for future climates, combined with the substantial variation in historic bloom dates that all models leave unexplained, indicates that climate change projections of tree phenology should be interpreted with caution.

5. Chill model comparisons

A number of studies have evaluated the performance of commonly used horticultural chilling models (summarized in Table 2). Several authors have argued that the structure of the Dynamic Model, or its homogeneous rate of chill accumulation, make it the most plausible among the common models (Erez et al., 1990; Allan et al., 1995, 1997; Perez et al., 2008; Luedeling et al., 2009a, 2009c, 2009d, 2011a, 2011b; Darbyshire et al., 2011; Luedeling and Brown,

Table 2
Comparative evaluations of horticultural chilling models.

Location	Species	Models tested	Approach	Best model	Author
South Africa	Generic, case study for nectarines	UM, DM	Theory-based	DM	Erez et al. (1990)
Réunion Island and France	Peach	UM, DM	Controlled forcing trials	All models failed	Balandier et al. (1993a)
South Africa	Generic	CH, UM, PUM, DM	Theory-based	DM	Allan et al. (1995)
South Africa	Generic	UM, PUM, DM	Theory-based	PUM, DM	Allan et al. (1997)
South Africa	Eucalyptus	UM, PUM, DM	Multi-site field trials	DM	Gardner and Bertling (2005)
Spain	Apricot	<7 °C, UM, DM	Controlled forcing trials	UM, DM	Ruiz et al. (2007)
Chile	Generic	CH, UM, PUM, DM	Theory-based	DM	Perez et al. (2008)
Spain	Cherry	<7 °C, UM, DM	Controlled forcing trials	UM, DM	Alburquerque et al. (2008)
Germany	Generic	DM, UM, PUM, DM + several others	Theory-based	DM	Luedeling et al. (2009a)
California	Generic	CH, UM, PUM, DM	Theory-based	DM	Luedeling et al. (2009c)
California	Generic	CH, DM	Theory-based	DM	Luedeling et al. (2009d)
California	Walnut	CH, UM, PUM, DM	Statistical evaluation of phenology records	DM	Luedeling et al. (2009e)
Spain and Italy	Apricot	UM, DM	Controlled forcing trials	DM	Viti et al. (2010)
Australia	Generic	CH, MUM, PUM, DM	Theory-based	DM	Darbyshire et al. (2011)
Global	Generic	CH, UM, DM	Theory-based	DM	Luedeling and Brown, 2011
Global	Generic	CH, UM, DM	Theory-based	DM	Luedeling et al. (2011a)
Germany	Generic	CH, UM, DM	Theory-based	DM	Luedeling et al. (2011b)
Australia	Pistachio	CH, UM, DM	Controlled forcing trials; statistical correlations	DM	Zhang and Taylor (2011)
Spain and South Africa	Apricot	<7 °C, UM, DM	Controlled forcing trials	DM	Campoy et al. (2012)

CH = Chilling Hours Model (Bennett, 1949), UM = Utah Model (Richardson et al., 1974), MUM = Modified Utah Model (Linville, 1990), PUM = Positive Utah Model (Linsley-Noakes and Allan, 1994), DM = Dynamic Model (Fishman et al., 1987a, 1987b).

2011). On several occasions, chilling model performance has also been tested in experiments.

Working on *Eucalyptus nitens*, Gardner and Bertling (2005) found that among three models tested (Utah Model, Positive Utah Model and Dynamic Model), the Dynamic Model was most successful in explaining the percentage of trees that had umbels, as well as the umbel score per tree (based on multiple regression analysis). These results were based on observations during a single season (2001) at 4 sites, with 5 trees per site.

Albuquerque et al. (2008) determined chilling requirements of seven cherry cultivars during two years at one location in Spain, by taking branches from dormant trees at various times during the winter, and exposing them to forcing temperatures. They found that the Utah Model and Dynamic Model produced equally consistent results, whereas the '<7 °C Model' (approximately equivalent to the Chilling Hours Model) performed poorly.

Ruiz et al. (2007) determined chilling requirements of apricots in Spain based on three years of experimentation. Branches were picked every 3–4 days during the dormancy season and exposed to forcing conditions. For the '<7 °C Model', the Utah Model and the Dynamic Model, chilling requirements were then compared. Mean coefficients of variation of chilling requirements over all ten tested cultivars were 26.4% for the '<7 °C Model', 7.2% for the Dynamic Model and 6.3% for the Utah Model. Even though the Utah Model provided the most consistent estimates, the authors concluded that the Dynamic and the Utah Model are equally suitable for calculating chill in this area.

Using a similar approach, Viti et al. (2010) compared the performance of the Utah and Dynamic Models in explaining budbreak of apricots under artificial forcing conditions in Murcia, Spain and Tuscany, Italy. Chill accumulation in the field was monitored using temperature loggers, and shoots were extracted at weekly intervals to be forced in a warm environment. The authors reported chilling requirements separately for each of two years and each of four cultivars, but they provided all necessary data for a cross-site evaluation. For individual cultivars, chilling requirements varied among site/year combinations with coefficients of variation of 8–14% for the Utah Model and 3–11% for the Dynamic Model, with the Dynamic Model providing a more precise estimate for all four cultivars.

Also with a similar methodology, Campoy et al. (2012) evaluated chilling requirements of twelve apricot cultivars in Murcia, Spain, based on 4 years of observation. For three of these cultivars, as well as for one not grown in Spain, 2 years of observations were also available from South Africa. Shoot samples were taken from trees at 3–4 day intervals and forced under controlled conditions. Based only on results from observations in Spain, chilling requirement estimates had coefficients of variation between 8% and 41% for the Utah Model, between 7% and 79% for the Chilling Hours Model, and between 5 and 12% for the Dynamic Model. In all cases, coefficients were lowest for the Dynamic Model. When adding observations from South Africa, two of the cultivars confirmed this impression, with coefficients of variation of chilling requirement estimates of 14% and 38% for the Utah Model, 19% and 43% for the Chilling Hours Model and 11% and 10% for the Dynamic Model. Only for the cultivar 'Palsteyn', the Chilling Hours Model had the lowest coefficient of variation at 14%, compared to 21% for the Dynamic Model and 42% for the Utah Model. The overall impression from this study is that for all cultivars except one (and then only when combining observations from both sites), the Dynamic Model provided the most precise estimate of the cultivars' chilling requirements.

Zhang and Taylor (2011) determined the date of fulfillment of the chilling requirement in 'Sirora' pistachios in New South Wales, Australia. They exposed branches taken from orchards at weekly intervals to forcing temperatures in a greenhouse. When 50% of buds broke on branches taken during three consecutive weeks, the

chilling requirement was considered fulfilled. Over five years of experimentation, chilling requirements estimated by the Dynamic Model showed a coefficient of variation of only 3%, compared to 15% for the Utah Model and 18% for the Chilling Hours Model. Comparison of evenness of budbreak over 7 years of observation with accumulated chill totals also produced conclusive results.

Luedeling et al. (2009e) statistically evaluated a dataset of 1297 phenological dates for seven developmental stages of four walnut cultivars at eight locations in California. Their analysis was based on the assumptions that chilling and heat requirements are fulfilled in sequence, that heat accumulation can be described according to Anderson et al. (1986), and that heat and chilling requirements do not vary across sites and years. Under these assumptions, the Dynamic Model was most successful at explaining observed phenological dates, closely followed by the Positive Utah Model. The Utah Model and the Chilling Hours Model were much less suitable for explaining observed variation in phenological dates.

