

The Physiology of Chilling Temperature Requirements for Dormancy Release and Bud-break in Temperate Fruit Trees Grown at Mild Winter Tropical Climate

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Abstract

It is studied that inadequate winter chilling may interfere with the normal processes of plant growth, reproductive development and subsequent yield. As much of the evidences behind these studies are subjective and region based, the available information was collated and evaluated to further investigate the impacts of winter chill that is currently an issue of fruit growers in mild winter areas. Though, the period of adequate low temperatures is insufficient in warmer regions to satisfy the chilling requirements of temperate fruit trees, this call up on many option for chill compensation; like planting low chill cultivars, use of dormancy breaking chemicals, forced defoliation, pruning and some other techniques as an alternative strategies. However, the diverse agro-climatic conditions due to major differences in altitude, rainfall as well as in slope characteristics showed the existence of different chilling temperature requirements across locations that favor many temperate fruit trees to grow: including apple, pear, grape, peach, nectarine, plum, cherry, walnut, almond and other fruit tree species. Temperate fruit production in mild winter areas now days increased rapidly and even more new industries are being developed in regions where none previously existed. To date, in tropical highlands, fruit productivity and quality have been gradually improved through introduction and selection of better adaptable varieties based on their chilling requirements. To supplement the present existing knowledge gap in relation to the cultivar-environment interactions, the use of chill models to quantify chill accumulation during winter months would help in classifying the environment (potential growing areas) according to the amount of chill hours existed in that location.

Up to date, a number of valid methods were applied for quantification of chill accumulation in tropical and sub-tropical conditions showed varying results depending on the types of species, existing warm temperature and other climatic variables. The limitation in their predictive performance from region to region is due to their designing approaches that were primarily for temperate climate. This requires a model comparison for specific location, i.e. by using more than one model to avoid the potential misleading in calculation and chill estimation. Of the chill models tested to quantify the chill accumulation in the mild winter areas, the use of dynamic model gave good estimation that it nullifies the chilling reversal by high temperature. Also, the model of Positive Chill Units (PCU, or Positive Utah) is a competent under warm climate, next to the dynamic model. The Positive Utah model, an iteration of the original Utah, excludes the negation influence of high temperatures. The procedure for PCU is the same as for the original Utah model except that, when negative, the chill unit value is set equal to zero. Therefore, the accumulated chill units are equal to zero until the temperatures drop into the effective zone and positive chill units begin to accumulate. Though, for these areas with warm climate, using the 0 - 7.2 °C model is not recommended, because of its sensitivity to changes in temperatures that represent different weighing factors recorded for other models. Other important alternatives to these classical models include, the Growing Degree Hour Model (GDH), the Mean Temperature Model, Exponential temperature response functions and others are applied as independently, or in combination with classical chill models for a better chill estimation. Winter chill should be studied like other weather dependent processes because the present trends in chill decline across locations significantly affect fruit culture in areas with mild winter. Therefore, identifying the

problems related with lack of insufficient winter chilling would help in designing possible strategies for the changing scenarios and understanding the current physiological responses of the plant against these changes.

Keywords: temperate fruits and nuts trees, chilling requirement, chill models, dormancy release, bud-break

1. Introduction

Temperate perennial crops that are growing in these seasonally restricted temperate regions require chilling temperatures that should be satisfied in order to initiate growth and flowering in spring (Saure, 1985). They undergo a cycle of dormancy requirement that inhibits growth until exposure to low winter temperatures (chilling), prior to spring bud break. The duration of the dormancy period minimizes subsequent low temperature damage to flowers by delaying bud break and flowering. For temperate fruit trees and other woody perennials in the region, chilling requirements can be adaptive whereas in areas with mild winters, fluctuating winter temperature causes highly variable ranges of chill (Seeley, 1996; Richardson et al., 1974; Samish, 1954) and short chilling requirements are evident. Failure to receive sufficient chilling can lead to serious consequences including reduction of flower quality, abscission of flower buds, protraction of the flowering process and reduced fruit set (Jackson et al., 1983; Erez & Lavee, 1971; Abbott, 1962). Also, lack of effective chilling during winters in tropical and sub-tropical areas result in prolonged dormancy leading to poor blooming, strong apical dominance, and unsynchronized growth patterns and, consequently, low yields (Cook and Jacobs, 1999). Similarly, reproductive development in perennial crops under mild winter conditions involves an extended and complex sequence of morphological, physiological and metabolic changes (Chmielewski et al., 2004; Jackson et al., 1983; Spiegel-Roy & Alston, 1979; Erez & Lavee, 1971). Moreover, the beginning of the tree blossom stage depends on annual deviations in air temperature, i.e., years with temperatures above normal in late winter and early spring are clearly showed irregularities in the date of the beginning of the blossom stage. This indicates that high winter temperature has a negative effect on accumulated winter-chill particularly in tropical and sub-tropical climates (Byrne, 2005).

Early studies by Weinberger (1950) assumed that the hourly temperatures that were accumulated over winter for temperature ranges between 0 and 7.2 °C was found successful for dormancy release and bud break. However, the chill requirements measured as chill hours (CH) by Weinberger (1950), without considering the temperature scenarios would be a poor indicator of the chill effectively accumulated by the buds. Later on, in Utah, Richardson et al. (1974) developed the chill model that estimated hourly chill exposure using a weighted step-function. The model supposes that chill accumulation occurs within a temperature range of 2.5 and 12.5 °C, outside of which, the accumulation is nil or negative. It revealed that different temperatures have different effectiveness in accumulating chilling and notably the most effective chilling occurs above 2.5 °C and below 7°C. The Utah model gives good results in cool and cold temperate climates; however, it yields a large quantity of negative chill values in tropical and sub-tropical climates. A modification of Utah model, the Positive Utah Model (Positive Chill Units (PCU)), has come up with better results in sub-tropical and tropical mild winter conditions (Linsley-Noakes et al., 1994). It assumed that previously accumulated chilling cannot be negated by the influence of high temperatures, but equal to zero for every raise in temperature above 12.5 °C and below 1.5°C. Fishman et al. (1987) developed the Dynamic Model for warm winter conditions, which takes a different approach to quantifying winter chill. It assumes that winter chill results from a two step process, in which an intermediate product is first formed in a process promoted by cold temperatures. Warm temperatures can destroy this intermediate product. As soon as a certain quantity of intermediate has accumulated, it is irreversibly transformed into a Chill Portion (CP), which can no longer be destroyed (Fishman et al., 1987; Erez et al., 1990).

An important alternative to the classical models are the growing Degree Hour Model (GDH), the Mean Temperature Model and Exponential temperature response function for mild winter areas. These models also give good result by nullifying the negative values generated by Utah model. (Linkosalo, 2000; Hänninen, 1990; Shaulout & Unrath, 1983; Gilreath & Buchanan, 1981). More recent work with apple and pear suggests that a wide range of chilling temperatures between 1°C and 13°C were equally effective in inducing dormancy release. This may explain that chill estimates derived from the classical models (Utah chill units; Richardson et al., 1974; 1975) fail to fully estimate bud dormancy progression in areas with mild winter (Jacobs et al., 2002).