All models failed in trying to explain chilling accumulation for peach production at three different altitudes on the island of Réunion and at Clermont-Ferrand, France (Balandier et al., 1993a). This highlights that the commonly used chilling models cannot explain budbreak across the full climatic range, in which peaches can be grown. In addition to pointing out potential shortcomings in the models, this study makes it seem likely that climatic conditions during dormancy induction or other stages of the growth cycle affect chilling requirements (Balandier et al., 1993b). Rea and Eccel (2006) showed that several existing chilling models did not explain apple bloom along an elevation gradient in Northern Italy, leading them to propose a new model for this region based on the Utah Model. Unfortunately, the Dynamic Model was not among those tested in this study.

In spite of a lack of standardization among the model comparison studies (Dennis, 2003), it can be concluded that the majority of studies have found the Dynamic Model to be relatively accurate in different climates, in particular in comparison with the most commonly used Chilling Hours approach. However, all of the models still leave a lot to be desired in terms of accuracy, and some dormancy-breaking behaviour at warm sites could not be explained at all. While studies on marginal production sites are scarce, evaluation of common modelling approaches for production at such sites could yield important insights into the empirical relationship between temperature and chill accumulation. For example, temperate fruits and nuts are grown under marginal conditions in the highlands of Oman (Gebauer et al., 2009), Kenya (Griesbach, 2007) and Ethiopia (Ashebir et al., 2010), in Northwest Vietnam (Newman et al., 2008), Thailand (Nissen et al., 2006) and many other locations throughout the Subtropics and even in the Tropics. At some sites, temperate fruits are even grown without winter chill, with dormancy induced artificially by manual or chemical defoliation (Edwards, 1987). Observations at these marginal production sites could contribute greatly to the development of new chilling models that more accurately represent the response of dormant trees across the full range of possible habitats of temperate tree crops.

6. Climate change impacts on winter chill

A number of authors have analysed historic changes in winter chill based on temperature records, or projected future chilling losses for climate change scenarios for several important growing regions, using a wide range of methods to quantify winter chill (summarized in Table 3). In light of the above discussions, not all of these projections are equally credible.

Sunley et al. (2006) evaluated winter chill changes across several locations in the United Kingdom between 1950 and 2002, using the Chilling Hours Model, the <7.2 °C Model, the Utah Model and the so-called 'Lantin' model. They compared winter chill of the

Table 3
Evaluations of past and projected future changes in chill availability.

Region	Chilling model	Time frame/climate	Principal finding	Authors
United Kingdom	<7.2 °C, CH, UM, Lantin	1950–2002	Moderate historic chill losses for most models; slight increases according to the Utah Model	Sunley et al. (2006)
United Kingdom	No model	Future	Fruit production in UK at risk from chill losses	Else and Atkinson (2010)
Southern Brazil	CH	Historic climate +1 °C, +3 °C, +5.8 °C	Severe chill decline; for higher warming scenarios, very few areas remain viable	Wrege et al. (2010)
Western Cape (South Africa)	PUM	1967–2007 +0.5, 1.0 and 1.5 °C warming	Mean chill losses by 26% during historic record; future losses projected at 10–30% for cool sites, 10–60% for warm locations	Midgley and Lötze (2011)
Mountain Oases in Oman	CH	1983–2008 +1 °C and +2 °C (WG)	Chill conditions marginal for most fruits; under warming scenarios most fruits no longer viable	Luedeling et al. (2009b)
Mountain Oases in Oman	DM	1983–2008 +1 °C and +2 °C (WG)	Severe chill losses, but much less pronounced than in the above study; production will probably remain possible	This article
Germany	CH, DM	1876–2009	High variation in annual chill, but no significant trends over time	Luedeling et al. (2009a)
Meckenheim, Germany	CH, UM, DM	1958–2011	Slight decrease over time for the CH (around –3 CH/year), no changes for UM and DM	Luedeling et al. (2011b)
California	CH	1950–2100	Severe historic and projected losses; production of most tree crops at risk	Baldocchi and Wong (2008)
California	CH, DM	1950, 2000, 2050, 2090 (WG)	Substantial losses historically and particularly for future scenarios; losses much more severe for CH than for DM	Luedeling et al. (2009c)
Australia	MUM	Historic climate +1 °C, +2 °C, +3 °C, + regionalized CM outputs	Severe losses projected for warm production sites; moderate losses for cooler sites; adaptation measures are recommended	Hennessy and Clayton-Greene (1995)
Australia	CH, MUM, PUM, DM	1911–2009	Historic chill decline at almost all sites, for all models; slight gains for MUM and PUM at two sites, DM at one site; big variation among models	Darbyshire et al. (2011)
Australia	CH, MUM, PUM, DM	1911–2009 + warming caused by 1, 2 and 3 °C global temperature increase	Chill losses projected for all sites, in particular warm locations; substantial variation across sites; DM typically indicated smallest change	Darbyshire et al. (in press)
Egypt	0–10 °C	1969/70, 1989/90, 2008/09 +CM outputs	Some historic losses, but no trend analysis possible; substantial losses projected for future scenarios	Farag et al. (2010)
Global	DM	1975, 2000, 2050, 2090 (WG)	Severe losses in warm growing regions (historically and projected); little change in temperature regions; chill gains in cold regions	Luedeling et al. (2011a)

CH = Chilling Hours Model (Bennett, 1949); UM = Utah Model (Richardson et al., 1974); PUM = Positive Utah Chill Units Model (Linsley-Noakes and Allan, 1994); DM = Dynamic Model (Fishman et al., 1987a, 1987b); Modified Utah Model (Linville, 1990); WG = weather generator used for making climate scenarios; CM = climate model.

decade 1969–1979 with chilling of 1987–1997, finding changes between –5.7 and –12.2% for the <7.2 °C model, between +2.3 and –10.9% for the Chilling Hours Model and between –1.6 and –4.8% for the Lantin Model. The Utah Model behaved differently, with change estimates ranging between –0.9% and +5.1%. Also working on the United Kingdom, Else and Atkinson (2010) predicted chill losses that might jeopardize the ability of fruit trees to satisfactorily break dormancy. They offer no quantitative projections and appear to base their conclusions on the assumption that temperatures between 3 and 7 °C are effective for chilling accumulation. Considering that other studies project no or only small changes in winter chill in cool temperate climates (Luedeling et al., 2011a), more work, including model comparison studies, is needed on projecting future occurrence of chill in this region.

Wrege et al. (2010) calculated winter chill changes in Southern Brazil using the Chilling Hours Model. Based on weather station records, they expressed minimum temperature as a function of latitude, longitude and elevation. The number of Chilling Hours (CH) was then expressed as a function of minimum temperature, and mapped for the states of Paraná, Santa Catarina, and Rio Grande do Sul. In addition to current climate, the authors added warming scenarios of +1, +3 and +5.8 °C. In these scenarios, the respective temperature increments were added to all daily minimum temperatures. Projections indicated that the proportion of the study area that received more than 300 CH will decline from 70.1% (current), to 61% under the +1 °C scenario and to 4.3% under the +3 °C scenario. Assuming a 5.8 °C warming, no place within the study area

was expected to receive more than 300 CH, and only 4.4% received more than 50 CH.

Midgley and Lötze (2011) analysed winter chill trends in the Western Cape region of South Africa using the Daily Positive Utah Chill Units Model (Linsley-Noakes and Allan, 1994), based on daily temperature records from 12 weather stations taken between 1967 and 2007. Chill Units (CU) were read from a conversion table, which assumes that hourly temperatures follow a sine curve during the day and a logarithmic decay function at night (Linville, 1990). On average, they found a chill decline by 224 CU for all stations between May and September. Relative to 40-years means, these losses corresponded to 26% on average, with losses as high as 36–47% for individual stations. In the coolest growing regions, trends were not significant, but strong reductions in May, at the beginning of the dormancy season, were observed even there. For uniform warming scenarios (same warming applied to all temperature readings) of 0.5, 1.0, 1.5 and 2.0 °C, the authors projected pronounced chill losses for all stations, with seasonal losses ranging between 10% and 30% for cool sites, across all four scenarios, and between 10% and 60% for warm sites. The highest relative losses were projected for warm sites and warm months. Midgley and Lötze (2011) report that growers are already transitioning to lower chill crops, such as grapes. They expect this trend to continue and the use of rest-breaking chemicals to increase in importance.

Luedeling et al. (2009b) evaluated the current and future potential of high-mountain oases in Oman to produce temperate fruit and nut crops. Such tree crops are only grown in very few

settlements in Oman (Gebauer et al., 2007), because the hot desert climate in the rest of the country only allows production of subtropical and tropical species (Nagieb et al., 2004). Because of their particular climatic setting, the mountain oases of Al Jabal al Akhdar have expanded their fruit and nut production in recent decades (Luedeling and Buerkert, 2008a). Using long-term daily temperature data calibrated with a shorter record of hourly measurements, Luedeling et al. (2009b) analysed the number of Chilling Hours that were historically available in these oases, as well as Chilling Hours for two future climate scenarios, in which all temperatures were increased by 1 and 2 °C, respectively. They compared results to minimum chilling requirements for important species from the literature. Results indicated that in the current scenario, winter chill was only rarely sufficient to sustain walnuts and apricots. In the +1 °C scenario, chilling requirements of peach were only rarely fulfilled, and in the +2 °C scenario, even pomegranate, the most widely cultivated tree crop, appeared unable to receive enough chilling in most winters. Because oasis agriculture is only possible where natural water sources are available (Luedeling and Buerkert, 2008b), and there are no locations at higher altitude where this is the case, the prospect for the production of temperate fruits in Oman's mountain oases was projected to be bleak. However, as shown in the above discussion, use of the Chilling Hours Model is not recommendable in such a hot climate. Recalculating winter chill according to the Dynamic Model produces quite different results. This model reduced projected losses in mean annual winter chill from 43% to 26% for the +1 °C scenario, and from 71 to 50% for the +2 °C scenario. Rather than with 80 Chilling Hours, the warmest scenario left farmers with 25 Chill Portions, which may be enough to sustain at least some of the currently grown species. This case study illustrates the importance of using appropriate models in projecting winter chill.

Historic changes in winter chill have been analysed for 43 weather stations in Germany and interpolated for the whole country (Luedeling et al., 2009a). This analysis relied on idealized daily temperature curves constructed from daily minimum and maximum temperatures. Chill changes were quantified in Chilling Hours and in Chill Portions, for records going back to the 1870s. While according to both models mean winter chill over all stations varied substantially over the years, neither model detected a significant trend. The number of Chilling Hours declined by 0.06 per year ($r^2 = 0.00$) and the number of Chill Portions by 0.04 per year ($r^2 = 0.03$). The lack of significance in these trends, in spite of a warming trend, probably stems from the structure of the chilling models, which do not count frost hours as effective for chilling. Given typical winter temperatures in Germany, warming may just as well lead to more chilling (if frost hours become non-freezing) as to less chilling (if cool hours become too warm to be effective). Apparently, these two processes have historically cancelled each other out in Germany.

Similar findings were reported by Luedeling et al. (2011b) for the Meckenheim fruit growing region in Germany. These authors used hourly temperature records to establish correlations between hourly and long-term daily records. Based on these relationships, long-term hourly temperature records since 1958 were reconstructed. Again, there was no significant trend in chilling over time, but the authors reported a correlation between mean winter temperature and the amount of chilling that accumulated. According to the Dynamic and Utah Models, maximum chill accumulated when mean temperatures (for the whole winter and for 15-day intervals during the winter) were around 6–7 °C. At colder and warmer temperatures, less chill was accumulated. For the Chilling Hours Model, the most effective temperature was around 2–3 °C, substantially lower than for the other models. The authors concluded that warming from a cold baseline may lead to increases in winter chill, whereas warming from a fairly warm baseline should lead to decreases.

Production in California, one of the world's most productive growing regions, in particular for nut crops, may also be threatened by winter chill losses (Baldocchi and Wong, 2008). Using the Chilling Hours Model, Baldocchi and Wong (2008) projected chill losses for weather stations within the state for future scenarios, and they detected historic declines for the majority of stations they analysed. They found historic losses between 50 and 260 Chilling Hours per decade, and projected further losses in the future at a rate of around 40 Chilling Hours per decade. Their projections indicate that by the end of the 21st century, orchards in California will experience less than 500 Chilling Hours, making the state marginal or unsuitable for many currently grown species and cultivars.

Also for California but using a different methodology, Luedeling et al. (2009c) projected future changes in winter chill. They used long-term daily weather records from weather stations all over California to calibrate a stochastic weather generator. This generator was then used to produce 100 replicates of daily weather records for a number of scenarios, representing typical climatic conditions around 1950, 2000, 2050 and 2090. For future scenarios, three General Circulation Models and two greenhouse gas emissions scenarios were considered. Using statistical relationships between measured hourly and daily temperature values, daily data were then converted to hourly data and winter chill was quantified according to the Chilling Hours and Dynamic Models. Based on the resulting distribution of winter chill estimates over 100 years of synthetic weather data, the authors defined a 'Safe Winter Chill' value as the 10% quantile of the distribution. This value is the amount of winter chill that is exceeded in 90% of all years, representing the assumed maximum chilling requirements of trees that can be produced with reasonable economic success. Luedeling et al. (2009c) detected changes in historic Safe Winter Chill by 2000 of up to –30%, compared to the 1950s baseline, according to the Chilling Hours Model. For future scenarios, losses were estimated at 30–60% by the middle of the 21st century, and up to 80% by the end of the century. Using Chill Portions, losses were much lower, at a maximum of 30–60% by the end of the 21st century. Both models agreed that Safe Winter Chill is likely to decline. However, losses according to the Chilling Hours Model painted a much bleaker picture for California's fruit producers than the Dynamic Model.

A few studies have focused on winter chill in Australia. Hennessy and Clayton-Greene (1995) provided the first estimate of climate change impacts, including an analysis of the sensitivity of fruit growing locations to three warming scenarios (+1, +2 and +3 °C, applied to all temperature readings), and an application of regionalized climate model outputs for 2030 to historic temperature records. The authors used the Modified Utah Model (Linville, 1990) for quantifying chill. They found that warm sites, and sites with wide diurnal temperature ranges, were more strongly affected by chilling decline than cooler sites with more homogenous temperature profiles. For climate change scenarios, Hennessy and Clayton-Greene expected chilling declines for all sites, and for the stronger warming scenarios, they anticipated that these losses should impact production. They recommended that growers should explore ways to artificially break dormancy and consider introducing lower-chill cultivars into Southern Australia.

Darbyshire et al. (2011) evaluated historic winter chill trends at 13 locations in Australia, using four common chilling models, the Chilling Hours Model, the Modified Utah Model, the Positive Utah Model and the Dynamic Model. They used idealized daily temperature curves to produce from daily temperature records the hourly data that is required for using common chilling models. A striking result of this study was that the ranking of the 13 stations differed substantially, depending on which model was used. For the extreme case of Lenswood, South Australia, the Chilling Hours Model ranked 4th among the stations analysed, while the other models placed this site between ranks 9 and 11. This result shows

that models differ substantially and that not all model can be accurate. Darbyshire et al. (2011) report a declining winter chill trend in response to warming at most sites, most notably at the warmest locations, according to all chill models. The only exceptions were the two versions of the Utah Model, which showed increasing chill for two sites. The Dynamic Model also indicated a slight increase for the coldest location (winter temperature 3.8–6.2°C). Overall, the study indicated chill declines for almost all weather stations, which varied strongly according to which chilling model was chosen.