In view of the widespread perception that chilling temperature requirements has a significant impact on flowering and fruit yield, these empirical modes have been widely used to determine the amount of chilling in a specific location. Also, chill models are used to predict the historical trends of weather dynamics, that how the chill accumulation increase or decline with time. Therefore, in application, all models are arbitrary and mainly dependent on temperature, day length and types of fruit tree grown. To avoid this limitation, applying more than

one model for a specific location would help in choosing the one with a better predictive performance that could reflect dormancy development and release more accurately..

2. Dormancy

Dormancy is a phenomenon when the buds remain dormant due to growth-arresting physiological conditions, as opposed to the quiescent period that the buds remain dormant due to unfavorable environmental conditions (Cesaraccio et al., 2004). This dormancy or sleeping stage protects these buds from oncoming cold weather. Once buds have entered dormancy, they will be tolerant to temperatures much below freezing and will not grow in response to mid-winter warm spells (Cannell & Smith, 1983). These buds remain dormant until they have accumulated sufficient chilling of cold weather. When enough chilling accumulates, the buds are ready to grow in response to warm temperatures during spring. As long as there have been enough chill, the flower and leaf buds develop normally. If the buds do not receive sufficient chilling temperatures during winter to completely release dormancy, trees will develop one or more of the physiological symptoms associated with insufficient chilling include delayed foliation, reduced fruit set and increased buttoning, and reduced fruit quality (Petri & Leite, 2004). Li et al. (2003a) reported that in the temperate climates of the Northern Hemisphere, most of the fruit trees and other woody plants enter into ecodormancy at the end of summer or beginning of autumn. This was followed by a shortened photoperiod which causes the cessation of growth and a change in the development of terminal shoots, which pass from leaf shoots to form primordia with protective scales, giving rise to autumn buds.

Although the term dormancy seems intuitively obvious, it is a complex term with a variety of definitions: Lang et al. (1987) defined dormancy as a state of reduced or stopped activity or development of specific plant tissues that will resume in the future. Many researchers separated dormancy into a period of rest and a period of 'quiescence' (Linkosalo, 2000; Hänninen, 1990; Cannell & Smith, 1983). For example, Sarvas (1974) defined rest as a period when buds are dormant due to physiological conditions, and he defined quiescence as a period when the buds remain dormant due to unfavorable environmental conditions. Several models described the breaking of rest and overcoming quiescence in terms of chill accumulation to abruptly break rest followed by a period of forcing temperature to overcome quiescence (Fuchigami & Nee, 1987; Cannell & Smith, 1983).

Horvath et al. (2003) reviewed three different states of dormancy in relation to the factors regulating seasonal progression from one state to another. (i) Paradormancy occurs due to the environmental factors that would be outside the bud but within the plant that affects growth and determine all the activities (Lang, 1987). Paradormancy is in similarity with apical dominance and correlative inhibition, as occurs with lateral buds; both can be overcome by physical (terminal bud removal) and chemical (growth regulators) treatments (Hillman, 1984). (ii) Winter-dormancy (endodormancy or rest) is a true dormancy that when the bud growth is prevented by an inhibitory system such as growth regulators operating within the bud and commences after leaf abscission. It strongly differs from paradormancy in that removing bud scales or leaves does not break this type of dormancy. Seasonal endodormancy in fruit trees, as well as other woody perennials, is a phase of development that allows the plant to survive periods of stress often associated with low winter temperatures or even drought. In this dormant state, resistance to low temperatures is at its highest. Overcoming endodormancy is achieved by a period of chilling exposure that can be of considerable duration in some cases. Endodormancy results from physiological changes in the bud which prevent untimely growth due to unsuitable climatic conditions. (iii) Imposed dormancy (ectodormancy) occurs when growth is prevented directly by external environmental factors and is reversible. This type of dormancy mainly occurs in late winter when buds are ready to grow and respond to increasing temperatures as evident during 'forcing' of bud break in some fruit production systems. Once the chill requirement has been met, buds grow when exposed to warm temperatures.

2.1 The Nature of Dormant State in Fruit Trees

Saure (1985) states dormancy as a period in which visible growth is not obviously apparent, but, cellular differentiation occurs in a slow and steady manner; for example, an increase in bud weight. In apple, the development of primordia during winter has been shown to continue with respect to differentiation and enlargement throughout the season with growth being greatest from February to March (Buban & Faust, 1995). Brown (1960) reported three phases of growth in apricot flowers within buds using detailed descriptive growth curves: the first in the autumn and early winter where growth rate is very slow, the second or transition phase in late winter shows a slightly greater growth rate than the first and the final phase, associated with the events that promote very rapid bud break. There is also active synthesis of RNA and protein during dormancy in pear (Zimmerman & Faust, 1969), peach (Bagni et al., 1977) and apple (Li et al., 1989). Durner and Poling (1987) states that dormancy induction in strawberry is clearly related to short days and declining temperatures. Thus,

there is a marked morphological difference between the leafless state and leafy strawberry plant as they enter dormancy. Nishizawa and Hori (1993b) reported that dormancy becomes noticeable in as strawberry leaf size declines along with leaf petiole length but, as with deciduous fruit trees, cooling the roots of strawberry is prerequisite for effective bud break. Brennan et al. (2013) states that using a system of cold storage of raspberry canes for subsequent cropping in greenhouse conditions for 6 weeks at 2 °C or below produced even bud break and eventual yields of greater than 0.9 kg per cane. Accordingly, the canes could be stored for longer periods, but the temperature should be reduced to 1 °C or below, to prevent premature bud break and poor development. Also, they found that once the chilling requirement was fulfilled, subsequent development is entirely temperature dependent and the raspberry growth cycle can be manipulated to produce fruit beyond the normal field fruiting season.

In humid tropical climates, the induction and release of seasonal dormancy are triggered by environmental signals, mainly temperature and photoperiod. In most temperate and boreal trees, dormancy is induced by the decreasing length of the photoperiod in autumn and cool temperatures, resulting in the cessation of growth and the formation of winter buds (Thomas & Vince-Prue, 1997; Vaartaja, 1959; Wareing, 1956). Photoperiod and low temperature may induce dormancy through independent pathways (Welling et al., 2002) and in a few species; low temperatures alone seem to be sufficient to induce endodormancy (Heide, 2011; Heide & Prestrud, 2005). In tree species adapted to cool climates endodormancy is generally released after sufficiently long exposure to cool, non-freezing temperatures (Sarvas, 1974; Perry, 1971). Yet, the actual range of effective temperatures for chilling is only vaguely known for forest trees, and cool, non-freezing temperatures up to 10 °C, most likely between 2 and 4 °C, are expected to be most effective (Battey, 2000). Higher temperatures may even negate previous chilling (Perry, 1971), while lower (sub-zero) temperatures are generally considered to be ineffective for the fulfillment of the chilling requirement, presumably because very low temperatures prevent a physiological integration of signals (too low metabolic activity). Once the chilling requirement is fulfilled, metabolic activity increases, hydrolytic enzymes are activated and carbohydrate reserves gradually become mobilized. As a first visually identifiable clue, the onset of bud swelling indicates that the transition from endodormancy to ecodormancy has occurred (Pallardy, 2008; Saure, 1985). The bud water content rises (Essiamah & Eschrich, 1986) and the buds become increasingly susceptible to freezing. Then the subsequent release of ecodormancy is modulated by favourable environmental conditions.

Chilling during early or late in the winter, would affect both the number of buds which break and their subsequent growth (Thompson et al., 1975). The rate of bud development in the spring was found to depend most heavily on the cold conditions of the preceding autumn or early winter (Abbott, 1977). Accordingly, the warmer autumn conditions promote further bud development (delayed onset of quiescence), which facilitates renewal and completion of growth once dormancy has ended. It consists of the following sequence: quiescence → preliminary rest → mid rest → after rest → quiescence. Here quiescence is a state of growth stoppage reversible by favorable conditions. Preliminary rest and after rest are characterized by a lack of growth, but an ability to be forced. Mid rest corresponds roughly to innate dormancy, the state in which forcing is difficult or impossible. Also, those buds which receive more chilling can leave the quiescent state at lower temperatures than those which get less chilling. Couvillon and Erez, (1985) reported that there is a correlation within the apple species between the date of bloom and the chilling requirement: those varieties which bloom late need more chilling during winter.

2.2 Physiological Changes During Dormancy Induction and Release

2.2.1 Dormancy Induction

Physiological changes that occur when plants perceive the environmental signals for the induction and release of dormancy are associated with the responses including phytohormones, phytochromes and carbohydrates (Chao et al., 2007). The gradual transitions between the different phases of dormancy involve numerous genetic, physiological biochemicals and anatomical alterations (Cooke et al., 2012; Horvath, 2010; Faust et al., 1997). Whitworth and Young (1989) found that there is a decline in starch: total carbohydrate ratios following the onset of winter chill, may be a mechanism in the preparation for winter chill by the accumulation of sugars such as sucrose and sorbitol for freezing tolerance. The rootstocks showed particularly marked changes in carbohydrate composition: hexose, and sucrose were shown to be of particular importance during early growth. However, it may be deemed that there is not enough evidence to support the suggestion that carbohydrate status may play a major role towards the completion of winter rest. Jennings and Carmichael (1975) suggesting that overwintering raspberries for observation on carbohydrate composition in the roots and canes during the onset of dormancy revealed that a genotype with prolonged leaf retention and delayed dormancy had unusually high starch concentrations in the tissues in December. It appears to be evidence that larger fruiting plants require a priming

of the plant carbohydrate status prior to bud break and flowering. One could speculate that the reasons for this may be associated with the provision of the appropriate energy substrate for the energy-intensive processes of leaf, flower and fruit development. Thus, carbohydrate stored in the root system, basal season's shoot system and resting buds of many perennial plants is used to support the next season's growth.

Thomas (1967) described the carbohydrate status of root storage organs were slowly depleted in the winter, at an increasing rate as new spring growth appeared. It was not until the shoot had sufficient leaf area to ensure photosynthetic self-support (April-May) that carbohydrate concentration no longer declined. Young et al. (1995) reported that changes in respiration rate the Q₁₀ and the energy of activation can be used to track bud development through endo- to ectodormancy and bud breaking. For example, when comparing the respiration characteristics of stratified and non stratified apple seeds, changes in respiration rate is higher in stratified seed when the raises in temperatures promote growth prior to imbibition. While the respiratory quotient (R_Q) during early dormancy in apple indicates that the use of lipids as the primary substrate increase after 990 chilling units, suggesting a shift towards carbohydrates as the primary substrate (Young et al., 1995).

Arnold and Young (1990) states that the amount of protein increase during chilling, reaching a maximum just prior to reach their chill requirement and are then used during bud break. Recently, a number of dormancy-specific RNAs, proteins and enzymes have been identified as signaling dormancy induction and release (Rowland & Arora, 1997). They found that dormancy proteins can be categorized into two groups; either bark storage proteins or dehydrins. As the name implies, the accumulation of dehydrins occurs in after the application of a dehydration stress, including low temperatures. Taylor and May (1967) suggesting that the concentration of bark storage protein increases dramatically (200 % in apple) in the autumn, subsequently declining when used to supply spring growth. Rowland and Arora (1997) further states that the decline or breakdown of bark storage proteins is likely to be linked to a hormonal communication mechanism involving gibberellins, cytokinins and auxin. However, neither bark storage proteins nor dehydrins have yet to be shown to be clearly linked with a regulatory role in influencing endodormancy (Coleman et al., 1992).

Frewen et al. (2000) reported that several quantitative trait loci (QTLs) have been identified for ecotypes of poplar (*Populus deltoid*) with different dormancy induction thresholds. Accordingly, mapping of some of these QTLs has been linked to chromosome regions that encode for a phytochrome gene. Phytochromes are family of plant photoreceptors proteins and act as important regulators of many plant developmental responses to light. Developmental regulation is thus achieved via the perception of radiation between 700 and 800nm (far red). This enables quality changes in sunlight caused by presence of plant canopies (shade) to be detected and revealed the developmental strategies of shade avoidance induced (Salter et al., 2003). Senescence can also be linked to the induction of endodormancy, and both ethylene and ABA have senescence inducing roles, suggesting a commonality of action or hormonal linkage (Horvath et al., 2003).

Freeman et al. (2003) further confirmed that dormancy breaking results in the upregulation of several genes early in cell cycle growth phase, including cyclins and histones. The transition to the next development phase ('S phase') in the growth cycle, in which DNA replication takes place, is known to be modulated by several groups of plant hormones, i.e. gibberellic acid, cytokinins and brassinosteroids, as well as sugars (Horvath et al., 2003). In a study of peach (*Prunus persica*), IAA bud concentration fell with chilling and was low during rest, while ABA concentration was high declining close to bud break, at which time zeatin riboside increased (Ramina et al., 1995; Powell, 1986; Mielke & Dennis, 1975). Regardless of this correlation, it has yet to be proved that ABA has a direct casual role in dormancy regulation (Powell, 1987). This conclusion is supported by studies that show ABA changes in the absence of any apparent alteration in bud dormancy and ABA application does not often promote dormancy (Meilke & Dennis, 1978; Singha & Powell, 1978).

2.2.2 Dormancy Release and Bud-break

Different approaches have been suggested to examine the mechanisms of dormancy release in temperate fruit trees. The first approach is the Apical Meristem Dynamics which is based on regulation within the apical meristem itself by changes in the cell-to-cell communication and plasmodesmatal connections or in the cell cycle (Rinne et al., 2001; MacDonald, 2000; Jian et al., 1997; van der Schoot, 1996). The second approach emphasizes on the regulation of super cooling of water inside the vascular connections into the bud (De Fay et al., 2000; Quamme et al., 1995; Sakai, 1979), they addressed the sequence and regulation of water uptake into the bud; and the importance of water status/availability during dormancy release. The third approach is based on the mechanism of dormancy induction and release via a metabolic or communication block, or a permeability barrier between the bud and adjacent tissues (Faust et al., 1997; Crabbe & Barnola, 1996). Gevaudant et al. (2001) confirmed that both the buds and the underlying tissue in peach (*Prunus persica*) contains a greater accumulation

of PPA (*Prunus persica* H⁺-ATPase) transcripts as compared to the buds themselves at the beginning of the dormancy period (October). This group attributed increased sucrose absorption in tissues underlying the bud during October to a stimulated H⁺/sucrose co-transport driven by PPA genes and suggested this to have a role in paradormancy. This study also described that chilling-induced specific decrease in certain PPA isoforms in tissues underlying the buds in November and December could be involved in the evolution from paradormancy to endodormancy. Finally, while most work to date has focused on hormonal control of dormancy release, which, when, how, and to what degree hormones are involved is still uncertain, regardless of the evidence supporting the activities of various growth regulators involved in the processes of dormancy induction and release.