Darbyshire et al. (in press) also evaluated likely effects of future warming on chill accumulation. Using the Chilling Hours Model, the Modified Utah Model and the Dynamic Model, they quantified expected chill losses for three warming scenarios, in which global temperatures were raised by 1, 2 and 3°C. These global temperature increases were translated into localized warming at 13 sites across Southern Australia, using a collection of 21 General Circulation Models. Out of this population, six models were strategically selected to bracket the range of temperature changes that must be expected. Historic daily temperature records, extracted from a gridded Australia-wide dataset (for 1911–2009), were then modified by adding localized temperature changes expected for the respective climate change scenarios. Linvill (1990)'s equations were used to translate daily temperature records into hourly values, and winter chill was summarized for all 99 winter seasons included in the records. Following Luedeling et al. (2009c), results were expressed as Safe Winter Chill, the 10% quantile of the distribution across all years of the weather records. Chilling estimates for the various climate scenarios with the three models varied widely. For the +3°C scenario, chill changes across all 13 locations ranged from –20 to –84% according to the Chilling Hours Model and from –3 to –99% for the Modified Utah Model. The Dynamic Model projected losses between –7 and –77%. Chill losses were consistently projected for all locations, with in particular the warmer sites experiencing severe chill decline.

Farag et al. (2010) calculated historic and projected future changes in winter chill for Egypt. While claiming to use the Chilling Hours Model of Weinberger (Bennett, 1949), they used a chilling model, in which temperatures between 0 and 10°C were considered equally effective for chilling, while temperatures outside of this range were considered ineffective. Using historic hourly temperature records for 14 weather stations, the authors calculated historic chill accumulation in 1969/70, 1989/90 and 2008/09. Three future climate scenarios for the 2050s were generated by raising the means of temperatures for these three past winter seasons by mean annual temperature changes according to three GCMs. Interpretation of the results is difficult because the description of the methodology is somewhat incomplete, and because the authors arbitrarily selected three past winters from the historic record, which may or may not be representative of long-term trends in temperature and winter chill. The data presented is thus not sufficient for analysis of historic trends, but mean winter chill over all stations was lower by 4% in 1989/90 and by 11% in 2008/09, compared to the 1969/70 baseline. For 2050s scenarios, losses were estimated at between 28 and 42%, compared to the baseline.

A global analysis of historic and projected future changes in winter chill has been provided by Luedeling et al. (2011a). Based on more than 4000 weather stations around the world, the authors used a weather generator calibrated with daily weather station data to produce daily weather data for 18 climate scenarios, for 1975, 2000, as well as scenarios for the middle and the end of the 21st century. For future projections, three General Circulation Models and two Greenhouse Gas Emissions scenarios were considered. For each scenario, 100 replicate years of daily weather data were produced and transformed into hourly temperature records using idealized daily temperature curves. In this study, only estimates produced by the Dynamic Model are reported. This circumstance was justified

by the higher credibility of projections with the Dynamic Model, in particular across climate gradients, than with all other major models. Projections indicated major chilling losses in all warm growing regions of temperate fruits, both in the past and in the future. In particular the warmest growing regions, in North Africa, South Africa, the Southern United States, Northern Mexico, Southern China and Southern Australia are projected to suffer substantial losses in winter chill during the 21st century. Cold growing regions, in contrast, may experience little change, or even increases in winter chill, as increasing numbers of days become frost-free.

While the studies listed above used different metrics to quantify chill changes and worked in different regions, some general conclusions can be drawn. For most fruit growing regions analysed, winter chill is expected to decline. The only exception among the published case studies is Germany, where little change has occurred in the past. Only the global analysis by Luedeling et al. (2011a) indicated that cold growing regions may experience increases in winter chill. This is likely due to a geographic bias among published case studies, which have focused on growing regions where chilling is considered an important factor in orchard management. This is the case predominantly in warm growing regions, while growers in colder locations have traditionally paid little attention to winter chill. From the array of case studies, it clearly emerges that the Chilling Hours Model consistently detected the strongest changes in winter chill, while in particular the Dynamic Model was more moderate in the amount of change it projected. In light of the studies that have shown the Dynamic Model to be more accurate, in particular in warm climates (see Section 5), the latter, more moderate estimates are more likely to be accurate.

7. Adaptation strategies

The need to anticipate and adapt to climatic changes is much more urgent for growers of tree crops than for farmers engaging in annual crop production. Annual farmers can change their crop species or varieties from one season to the next, or they can plant their crops earlier or later if they sense changes in the duration of the growing season. In contrast, once orchard managers have selected and planted their tree cultivars, they require these trees to remain in production for decades. Orchard establishment is expensive, especially when low fruit or nut yields during the first few years are considered. Short-term adjustments in tree cultivars are thus very costly and would be a severe economic blow to many growers. Growers must therefore pay very close attention to growing the right trees in the right places, or they must be equipped with an arsenal of management tools to overcome slight climatic mismatches of cultivar and climate.

7.1. Better metrics

Strategies that have been used to expand the range of temperate fruit species offer potential applications in adapting production to climate change. The first strategy worth mentioning in this respect is careful selection of cultivars that are adapted to the particular climate conditions of a production site. In a slight modification of traditional practice, however, this adaptation should now consider future projected agroclimate, rather than historically observed conditions. This of course requires accurate concepts of the climatic requirements of tree crops. While this is equally true for heat requirements, this review is only concerned with chilling. As outlined above, substantial work is still needed to produce and widely introduce accurate chill metrics. Where growers use inaccurate metrics, species and cultivar selections may be poorly informed. For example, assuming that the Dynamic Model is the appropriate choice of model, the notion that one Chilling Hour indicates exactly the same amount of chill everywhere could be a problem. When

using inadequate chill metrics for selecting new cultivars for a particular growing region, growers might import trees that turn out to be very poorly adapted, even though – according to the chosen chill metric – chilling requirements should be similar to those of traditional cultivars in the region. A lot of experimentation is still needed to come to a consensus of which approach to modelling winter chill is appropriate. Until this experimental gap is closed, it appears that the Dynamic Model is preferable among the existing approaches, and it would be advantageous to determine chilling requirements in Chill Portions for many more cultivars than have been characterized to date. Where long-term bloom records and matching temperature records are available, statistical methods can help determine the chilling requirements of tree cultivars (Luedeling et al., 2009e; Yu et al., 2010; Luedeling and Gassner, 2012).

7.2. Low-chill cultivars

Breeding for low chilling requirements has also been successful in the past. The array of cultivars that is available for many species spans a wide range of climatic requirements. For example, Guerriero et al. (2010) evaluated bloom dates of 229 apricot varieties, grown in a germplasm collection in Venturina, Italy, during the warm winter of 2006/07. They found that many genotypes from northern climates did not flower at all in that year, whereas cultivars from Southern Italy flowered more profusely than in normal years. Such trials can certainly identify valuable genetic resources for further breeding. In pursuing this strategy, it must be considered that breeding for new tree cultivars can take a long time. Modern breeding techniques, as well as advances in mapping the genetic determinism of chilling are required to speed up the breeding process, so that appropriate cultivars can be developed for all major fruits within a reasonable time frame. Due to past efforts to expand cultivation to warmer regions, low-chill cultivars are already available for several species (e.g. Lesley and Winslow, 1952; Sharpe, 1961; Scorza and Miramendy, 1981; Stino et al., 1982; Griesbach, 2007).