Cannell (1989) states that bud break follows fulfillment of the chilling requirements and is normally initiated during ecodormancy as the temperature increases. Also, the time of bud break appears to be strongly influenced by the time when chilling is received rather than chilling intensity (Abbott, 1970). In apple, differences in the flowering time of various cultivars described as early or late blooming have markedly different heat sum requirements, with late blooming cultivars having the higher heat accumulation requirements (Swartz & Powell, 1981). In Pears (*Pyrus communis*), artificially warmed in the autumn, are known to show delayed bud break and flowering (Atkinson & Lucas, 1996; Atkinson & Taylor, 1994). The heat sum requirements for bud break depends on the amount of chilling received; such that the longer the chilling the lower the heat sum required (Sparks, 1993; Couvillon & Erez, 1985; Swartz & Powell, 1981; Campbell & Sugand, 1979; Spiegel-Roy & Alston, 1979). However, the interaction between heat sum requirements and chilling received is important, as this may provide a poor estimate of bud break and flowering (Couvillon & Erez, 1985).

With respect to time of bud break, there is a clear difference observed in response of buds from different shoot positions (Jacobs et al., 1981). Accordingly, terminal and apical buds require much less chilling than lateral or basal buds, while the high chilling requirements of some cultivars appears to be correlated with strong apical dominance (Faust et al., 1995b). These positional effects are complex because once the buds are excised these positional responses are lost (Borkowska & Powell, 1979). Endogenous cytokinins have been shown to increase in spring prior to and during bud break (Cutting et al., 1991; Young, 1989), particularly in terminal shoot buds, relative to more distally located lateral buds (Cook & Belstedt, 2001).

Young et al. (1995) suggested that in cherry, dormancy breaking is accompanied by increases in bud nucleic acids, proteins and polyamines. This study also explains the resumption of growth that is associated with an increase in maintenance of respiration rate, fatty acid saturation and a decline in membrane sterol content. A study by Sagisaka (1974) also suggested that dormant to non-dormant buds show a change in respiratory metabolism from one which provides reducing power (pentose-phosphate cycle) to one providing energy for growth (glycolytic pathway and the TCA cycle). There is evidence from a number of studies that bud break is associated with free radical removal by activated peroxide-scavenging system, but it is unclear whether this is a simple correlation or a casual relationship (Rowland & Arora, 1997).

Gianfagna and Mehlenbacher (1985) suggests that, flowering time in apple actually dependent upon the temperature for bud growth and its heat sum requirement than a cultivars chilling requirement. They found that differences in cumulative temperatures for 'Delicious' apple between February and April showed above a day-degree value of 700 (°F), not only was flowering earlier but the variation in actual flowering date was much smaller compared to values at or below 300 (°F). Thus, the base temperature requirements for heat accumulation vary with species, ranging from 2.5 °C for peach to 4.5 °C for pear (Spiegel-Roy & Alston, 1979). It would appear in some species, cherry and blueberry for example, that chilling and heat sum requirements can be accumulated simultaneously (Felker and Robitaille, 1985). The case is different with peach, where exposure to temperature above 21 °C has a negative influence on accumulated chill hours (Erez et al., 1979a, b).

2.3 Bud-break by Chemicals and Cultural Practices

2.3.1 Chemical Application to Top Fruit

Chemical breaking of dormancy has been achieved initially through the use of simple plant and animal oils for a long time to compensate lack of chilling (Subhadrabandhu, 1995). Their mode of action appears two-fold; firstly they coat the branch creating an oxygen shortage. As oxygen starvation develops, the products of anaerobic respiration are implicated in breaking dormancy. These mineral oils have subsequently been modified with the addition of phenolic substances to increase their efficacy under conditions where chilling is low. Later on, other dormancy breaking chemicals have been developed and many of the substances act as respiration uncouplers. Normally in the process of respiration, electron transport and oxidative phosphorylation are tightly coupled. Uncoupling of these processes allows electron transport to proceed unlimited in the absence of ATP synthesis

that producing heat. This can have the effects of inducing anaerobic conditions with the production of ethanol in the bud (Erez, 1995).

Important dormancy breaking chemicals include cyanamide, as a calcium salt, Hydrogen cyanamide, thiourea, oil-DNOC, KNO_3 winter oil and others. Hydrogen cyanamide has been shown to be very effective in dormancy breaking of apple, pears, plum, apricot, raspberry and sweet cherry, as well as, peach cultivars with high chill requirements (Erez, 1995; Snir & Erez, 1988; Erez, 1987). Cyanamide, as a calcium salt, has also become the leading dormancy breaking chemical. However, the application of cyanamides require careful measures because of its toxicity effect. Other dormancy breaking chemicals include thiourea, which is very effective in combination with KNO_3 and oil-DNOC, but also is toxicity to humans (Erez, 1987). Plant growth regulators such a gibberellic acid and cytokinins have also been shown to break dormancy, but the high concentrations required appeal significant costs (Erez, 1987). Another problem with gibberellic acid is that the shoots often appear thin and spindly (Anonymous, 1994). Responses to GA_3 appear to be more effective depending on time of application and extent of chilling (Couvillon & Hendershott, 1974). Recently, introduction of 'Armobreak' a fatty amine, which enhances cuticular penetration, may reduce the concentration required of these rest breaking chemical agents (Erez, 1995). This would impact on key environmental issues associated with the use of these types of chemicals. Erez, (1995) also suggesting that the efficacy of KNO_3 and gibberellic acid was enhanced by Armobreak.

2.3.2 Chemical Application to Soft Fruit

Snir (1986) states that application of cyanamide to low chill cultivars of raspberry (i.e. cv. Dormanred) adapted to subtropical Israeli conditions showed improved bud break. This revealed that the use of dormancy breaking agents in combination with low chill cultivars promote better blooming and fruit set, regardless of environmental influence in mild winter areas. Linsley-Noakes (1989) conducted a series of trials in South Africa involving the application of hydrogen cyanamide solutions during the late summer/early autumn to alter bud break behaviour in other raspberry cultivars. This study indicates that after determining the optimum treatment regime, the bud break was possibly raise from 22-51% in some cases, which led to improved yields.

Also, different chemicals and growth regulators have been tested for improving bud break in fruit crops where lack of adequate winter chill may inhibit robust synchronous bud break. For instance, the application of compounds like potassium nitrate and thiourea were found to improve bud break and yield, with cyanamide again producing the better effects (Snir, 1983). Similarly, chemical defoliant such as maleic hydrazide have also been used to stimulate and synchronize flowering in fruit crops grown in mild winter areas of tropical and sub tropical regions.

Also, the application of growth regulators in late summer/early autumn has successfully affected the apparent accumulation of winter chill and bud break. Treatments with PP 333 (paclobutrazol) has inhibiting late season growth, inducing early leaf fall and therefore early dormancy, while the application of gibberellic acid (GA) would result in prolonged vegetative growth and delay leaf fall (Måge, 1986). Such a control mechanisms may be used to tailor growth and onset of dormancy to the local growing conditions by considering the local climate characteristics in order to maximize the efficiency of chill accumulation in that location. Other plant growth regulator such as ethephon is known to affect dormancy and can delay the bud break by up to 16 days (Durner 1995). Accordingly, this practice has been found to be useful particularly in continental North America where dehardening of the flower buds in late winter and early spring makes them highly susceptible to harsh frosts causing pistil damage or death.

2.4 Cultural Practices

2.4.1 Irrigation and Fertilization

Because of human health hazards and harmful environmental impacts, chemical applications are unlikely to be accepted by consumer and preferences shifts to organic alternatives. The routine agricultural practices such as watering, fertilizing, and pruning in the late season have all been shown to promote new growth and prolong succulent stage, with the consequent effect of increasing the chilling hours required to complete rest; thus delaying bloom in the following spring (Walser et al., 1981). Also some techniques like regulated deficit irrigation (RDI) or even partial root drying (PRD) which limit soil water availability could be worth examining with respect to control of dormancy and subsequent regulation of bud break. Spiers and Draper (1974) reported that in many fruit tree species, early leaf removal, either artificially or induced by late summer drought, can reduce the bud rest period, or synchronize flowering. Such trials have also demonstrated improved shoot growth and earlier spring flowering.

2.4.2 Pruning

Costes et al. (2006) studied the relationship between bud break and effect of pruning on shoot growth, source leaf area, current photosynthesis and annual building of storage reserves. They found that timing and severity of pruning can play a crucial role in the partitioning of photo assimilates during early and late summer. Thus, early summer pruning can stimulate the reallocation of reserves to renewing bud break and leaf growth, whereas late summer pruning may reduce leaf demand and has been shown to increase assimilates to the current season's growth. White et al. (1999, 1998) carried out cane-pruning experiments on northern European raspberry cultivars to see the effects on bud break. The study revealed that pruning in some cases increase the level of bud break compared to intact canes when exposed to simulated limiting winter chill conditions. The results also suggested that the phenomenon may be due to the reduction of apical dominance, and that management systems that include apical tip removal at the crucial phase of development may offer another method for improving bud break.

2.5 Plant and Environment Management

In warm climatic conditions, chilling requirements can be overcome by using evaporative cooling achieved through the use of overhead irrigation system (sprinklers) to reduce bud temperature (Erez, 1995). This approach is known to increase bud break and enhance uniformity of leafing out (Erez & Couvillon, 1983). Evaporative cooling also has the potential to be used with other physical methods, apart from low chill requiring cultivars, such as orchard/tree management practices that reduce bud chill requirement. These include reducing tree vigour by orientating branches to a more horizontal angle, preventing vegetative growth late in the season and delaying dormant season pruning. Thus deeper dormancy would be induced when stronger tree vigour, associated with vertically orientated branches (Erez, 1995).

3. Floral Initiation

Westwood (1993) suggested that flower buds formation is considered to involve signaling processes within the cells and also on a whole plant scale, resulting in a synchronous physiological event. As studied by many authors, floral initiation varies with all crops; in apple it requires the production of around 20 growth nodes (Luckwill & Silva, 1979; Abbott, 1977; Landsberg, 1974). Growth nodes or 'plastochron' are units of time recorded between successive development of primordia (i.e. morphological structures such as leaves, bud scales or flowers). An increase in apical meristem diameter signals the beginning of floral development, which is followed by differentiation and development of floral organs acropetally (Diaz et al., 1981). These events take place in late summer around the time shoot extension growth has terminated in August.

The rate at which initiation of apple primordia takes place has important implications in firstly determining the fate of the bud (reproductive versus vegetative), as well as its quality and fruit setting potential (Abbott, 1970). A short time to achieve the 20 growth node threshold promotes flower initiation, whereas too slow a production rate produces only a vegetative bud. Abbott (1977) also confirmed that the longer floral primordia has been initiated, the older it will be at the onset of dormancy when compared to the new fruit bud with a longer plastochron. The age of a primordium when entering dormancy can have important implications for subsequent development and performance. It is suggested that plastochron interval may have an optimal length that achieves the most effective fruit setting blossom characteristics. Variation in time of flower initiation has not, however, been shown to directly influence on blossom quality (Abbott, 1977). Accordingly, once formed, buds consist of bud scales, leaf and bract primordia and floral initials.

Felker et al. (1983) suggested that the reproductive bud scales having begun formation in early May remain in a dormant state due to correlative inhibition. The cessation of vegetative growth and terminal bud formation can be delayed in extreme cases until October, but it is normally finished by August. Accordingly, factors such as dwarfing rootstocks, heavy cropping and drought stress can all induce earlier termination of shoot growth and the production of 'resting' buds in apples.

The differentiation of organs in apple, such as the ovules and pollen sac, occurs at the end of the winter period (Bergh, 1985), while bud connecting xylem in some *Prunus* species does not appear until around 5 weeks before bloom (Hanson & Breen, 1985). There are many studies that have reported the influences of nitrogen, irrigation, light and temperature on floral initiation (Sedgley, 1990). There are also important impacts on floral abundance from management practices; one of the most prominent being pruning, particularly in the summer, removing sites for floral initiation (Webster & Shepherd, 1984; Lord et al., 1979).

Gutteridge, (1958) reported a similar situation exists in strawberry, in which flower initiation takes place in the autumn followed by a period of rest or dormancy. Floral induction is driven by changes in the plant's environment and occurs in short-day plants as day length declines and temperatures are reduced (Battey et al., 1998; Piringer & Scott, 1964). Even though in June bearing strawberry being a facultative, short day plant, its photoperiodic response is modified by temperature (Le Miere et al., 1996; Nishizawa & Hori, 1993a). They suggested that flower induction is primarily induced by photoperiodic reduction in the autumn, rather than the associated low night temperatures. However, Brown and Wareing (1965) suggest that with *Fragaria vesca*, temperature is more important than photoperiod. More recent work shows that flower induction with ever bearer strawberries may occur irrespective of daylength or temperature (Smeets, 1980).

Also, the formation of floral initials in straw berry starts over the winter from August through to the following in spring with differentiation of the initials occurring throughout this period. The change of apical meristems from vegetative to reproductive was stimulated by shortening day length (Williams, 1959a, b). Thus, floral initiation and development of dormancy occurred concurrently, but independently, in response to shorter days and lower temperatures as autumn progressed. For example, in cultivar 'Lloyd George', Williams (1959b) suggest that flowers were initiated without the occurrence of dormancy, suggesting separate processes, although other cultivars responded differently. It indicates that floral initiation had occurred after dormancy broken, subsequent development was temperature dependent, with little influence of day length. The age of the cane was found to influence initiation, with canes comprising no less than 15 nodes failing to initiate flowers even under long inductive treatments. Williams also found that initiation begins near the tips of canes and proceeds downwards.

3.1 Hormonal Control of Flowering

Hayama and Coupland (2003) described that light is mediated by phytochrome and cryptochrome photoreceptors found in the shoot meristems, and play a substantial role in the induction and timing of flowering, as well as many other plant physiological factors. This light regime information is fed into the plant clock systems (circadian clock) via biochemical pathways that are far unsynchronized. Recently, a model has been developed to describe the mechanism of the core of the circadian clock (the central oscillator) to synchronize the day/night photoperiod that provide a direct evidence in characterizing the molecular links between the central oscillator system and the timing of flowering (Suarez-Lopez et al., 2001; Onouchi et al., 2000). Also related here is the influence of light quality on flowering time. Simpson and Dean, (2002) reviewed the evidence collated from the generation of a number of phytochrome and cryptochrome mutants revealed that the wavelength of incident light can influence flowering time. Accordingly, the environmental significance of this appears to be in shade avoidance and competition: thus, shading by neighboring vegetation increases the relative abundance of far-red light since the absorption of red light by chlorophyll reduces the local red/far-red light ratio. The sensing of relative increases in far-red light abundance forms a signal of ecological competition resulting in accelerated flowering and quicker life cycle completion.