7.3. Dormancy avoidance

In tropical climates without pronounced seasonality, it is possible to artificially induce tree dormancy by defoliating trees after harvest (Edwards, 1987; Griesbach, 2007). If this is practiced, trees appear to be able to resume their annual cycle without requiring chill. This type of management has enabled the production of temperate fruits in places like India and Kenya, but it cannot be recommended at colder sites with pronounced seasonal cycles. However, research into effects of certain management practices, such as defoliation, during the dormancy induction period should be explored. Research has shown a quantitative effect of temperature treatments during this period on the depth of dormancy (Westergaard and Eriksen, 1997; Heide and Prestrud, 2005; Tanino et al., 2010), and it may be possible to exploit such effects for practical orchard management.

7.4. Microclimate manipulation

Microclimate manipulation can also affect chill accumulation. Campoy et al. (2010) showed that shading during endodormancy can slightly advance bloom dates of apricots in Spain. Targeted irrigation can also influence microclimates. Overhead irrigation has successfully been applied in Israel for cooling buds during the hottest hours of the day (Erez, 1995).

7.5. Chemical rest-breaking

A number of chemicals have been found to promote budbreak. Many of these compounds can be phytotoxic, when applied at the wrong time, but some have been very successful in breaking dormancy, even when chilling requirements were not fulfilled (Erez et al., 2008). For example, application of hydrogen cyanamide spray has been effective in promoting bloom in Ethiopia (Ashebir et al., 2010), Israel (Erez et al., 2008), Tunisia (Chabchoub et al., 2010) and the Southern United States (Dozier et al., 1990). The same compound also proved effective in Italy (de Salvador and di Tommaso, 2003). However, hydrogen cyanamide has also been shown to be phytotoxic and to cause strong yield reductions (George et al., 1992; Siller-Cepeda et al., 1992), and due to health hazards it has already been banned in several countries. Alternative chemicals, such as plant growth regulators containing thidiazuron (Campoy et al., 2010) or certain nitrogen compounds (de Salvador and di Tommaso, 2003), have also proven effective, and human toxicity has not been reported. Rest-breaking chemicals are widely used for compensating for insufficient budbreak and for promotion of homogeneous fruit set.

8. Adaptation in the absence of thorough understanding

In spite of over 200 years of scientific interest in tree dormancy (at least since Knight, 1801), the process itself as well as the environmental factors that induce and break dormancy are not completely understood (Campoy et al., 2011b). Major knowledge gaps concern the genetics of chilling requirements (in spite of recent advances, e.g. by Celton et al., 2011; Leida et al., 2012), the timing of bud responsiveness to chilling (Campoy et al., 2011a), the effects of dormancy induction conditions on chilling requirements (Heide and Prestrud, 2005) and possible interactions between chilling and forcing during the dormancy season (Harrington et al., 2010). Due to these knowledge gaps, none of the common chilling models can strictly be called process-based; all are merely empirical. As long as models are developed without a thorough understanding of the underlying processes, we should not be surprised if they turn out to be inaccurate. Moreover, with purely empirical models, extrapolating beyond the climatic ranges that models were developed in is quite risky, and the validity of locally calibrated chilling models for climate change adaptation planning is questionable.

Given the width of prevalent knowledge gaps, it seems unlikely that a thorough understanding of which tree cultivars will be best adapted in the future will emerge soon. It should also be considered that in addition to chilling, knowledge about climate responses during several other phases of the growing cycle needs to be available in order to project yields with relative certainty (Hänninen and Tanino, 2011). Also in light of the relatively scarce resources being invested in adapting tree crops to climate change (at least compared to cereals), growers certainly cannot wait for science to produce models that will be sufficient for adaptation planning. Particularly in marginal growing regions, trees planted today will experience changes in climate that may render their production unprofitable.

An elegant way around the need for exhaustive knowledge is climate analogue analysis, a novel approach to adaptation planning (Ramirez-Villegas et al., 2011). The premise of this strategy is that most climatic settings that are projected for a given location can already be found at present, though in a different location. For example, the climate projected for a particular target growing region for 2050 (according to a given climate model and greenhouse gas emissions scenario) can currently be found at a different location. These analogue locations can inform adaptation planning at the target growing region. Tree cultivars that are

grown successfully at the analogue location may be candidates for planting in the target region today, and new cultivars slated for introduction into the target region should possibly be tested at the analogue site rather than the target site, to ensure that they are viable in a warmer climate. Lastly, observations of tree phenology and productivity across target and a suite of analogue sites (for different climate models and greenhouse gas emissions scenarios) can help develop models that actually are suitable for climate change projections. Such empirical models would be valid for the range of climates that can plausibly be expected at the target site. Geospatial procedures for identifying analogue locations exist (Luedeling and Neufeldt, *in press*), but to my knowledge they have not been applied for planning the adaptation of tree crop systems to climate change. In the face of the substantial knowledge gaps in tree physiology, climate analogues may be a useful strategy for ensuring productive orchards in the future.

9. Concluding remarks

Temperate orchards are in urgent need of climate change adaptation strategies because of the high investments incurred in orchard development and the long productive life span of trees. Yet scientific understanding of the complex processes involved in tree physiology lags far behind knowledge about processes in annual crops. While winter chill has been studied more than many other weather-dependent processes, all existing modelling approaches are purely empirical, and there is little reason to believe that their mathematical equations are related in a biologically meaningful way to tree physiology. Yet even within the array of existing models, accuracy differs substantially, as indicated by the model comparison studies mentioned above (Section 5). The Dynamic Model currently seems to be the frontrunner in terms of accuracy, but it seems like a far greater number of growers use the Chilling Hours approach to chilling quantification. The latter is easy to understand and intuitive, while explaining the Dynamic Model to practitioners (or anyone else) is quite a challenge. Nevertheless, temperate fruit and nut industries should attempt to make the transition, in particular in marginal growing regions. Time series analyses and projections have shown dramatic losses in the number of Chilling Hours for California, Australia, South Africa and most warm growing regions. The extent of these projected losses, in combination with assumed chilling requirements of tree cultivars, makes the future look very bleak for many growers, and adaptation seems barely possible. The Dynamic Model typically also projects problems, but not nearly the catastrophic losses indicated by the Chilling Hours approach. Finding suitable tree species and cultivars looks much more possible.

The considerable number of studies that have shown the Chilling Hours Model to be inferior to the other approaches, especially when considering different climatic settings, provides a strong indication that the Chilling Hours Model should not be used for climate change projections. Moreover, its usefulness for comparing chilling requirements across growing regions appears very limited, and even for practical orchard management under stationary climatic conditions, other models have consistently proven more accurate. It may thus be time for tree crop industries to transition to the more accurate models. This is particularly important for avoiding misleading projections about the impacts of climate change, which growers are likely to increasingly consider in the future due to the long planning horizons involved in orchard operations. The Dynamic Model seems like the best bet for all growing regions at the moment.

Currently, locating adapted germplasm is hindered by the lack of estimates of chilling requirements in accurate units. As shown in particular by Luedeling and Brown (2011), Chilling Hour estimates,

which are available for many cultivars, cannot easily be transferred to a new location other than where requirements were determined. Standardization is needed in order to facilitate effective deployment of appropriate cultivars to places that will need these trees in the future, and the Dynamic Model seems like a good approach for producing such standardized estimates. A global effort is needed to determine chilling requirements of cultivars and assemble a comprehensive database of these. Such a database should contain climatic requirements as well as information on where and how these were determined. It would also be desirable to collect multi-locational datasets on the breaking of dormancy and tree phenology, coupled with detailed weather records. If such records were available for a wide range of climates, statistical means (e.g. Luedeling and Gassner, 2012) could be applied for expanding our understanding of the temperature responses of trees during the dormancy phase. Such a compilation will be particularly valuable if it includes records of other environmental factors that may influence dormancy and if it expands into marginal production sites where common modelling approaches often fail.