Plant hormones that have been associated with the control of flowering time include auxins, gibberellic acids (GAs) and cytokinins (Bernier, 1988). Physiological studies on the interaction of gibberellic acid in defoliation also implicate a role in the rest process. Autumn applications of gibberellic acid have been demonstrated to delay the development of autumnal leaf colour, leaf abscission, and the subsequent emergence from rest at bud break in the following spring (Walser et al., 1981; Brian et al., 1959). Molecular control studies involving phytohormones have been limited however, although a limited amount of information is now known for GA though work on *Arabidopsis* (e.g. Blazquez et al., 2002). Mutants in GA signalling or its synthesis show delayed flowering characteristics, though further work is required to determine the upstream factors that control GA activity.

3.2 The Role of Chilling in Bud Break and Floral Initiation

The developed floral buds of perennials (top and soft fruit) do not normally burst until they have received sufficient exposure to low temperatures. Time to flowering is therefore highly dependent on chilling, which is itself determined by the average daily temperature and the number of days at a species-specific temperature (Landsberg, 1974). Different combinations of the temperatures during the dormant phase and the duration of the chilling period satisfy the plant's chilling requirements (Jacobs et al., 2002). In strawberry for instance, increases in chilling leads to increased stimulation of stolon production, vegetative vigour, and floral capability (Battey et al., 1998; Smeets, 1982). However, reducing the chilling index below a threshold value dramatically increases the time to anthesis.

Tehranifar et al. (1998) suggested that chilling in strawberry is not a prerequisite for flower production – for example, with ‘Catskill’ and ‘Elsanta’, there was no negative effect of chilling, cold storage temperature or lifting date on flower numbers. However, fruit production is influenced by temperature and the duration of chill.

Short-day cultivars of strawberry, which are adapted to cooler winters, will have a better performance in tropical and sub tropical regions, but still require chilling if they are to achieve full production potential. With respect to the chill requirements among strawberry cultivars adapted to different climatic region, there are large differences observed in time length for chilling completion. For example, ‘Tioga’ requires between 2 to 4 weeks, while ‘Glasa’, ‘Elsanta’, ‘Gorella’ and ‘Sequoia’ have a 5 to 8 week requirement, with ‘Redgaunlet’ needing 8 weeks (Durner, 1999). In low chill strawberry cultivar (Douglas), flower bud induction is inhibited by chilling (Kronenberg & Wassenaar, 1972), but enhanced in high-chill cultivars (Durner & Poling, 1987). Tehranifar et al. (1998) in their work with cultivar ‘Elsanta’ suggests that the way chilling is achieved may influence its effectiveness; i.e. field chilling may be more effective than cold storage for this cultivar. The reason for this may be due to oscillating changes in temperature in the field compared to cold-stored plants, or possible differences in radiation, although no mention is made in this work about whether the cold-stored plants were illuminated. Chilling requirements vary with the type of rootstock and bud positions (Couvillon & Werner, 1985), besides with species and cultivar for both top and soft fruits. For example, in vegetative buds of peach and apple, terminal buds have the lowest chill requirements, while laterals are higher and floral buds are generally in between (Faust et al., 1995b; Scalabrelli & Couvillon, 1986). In apple, there is a significant genetic difference between early and late flowering cultivars, that the late flowering cultivars have a greater chill requirement than early flowering cultivars, while additional chilling hours can eliminate these date differences (Swartz & Powell, 1981). Similarly, Chandler (1960) reported that the late autumn and early winter is conducive for apple leaves being maintained longer on the tree; then more chilling is required to induce bud break. However, this situation would result in insufficient chilling in mild winter areas that potentially causes a delay in bud break: where effective chilling does not occur until a degree of physiological bud maturity has been achieved (Walser et al., 1981).

Also, there is an interaction between chill requirements and the subsequent heating (forcing) to achieve bud break. For example, partially chilled apple trees are known to require more heat units before flowering, than fully chilled trees (Swartz & Powell, 1981). This indicates that in those years where cold winter temperatures were above threshold and effective for chilling resulted in lower apple yield. Beattie and Folley (1977) analyzed the yields of ‘Cox’s Orange Pippin’ in Kent and Sussex (UK) from 18 orchards, managed in a similar manner, over the period 1971 to 1975. They found that there was very close correlation between mean ‘Cox’ yield and the temperature accumulated from February to April, each year. This analysis also showed that when the calculated temperature accumulation values were higher than average, yield was reduced. The higher accumulated temperatures are a reflection of years when the late winter and spring temperatures were higher. Atkinson and Lucas (1996) also produced similar reports regarding the influence of high temperature accumulation on yield reduction in their study of northern European fruit growing regions.

Chandler (1960), suggesting that in peaches, chilling temperatures in the presence of a certain amount of leaf area was not as effective as when leaves are absent. Thus, the time of fall leaf abscission could be correlated with the duration and intensity of rest in peach terminal vegetative buds (Walser et al., 1981). Also the time of blooming is influenced by different orchard management practices: For example, the application of foliar nitrogen in the autumn delayed the bloom of peaches compared to untreated controls (Reeder & Bowen, 1981). Similarly, trees treated with gibberellic acid showed delayed leaf abscission and retained their leaves (Walser et al., 1981). Leaf-derived gibberellic acid is the most likely candidate to be involved in delaying bud break and flowering, as its application temporally delays leaf senescence.

In semi-temperate locations, such as California, and in mild winter areas of tropical and sub tropical regions, lack of sufficient chilling was an issue for deciduous fruit cultivation (Cook & Jacobs, 1999). Advances have been made in response to this lack of chilling, with the breeding of low-chill cultivars and the development of chemical and orchard management practices to induce bud break (Sedgley, 1990). Under tropical conditions, defoliation after the first crop in low chill cultivars induced early bud break as in the case of low chill nectarine and peaches (Sherman & Lyrene, 1984). Similarly, defoliation prior to endodormancy of apple grown in the tropics will induce a second crop (Janick, 1974).

Thompson et al. (1975) suggested that the seasonal timing of chilling is also important, in that early chilling appears less effective in satisfying requirements, compared to chilling received in the latter part of the winter. This was in conformity with the results of Beattie and Folley (1977) where their correlative analysis of yearly apple yields with climate showed a negative influence of February to April cumulated temperatures with

cropping. This implies that variation in effective chilling temperatures for apple, peaches and pears, can also change if continuous chilling is not given. It appears in some cases where temperatures that were not initially chilling effective, if applied constantly, can become as effective when interrupted by warmer temperatures (Erez & Couvillon, 1987; Couvillon & Erez, 1985). It is equally evident that when chilling is interrupted by warmer periods, even over a short-term diurnal frequency, apparent chill accumulation and subsequent bud break can be influenced (Erez & Lavee, 1971).