Overall, a lot more research is needed into what exactly drives the progression of trees through the dormancy phase, what physiological processes and genetic mechanisms underlie this progression, and how these processes can be manipulated. In the (probably long) meantime, until knowledge gaps are filled, more work is needed on manipulating orchard climates and the breaking of individual buds. Another approach that can be effective in the absence of good scientific understanding is climate analogue analysis. For complex agricultural systems, searching for future climates among present-day locations and extracting adaptation lessons from such sites, may be the most promising strategy for ensuring that production remains viable in a climatically changing future.

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.
- Allan, P., Linsley-Noakes, G.C., Holcroft, D.M., Brunette, S.A., Burnett, M.J., Cathcart-Kay, A., 1997. Kiwifruit research in a subtropical area. *Acta Hortic.* 444, 37–42.
- Allan, P., Rufus, G., Linsley-Noakes, G.C., Matthee, G.V., 1995. Winter chill models in a mild subtropical area and effects of constant 6° C chilling on peach budbreak. *Acta Hortic.* 409, 9–17.
- Anderson, J.L., Richardson, E.A., Kesner, C.D., 1986. Validation of chill unit and flower bud phenology models for 'Montmorency' sour cherry. *Acta Hortic.* 184, 71–78.
- Anderson, J.L., Seeley, S.D., 1992. Modelling strategies in pomology: development of the Utah Models. *Acta Hortic.* 313, 297–306.
- Ashebir, D., Deckers, T., Nyssen, J., Bihon, W., Tsegay, A., Tekie, H., Poesen, J., Haile, M., Wondumagegnehu, F., Raes, D., Behailu, M., Deckers, J., 2010. Growing apple (*Malus domestica*) under tropical mountain climate conditions in northern Ethiopia. *Exp. Agric.* 46, 53–65.
- Balandier, P., Bonhomme, M., Rageau, R., Capitan, F., Parisot, E., 1993a. Leaf bud endodormancy release in peach trees—evaluation of temperature models in temperate and tropical climates. *Agric. For. Meteorol.* 67, 95–113.
- Balandier, P., Gendraud, M., Rageau, R., Bonhomme, M., Richard, J.P., Parisot, E., 1993b. Bud break delay on single node cuttings and bud capacity for nucleotide accumulation as parameters for endodormancy and paradormancy in peach trees in a tropical climate. *Sci. Hortic.* 55, 249–261.
- Baldocchi, D., Wong, S., 2008. Accumulated winter chill is decreasing in the fruit growing regions of California. *Clim. Change* 87, S153–S166.
- Bennett, J.P., 1949. Temperature and bud rest period. *Calif. Agric.* 3 (9), 12.
- Bidabé, B., 1965. Contrôle de l'époque de floraison du pommier par une nouvelle conception de l'action de températures. *C. R. Acad. Agric. Fr.* 49, 934–945.
- Campoy, J.A., Ruiz, D., Allderman, L., Cook, N., Egea, J., 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.
- Campoy, J.A., Ruiz, D., Cook, N., Allderman, L., Egea, J., 2011a. Clinal variation of dormancy progression in apricot. *S. Afr. J. Bot.* 77, 618–630.
- Campoy, J.A., Ruiz, D., Egea, J., 2010. Effects of shading and thidiazuron + oil treatment on dormancy breaking, blooming and fruit set in apricot in a warm-winter climate. *Sci. Hortic.* 125, 203–210.
- Campoy, J.A., Ruiz, D., Egea, J., 2011b. Dormancy in temperate fruit trees in a global warming context: a review. *Sci. Hortic.* 130, 357–372.

- Celton, J.M., Martinez, S., Jammes, M.J., Bechti, A., Salvi, S., Legave, J.M., Costes, E., 2011. Deciphering the genetic determinism of bud phenology in apple progenies: a new insight into chilling and heat requirement effects on flowering dates and positional candidate genes. *New Phytol.* 192, 378–392.
- Cesaraccio, C., Spano, D., Snyder, R.L., Duce, P., 2004. Chilling and forcing model to predict bud-burst of crop and forest species. *Agric. For. Meteorol.* 126, 1–13.
- Chabchoub, M.A., Aounallah, M.K., Sahli, A., 2010. Effect of hydrogen cyanamide on bud break, flowering and fruit growth of two pear cultivars (*Pyrus communis*) under Tunisian condition. *Acta Hortic.* 884, 427–432.
- Chandler, W.H., 1942. *Deciduous Orchards*. Lea & Febiger, Philadelphia, USA.
- Chmielewski, F.M., Blümel, K., Henniges, Y., Blanke, M., Weber, R.W.S., Zoth, M., 2011. Phenological models for the beginning of apple blossom in Germany. *Meteorol. Z.* 20, 487–496.
- Chaine, I., Cour, P., Rousseau, D.D., 1998. Fitting models predicting dates of flowering of temperate-zone trees using simulated annealing. *Plant Cell Environ.* 21, 455–466.
- Chaine, I., Cour, P., 1999. Climatic determinants of budburst seasonality in four temperate-zone tree species. *New Phytol.* 143, 339–349.
- Couvillon, G.A., Erez, A., 1985. Effect of level and duration of high temperatures on rest in the peach. *J. Am. Soc. Hortic. Sci.* 110, 579–581.
- Darbyshire, R., Webb, L., Goodwin, I., Barlow, E.W.R. Impact of future warming on winter chilling in Australia. *Int. J. Biometeorol.*, <http://dx.doi.org/10.1007/s00484-012-0558-2>, in press.
- Darbyshire, R., Webb, L., Goodwin, I., Barlow, S., 2011. Winter chilling trends for deciduous fruit trees in Australia. *Agric. For. Meteorol.* 151, 1074–1085.
- de Salvador, F.R., di Tommaso, G., 2003. Dormancy control in cherry. *Inform. Agric.* 59, 63–66.
- Dennis, F.G., 2003. Problems in standardizing methods for evaluating the chilling requirements for the breaking of dormancy in buds of woody plants. *HortScience* 38, 347–350.
- Dozier, W.A., Powell, A.A., Caylor, A.W., McDaniel, N.R., Carden, E.L., McGuire, J.A., 1990. Hydrogen cyanamide induces budbreak of peaches and nectarines following inadequate chilling. *HortScience* 25, 1573–1575.
- Edwards, G.R., 1987. Producing temperate-zone fruit at low latitudes—avoiding rest and the chilling requirement. *HortScience* 22, 1236–1240.
- Else, M., Atkinson, C., 2010. Climate change impacts on UK top and soft fruit production. *Outlook Agric.* 39, 257–262.
- Erez, A., 1995. Means to compensate for insufficient chilling to improve bloom and leafing. *Acta Hortic.* 395, 81–95.
- Erez, A., Couvillon, G.A., 1987. Characterization of the influence of moderate temperatures on rest completion in peach. *J. Am. Soc. Hortic. Sci.* 112, 677–680.
- Erez, A., Couvillon, G.A., Hendershott, C.H., 1979. Effect of cycle length on chilling negation by high temperatures in dormant peach leaf buds. *J. Am. Soc. Hortic. Sci.* 104, 573–576.
- Erez, A., Fishman, S., Linsley-Noakes, G.C., Allan, P., 1990. The dynamic model for rest completion in peach buds. *Acta Hortic.* 276, 165–174.
- Erez, A., Yablowitz, Z., Aronovitz, A., Hadar, A., 2008. Dormancy breaking chemicals—efficiency with reduced phytotoxicity. *Acta Hort* 772, 105–112.
- Farag, A.A., Khalil, A.A., Hassanein, M.K., 2010. Chilling requirement for deciduous fruits under climate change in Egypt. *Res. J. Agric. Biol. Sci.* 6, 815–822.
- Fishman, S., Erez, A., Couvillon, G.A., 1987a. The temperature dependence of dormancy breaking in plants—computer simulation of processes studied under controlled temperatures. *J. Theor. Biol.* 126, 309–321.
- Fishman, S., Erez, A., Couvillon, G.A., 1987b. 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.
- Gardner, R.A.W., Bertling, I., 2005. Effect of winter chilling and paclobutrazol on floral bud production in *Eucalyptus nitens*. *S. Afr. J. Bot.* 71, 238–249.
- Gebauer, J., Luedeling, E., Hammer, K., Buerkert, A., 2009. Agro-horticultural biodiversity in mountain oases of northern Oman. *Acta Hortic.* 817, 325–332.
- Gebauer, J., Luedeling, E., Hammer, K., Nagieb, M., Buerkert, A., 2007. Mountain oases in northern Oman: an environment for evolution and in situ conservation of plant genetic resources. *Genet. Resour. Crop Environ.* 54, 465–481.
- George, A.P., Lloyd, J., Nissen, R.J., 1992. Effects of hydrogen cyanamide, paclobutrazol and pruning date on dormancy release of the low-chill peach cultivar Flordaprince in subtropical Australia. *Aust. J. Exp. Agric.* 32, 89–95.
- Gilreath, P.R., Buchanan, D.W., 1981. Rest prediction model for low-chilling Sungold nectarine. *J. Am. Soc. Hortic. Sci.* 106, 426–429.
- Griesbach, J., 2007. Growing Temperate Fruit Trees in Kenya. *World Agroforestry Center (ICRAF)*, Nairobi, Kenya.
- Guédon, Y., Legave, J.M., 2008. Analyzing the time-course variation of apple and pear tree dates of flowering stages in the global warming context. *Ecol. Model* 219, 189–199.
- Guerriero, R., Viti, R., Iacona, C., Bartolini, S., 2010. Is apricot germplasm capable of withstanding warmer winters? This is what we learned from last winter. *Acta Hortic.* 862, 265–272.
- Hänninen, H., Kramer, K., 2007. A framework for modelling the annual cycle of trees in boreal and temperate regions. *Silva Fenn.* 41, 167–205.
- Hänninen, H., Tanino, K., 2011. Tree seasonality in a warming climate. *Trends Plant Sci.* 16, 412–416.
- Harrington, C.A., Gould, P.J., St Clair, J.B., 2010. Modeling the effects of winter environment on dormancy release of Douglas-fir. *For. Ecol. Manage.* 259, 798–808.
- Heide, O.M., Prestrud, A.K., 2005. Low temperature, but not photoperiod, controls growth cessation and dormancy induction and release in apple and pear. *Tree Physiol.* 25, 109–114.
- Hennessy, K.J., Clayton-Greene, K., 1995. Greenhouse warming and vernalization of high-chill fruit in Southern Australia. *Clim. Change* 30, 327–348.
- IPCC, 2007. *Climate change 2007—synthesis report*. Contributions of working groups I, II and III to the fourth assessment report of the Intergovernmental Panel on Climate Change. Intergovernmental Panel on Climate Change, Geneva, Switzerland.
- Knight, T.A., 1801. Account of some experiments on the ascent of the sap in trees. *Philos. Trans. R. Soc. London* 91, 333–353.
- Lammerts, W.E., 1941. An evaluation of peach and nectarine varieties in terms of winter chilling requirements and breeding possibilities. *P. Am. Soc. Hortic. Sci.* 39, 205–211.
- Lammerts, W.E., 1945. The breeding of ornamental edible peaches for mild climates. 1. Inheritance of tree and flower characters. *Am. J. Bot.* 32, 53–61.
- Legave, J.M., Farrera, I., Almeras, T., Calleja, M., 2008. Selecting models of apple flowering time and understanding how global warming has had an impact on this trait. *J. Hortic. Sci. Biotechnol.* 83, 76–84.
- Legave, J.M., Giovannini, D., Christen, D., Oger, R., 2009. Global warming in Europe and its impacts on floral bud phenology in fruit species. *Acta Hortic.* 838, 21–26.
- Leida, C., Conesa, A., Llacer, G., Badenes, M.L., Rios, G., 2012. Histone modifications and expression of DAM6 gene in peach are modulated during bud dormancy release in a cultivar-dependent manner. *New Phytol.* 193, 67–80.
- Lesley, J.W., Winslow, M.M., 1952. Peach varieties for a warm winter climate. *Circ. Calif. Agric. Expt. Sta.* 406, 2–7.
- Linkosalo, T., Lappalainen, H.K., Hari, P., 2008. A comparison of phenological models of leaf bud burst and flowering of boreal trees using independent observations. *Tree Physiol.* 28, 1873–1882.
- Linkosalo, T., Ranta, H., Oksanen, A., Siljamo, P., Luomajoki, A., Kukkonen, J., Sofiev, M., 2010. A double-threshold temperature sum model for predicting the flowering duration and relative intensity of *Betula pendula* and *B. pubescens*. *Agric. For. Meteorol.* 150, 1579–1584.
- Linsley-Noakes, G.C., Allan, P., 1994. Comparison of 2 models for the prediction of rest completion in peaches. *Sci. Hortic.* 59, 107–113.
- Linville, D.E., 1990. Calculating chilling hours and chill units from daily maximum and minimum temperature observations. *HortScience* 25, 14–16.
- Luedeling, E., Blanke, M., Gebauer, J., 2009a. Climate change effects on winter chill for fruit crops in Germany—Auswirkungen des Klimawandels auf die Verfügbarkeit von Kältewirkung (Chilling) für Obstgehölze in Deutschland. *Erwerbs-Obstbau* 51, 81–94.
- Luedeling, E., Brown, P.H., 2011. A global analysis of the comparability of winter chill models for fruit and nut trees. *Int. J. Biometeorol.* 55, 411–421.
- Luedeling, E., Buerkert, A., 2008a. Effects of land use changes on the hydrological sustainability of mountain oases in northern Oman. *Plant Soil* 304, 1–20.
- Luedeling, E., Buerkert, A., 2008b. Typology of oases in northern Oman based on Landsat and SRIM imagery and geological survey data. *Remote Sens. Environ.* 112, 1181–1195.
- Luedeling, E., Gassner, A., 2012. Partial Least Squares regression for analyzing walnut phenology in California. *Agric. For. Meteorol.* 158, 43–52.
- Luedeling, E., Gebauer, J., Buerkert, A., 2009b. Climate change effects on winter chill for tree crops with chilling requirements on the Arabian Peninsula. *Clim. Change* 96, 219–237.
- Luedeling, E., Girvetz, E.H., Semenov, M.A., Brown, P.H., 2011a. Climate change affects winter chill for temperate fruit and nut trees. *PLoS ONE* 6, e20155.
- Luedeling, E., Kunz, A., Blanke, M., 2011b. More winter chill for fruit trees in warmer winters?—Mehr Chilling für Obstbäume in wärmeren Wintern? *Erwerbs-Obstbau* 53, 145–155.
- Luedeling, E., Neufeldt, H. Carbon sequestration potential of parkland agroforestry in the Sahel. *Clim. Change*, <http://dx.doi.org/10.1007/s10584-012-0438-0>, in press.
- Luedeling, E., Zhang, M., Girvetz, E.H., 2009c. Climatic changes lead to declining winter chill for fruit and nut trees in California during 1950–2099. *PLoS One* 4, e6166.
- Luedeling, E., Zhang, M., Luedeling, V., Girvetz, E.H., 2009d. Sensitivity of winter chill models for fruit and nut trees to climate change. *Agric. Ecosyst. Environ.* 133, 23–31.
- Luedeling, E., Zhang, M., McGranahan, G., Leslie, C., 2009e. Validation of winter chill models using historic records of walnut phenology. *Agric. For. Meteorol.* 149, 1854–1864.
- Luedeling, E., Zhang, M., Luedeling, V., Girvetz, E.H., 2010. Erratum to Sensitivity of winter chill models for fruit and nut trees to climatic changes expected in California's Central Valley [Agric. Ecosyst. Environ., 133, (2009), 23–31]. *Agric. Ecosyst. Environ.* 138, 357.
- Midgley, S.J.E., Lötze, E., 2011. Climate change in the Western Cape of South Africa: trends, projections and implications for chill unit accumulation. *Acta Hortic.* 903, 1127–1134.
- Nagieb, M., Häser, J., Siebert, S., Luedeling, E., Buerkert, A., 2004. Settlement history of a mountain oases in Northern Oman—evidence from land-use and archaeological studies. *Die Erde* 135, 81–106.
- Newman, S.M., Ku, V.V.V., Hetherington, S.D., Nissen, R.J., Chu, T.D., Tran, D.L., 2008. Mapping stone fruit supply chains in North West Vietnam. *Hanoi*, 261–267.
- Nissen, R.J., George, A.P., Broadley, R.H., Newman, S.M., Hetherington, S., 2006. Developing improved supply chains for temperate fruits in transitional Asian economies of Thailand and Vietnam. *Acta Hortic.* 699, 335–342.
- Overcash, J.P., Campbell, J.A., 1955. The effects of intermittent warm and cold periods on breaking the rest period of peach leaf buds. *Proc. Am. Soc. Hortic. Sci.* 66, 87–92.