3.3 Physiological Basis of Chilling Responses

(i) Phases of vernalization and chill accumulation

Couvillon and Erez (1985) suggested two phases of vernalization in chill accumulation processes: The first phase involves the conversion of a product from unchilled to chilled state by chilling temperatures, which can be reversed by high non-chilling temperatures. For example, for several fruit species, 2, 4, 6 and 8 hours of 24°C within a 24 hour cycle at 4°C negated the applied chilling by 14, 45, 82 and 100% respectively. This approach permits the effects of corresponding warm modulating temperatures to negate chilling to be derived. The second phase in the process of vernalization involves the conversion of the unstable product from phase one into a stable form (Erez, 1987a, b). When this reaction takes place it is not reversible and the accumulation of the product to a certain level results in dormancy completion (Erez & Couvillon, 1987).

Erez (1995) suggests that the dynamic model based on the effects of temperature on dormancy through a determination of climatic events on accumulated product (the chill). Following temperature induction, a steady-state level of intermediate is determined by production and breakdown. It states that chilling accumulation is acquired by quanta of the intermediate product as it is transferred in to stable product. A number of other events are also suggested to impact on how effective chilling accumulation is achieved. These include the influence of the level of intermediate, such as negative effects of heat and the duration of the daily temperature cycle. The process has been described as dynamic and biochemically active (Rowland & Arora, 1997).

(ii) Changes in protein levels

Protein levels of peach flower buds during chilling have been linked to the chill requirements to satisfy chill (Lang & Tao, 1991). Protein analysis in peach plants has revealed that a 61 kD protein which declines as the chilling requirement is met, while the reverse happens in blueberry with the accumulation of two proteins as the chilling requirement is met (Lang, 1985). During dormant season, there is a loss of cold hardiness that may induces protein changes independent of chilling and it has proved difficult to separate the various processes. However, Lang (1994) has characterized dormant season protein expression and suggests, with peach, that the observed decline in a specific protein (61 kD) was associated with dormancy rather than cold acclimation. Lang (1994) also noted that the effects observed may have been due to increased bud development and deacclimation. The 61 kD peach protein was also shown to decrease in response to the application of dormancy-breaking compounds such as gibberellic acid and hydrogen cyanamide. Also, Muthalif and Rowland (1994a, b) further quantified the protein changes in response to chilling phases and requirements in two blueberry cultivars with contrasting chill requirements (low and high), and found that three major proteins accumulated during chilling.

The increase in protein accumulation was greatest at the beginning of chill period and subsequently declined rapidly on forcing and resumption of bud growth. However, for both the low and high chill- requiring blueberry, the accumulation of the chill proteins was closely associated, temporally and quantitatively, with cold acclimation (Muthalif & Rowland, 1994a). These proteins have highly conserved regions which are lysine-rich, as with all dehydrins. However, further analysis by (Lang, 1994) showed that the dehydrin proteins to be closely related to cold acclimation rather than degree of dormancy (Rowland & Arora, 1997).

(iii) Activity of enzymes

The enzyme acid lipase examined in apple buds from cultivars with different chill requirements showed an increase in its activity correlated with satisfying chill (Liu & Norman, 1991). Accordingly, the hydrolysis of lipids affects the freezing point of water, which itself may be involved in dormancy breaking. Faust et al. (1991) noted from the analysis of NMR scans of the apple buds showed an increase in free water, compared to that bound with proteins and cell walls, as apple buds accumulate chill. Studies with apple shown the processes involved with satisfying chilling requirement also convert bound water in the bud into free water, implying the necessity of free water for growth (Faust et al., 1991). The conversion of bound water to free has been shown to be incremental in relation to chilling, and the rate at which a threshold value is achieved differs between high and low-chill requiring cultivars (Faust et al., 1995a). Studies of different peach cultivars indicates that Catalase

activity in flower buds has been shown to decrease during chilling and increase with bud break (Kaminski & Rom, 1974). However, in grapes catalase activity has been shown to decline on the application of bud breaking chemicals (cyanamide & thiorea) (Nir et al., 1986).

(iv) Changes in carbohydrate levels

In deciduous fruit trees, carbohydrate storage parenchyma on bud tissues has begin to accumulate starch in the autumn, and there is an evidence that roots provide an important sink for marked increase in the storage of reducing sugars and sucrose (Nishizawa, 1994). With subsequent chilling (350-400 h), the amount of starch declines and other factors must be responsible for the fact that plants remain dormant. Further chilling, not due to correlative inhibition, appears to be induced by a reduced ability to synthesize nucleotides (Robert et al., 1997). The physiological state of tissues during chilling can be detected through measurements of changes in ATP content and NTP, reflecting non-specific energy demands and protein synthesis (Robert et al., 1997).

Starch concentration has been shown to decline during apple chilling and forcing, while sorbitol changed very little during forcing (Whitworth & Young, 1992). Sucrose increased with chilling only to the point where around 50% bud break was obtained. These results most likely indicate only the pattern of carbohydrate utilization, particularly with respect to its metabolism during chilling and forcing. Winter carbohydrate accumulation for cold hardiness, freeze protection and respiratory consumption are all well-documented (Raese et al., 1978; Hansen & Grauslund, 1973). Work with June-bearing strawberry demonstrated an autumnal increase in root starch at a rate negatively correlated with temperature (Le Miere et al., 1996). Therefore, it can be concluded that amount of root starch was not an indicator of dormancy, so it is therefore unlikely to be a driver of dormancy.

(v) Changes in levels of growth regulators

Swartz and Powell (1981) worked in apple buds with known differences in chilling requirements. Chemical analysis of this experiment revealed that there is a distinct decline in abscisic acid (ABA) concentration in bud primordia collected in January through spring, while little difference was observed in ABA concentration for those collected in December irrespective of chilling requirements. Though, the rate of decline in ABA concentration was most rapid with low chill compared to high chill cultivars. The ABA concentration at bud break was similar, but the dates of bud break as expected were not, because no warm controls were used and differences in ABA concentration may simply be to other changes rather than ABA acting as a casual factor. ABA concentration declines in sour cherry buds under both cold and warm conditions (Mielke & Dennis, 1978). Conversely, the concentration of giberellins in buds increases during chilling (Eagles & Wareing, 1964; Frankland & Wareing, 1962).

(vi) Rootstock influence of chilling

Variability in chilling requirements of different apple rootstocks suggests that the chilling responses of scion, with respect to bud break, can be influenced by the rootstocks (Young & Werner, 1985; Couvillon *et al.*, 1984). This may be achieved through the transfer of a phloem- mobile element (or chemical 'signal'), which is initially synthesized in the roots. Such a hypothesis would fit with the idea of Erez (1995) that the timing requirements of chilling and bud break are controlled by the actual accumulation of as yet unidentified product.

4. Chill Accumulation and Estimation

4.1 Quantifying Winter Chill

Richardson et al. (1974) developed the concept of determining 'chill units', from measurements of temperature, to calculate the amount of chilling received by simple predictive method that revealed weight step function. Firstly, one chill unit was defined as an hour exposure at the optimum temperature required meeting the species or cultivar's chilling requirement. A cultivar's chilling requirement was therefore measured by the number of hours required, at a set temperature, below which chilling is received. For example, early peach chill models (Weinberger, 1950) cumulated the number of hours below 7.2°C (45°F) as a guide to adequacy of breaking dormancy. For this, optimal chilling temperatures were found to be 6°C for peach but are lower (2°C) for apple (Thompson et al., 1975). Afterwards, there have been various attempts to refine the limitation of this early approach to take account that the rate of chilling process varied with temperature (Richardson et al., 1974).