- Perez, F.J., Ormeno, N., Reynaert, J., Rubio B., B., 2008. Use of the Dynamic Model for the assessment of winter chilling in a temperate and a subtropical climatic zone of Chile. *Chil. J. Agric. Res.* 68, 198–206.
- Ramirez-Villegas, J., Lau, C., Köhler, A.-K., Signer, J., Jarvis, A., Arnell, N., Osborne, T., Hooker, J., 2011. Climate Analogues: Finding Tomorrow's Agriculture Today. CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS), Cali, Colombia.
- Rea, R., Eccel, E., 2006. Phenological models for blooming in apple in a mountainous region. *Int. J. Biometeorol.* 51, 1–16.
- Richardson, E.A., Seeley, S.D., Walker, D.R., 1974. A model for estimating the completion of rest for Redhaven and Elberta peach trees. *HortScience* 9, 331–332.
- Ruiz, D., Campoy, J.A., Egea, J., 2007. Chilling and heat requirements of apricot cultivars for flowering. *Environ. Exp. Bot.* 61, 254–263.
- Rumayor-Rodriguez, A., 1995. Multiple-regression models for the analysis of potential cultivation areas for Japanese plums. *HortScience* 30, 605–610.
- Samish, R.M., 1954. Dormancy in woody plants. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 5, 183–204.
- Saure, M.C., 1985. Dormancy release in deciduous fruit trees. *Hortic. Rev.* 7, 239–300.
- Schwartz, M.D., 1999. Advancing to full bloom: planning phenological research for the 21st century. *Int. J. Biometeorol.* 42, 113–118.
- Scorza, R., Miramendy, H., 1981. Introduction and evaluation of low chilling peach and nectarine cultivars in the Bolivian Highlands. *Fruit Var. J.* 35, 122–125.
- Shaltout, A.D., Unrath, C.R., 1983. Rest completion prediction model for Starkrimson Delicious apples. *J. Am. Soc. Hortic. Sci.* 108, 957–961.
- Sharpe, R.H., 1961. Flordawo. A peach for central Florida. *Circ. Florida Agric. Expt. Sta.* S-126, 1–3.
- Siller-Cepeda, J.H., Fuchigami, L.H., Chen, T.H.H., 1992. Hydrogen cyanamide-induced budbreak and phytotoxicity in Redhaven peach buds. *HortScience* 27, 874–876.
- Stino, G.R., Mansour, N.M., Hamouda, A., El-Sheikh, A.R., 1982. Adaptability of 3 Imported Peach Cultivars in Egypt. *Ain Shams University, Faculty of Agriculture Research Bulletin*, pp. 1–21.
- Sunley, R.J., Atkinson, C.J., Jones, H.G., 2006. Chill unit models and recent changes in the occurrence of winter chill and spring frost in the United Kingdom. *J. Hortic. Sci. Biotechnol.* 81, 949–958.
- Tanino, K.K., Kalcsits, L., Silim, S., Kendall, E., Gray, G.R., 2010. Temperature-driven plasticity in growth cessation and dormancy development in deciduous woody plants: a working hypothesis suggesting how molecular and cellular function is affected by temperature during dormancy induction. *Plant Mol. Biol.* 73, 49–65.
- Thompson, W.K., Jones, D.L., Nichols, D.G., 1975. Effects of dormancy factors on growth of vegetative buds of young apple trees. *Aust. J. Agric. Res.* 26, 989–996.
- Valentini, N., Me, G., Ferrero, R., Spanna, F., 2001. Use of bioclimatic indexes to characterize phenological phases of apple varieties in Northern Italy. *Int. J. Biometeorol.* 45, 191–195.
- Vegis, A., 1961. Samenkeimung und vegetative Entwicklung der Knospen. *Handbuch der Pflanzenphysiologie – Encyclopedia of Plant Physiology*, vol. 16, pp. 168–298.
- Vegis, A., 1964. Dormancy in higher plants. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 15, 185–224.
- Vergara, R., Pérez, F.J., 2010. Similarities between natural and chemically induced bud-endodormancy release in grapevine *Vitis vinifera* L. *Sci. Hortic.* 125, 648–653.
- Viti, R., Andreini, L., Ruiz, D., Egea, J., Bartolini, S., Iacona, C., Campoy, J.A., 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.
- Warmund, M.R., Krumme, J., 2005. A chilling model to estimate rest completion of erect blackberries. *HortScience* 40, 1259–1262.
- Weinberger, J.H., 1950. Chilling requirements of peach varieties. *P. Am. Soc. Hortic. Sci.* 56, 122–128.
- Westergaard, L., Eriksen, E.N., 1997. Autumn temperature affects the induction of dormancy in first-year seedlings of *Acer platanoides* L. *Scand. J. Forest Res.* 12, 11–16.
- Wrege, M.S., Herter, F.G., Steinmetz, S., Reisser Jr., C., Caramori, P.H., Matzenauer, R., Braga, H.J., 2010. Impact of global warming on the accumulated chilling hours in the southern region of Brazil. *Acta Hortic.* 872, 31–40.
- Yu, H., Luedeling, E., Xu, J., 2010. Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. *Proc. Nat. Acad. Sci. U.S.A.* 107, 22151–22156.
- Zhang, J., Taylor, C., 2011. The Dynamic Model provides the best description of the chill process on 'Sirora' pistachio trees in Australia. *HortScience* 46, 420–425.