Consequently, temperature readings between 7 and 10°C are used in calculating a plant's chill requirement; with 6°C as the optimum, while temperatures below 1.5°C do not contribute and temperatures above 13°C reduce accumulated chill units. Though, numerous studies shows that optimal temperatures (effective cut off temperatures), within the range (1.5°C to 13°C), vary with species and cultivar (Couvillon, 1995; Anderson & Richardson, 1987). Mahmood et al. (2000b) reported that for *Prunus avium*, temperatures below -4.5°C and above 12°C are ineffective in breaking dormancy and specific cultivars, i.e. Stella, Summit and Sunburst had

optimum chilling temperatures of 3.2°C and 3.7°C respectively. While with peach, temperatures around 8°C are the most effective in satisfying chilling requirements, and above which, 10°C and 12°C were only 46% and 33% as effective, respectively (Erez & Couvillon, 1987).

When applying these chill models, they commonly accumulate chill over time and when a threshold amount of chill has been amassed for tree species that require different threshold amounts of chill to break dormancy. Zhang and Taylor (2011) reported the chilling requirement of *Sirora pistachio* (*Pistacia vera* L.) in Australia by monitoring winter chill accumulation from 2006 to 2010. Three chill models (Chill Hour, Utah, and Dynamic) were compared both in the greenhouse and under field conditions to evaluate their predictive performance. The result indicates that Dynamic Model produced the best determination for fulfillment of chilling requirement with 59 chill portions in 2006 and with little variation in the following years (Table 1). However, the relationship among the level of fulfillment of chilling requirement (low, moderate or high), showed a significant variation for Chill Hours and Chill Units between years (Table 1).

Table 1. Estimated chill accumulation of *Sirora pistachio* (*Pistacia vera* L.) in (chill hours, chill units, and chill portions) at Dareton Research Station, New South Wales (Zhang & Taylor, 2011).

Winter	Chill fulfillment date	Chilling hours	Chill Units	Chill Portions	GDH	50% bloom date predicted	50% bloom date in the field	Chill categorization
2006	10 Aug.	645	990	59	9633		20 Sept.	Moderate - High
2007	13 Sept.	677	919	58	17297	8 Oct.	7 Nov.	Moderate - High
2008	3 Sept.	569	1078	62	9818	9 Oct.	10 Oct.	High
2009	9 Sept.	412	752	60	9411	17 Oct.	16 Oct.	Moderate - High
2010	25 Aug	535	1123	61	10063	9 Oct.	10 Oct.	Moderate - High

4.2 Estimate of Hourly Temperatures Required for Winter Chill

The accuracy of chill models is sometimes reported to be better when hourly temperatures are used. The Utah model (Richardson et al., 1974) requires hourly temperature data, while the <7.2°C and 0-7.2°C models can use either daily or hourly data. Richardson *et al.* (1974) used a simple linear interpolation to obtain hourly temperatures from daily data: this involved segmenting a daily max/min temperature plot, connected by straight lines into equal segments (Figure 1). However, <7.2°C and 0-7.2°C models were used daily and hourly values for a site where both hourly and daily data were available. This indicates that hourly chill can be estimated simply from daily temperature data using relationships between the annual values of daily and hourly temperatures.

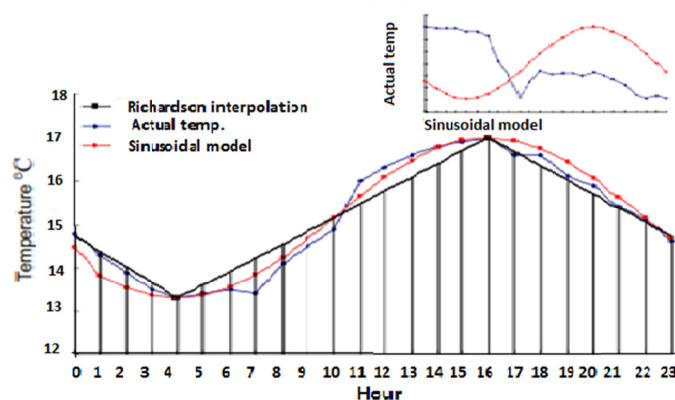


Figure 1. Method for the estimation of hourly temperature from daily maximum/minimum temperatures by simple linear interpolation (Richardson et al., 1974)

The data from the interpolation models (Richardson et al., 1974) were calculated from the maximum/minimum temperature data for the same location on the same day. Although most days follow a general sinusoidal trend (Figure 1), variability can be high due to other climatic factors: inset - plot from a winter day at the same location.

Monteith and Unsworth (1990) suggested better interpolation method is to utilize a sine function for diurnal temperature trends, so that the hourly mean temperatures can be estimated from:

$$\text{Hourly temperature} = (T_{\min} + T_{\max})/2 + ((T_{\max} - T_{\min})/2) * \sin(\text{radian}(H * 15 + 210)) \text{ (Equ...1)}$$

Where:

$T_{\max}$ = Daily maximum temperature

$T_{\min}$ = daily minimum temperature

H = hour of day, indexed from 0 – 23

Sanders (1975) suggest that these approaches should be further improved by considering the fact that the diurnal temperature increase tends to be more rapid than the decrease in the afternoon/evening with the time $T_{\min}$ - $T_{\max}$ often averaging 10-11 hours and the time between $T_{\max}$ - $T_{\min}$ averaging 13-14 hours. However, as illustrated by Aron (1975) in a critique of the temperature estimation methods developed by Richardson *et al.*, (1974) care must be taken in the use of these models: regions such as the Californian coastline experience regular daily changes in air mass due to coastal breezes that at times may extend well inland. Also, locations that experience the passing of a large number of fronts will also diverge from the model. The application of the method is likely to be successful in regions that generally experience sinusoidal daily temperature regimes.

4.3 Chill Calculation Methods

Calculating winter chilling can assist the fruit industry in predicting/forecasting the quality and quantity of fruit in the subsequent season. Chilling units accumulated during the cold season enable the plant to release dormancy in spring. Studies indicates that chill models used to calculate chill accumulation require different temperature ranges, above or below which the chill accumulation is negative or nil: For example, temperatures of 1.5–12.4 in the Utah Model (Richardson et al., 1974), 1.6–13°C in Modified Utah Model ((Linsley-Noakes et al., 1995) and 1.8–16.9°C in North Carolina Model (Shaultout & Unrath, 1983; Gilreath & Buchanan, 1981) were used and assigned for different weighing values of chill accumulation in a hourly basis. Gilreath and Buchanan (1981) states that, low chill requiring sungold nectarine cultivar in Florida shown faster bead break at 10°C after exposure to constant temperatures of 24 hours in the dark, while in the same cultivar at similar exposure, flower bud occurred at 7°C. Similarly, Erez et al. (1979a) reported from California that peaches require 9.6 to 9.8°C threshold temperatures which favor flower bud development.

Richardson et al. (1974) described the chilling requirements of 'Redhaven' and 'Elberta' peach trees growing in Utah, and found that the temperature at 6°C was the most effective chilling temperature and below 1.4°C did not contribute towards chilling. The same study indicates that temperatures above 16.5 °C caused the reversion of accumulated chilling for Utah model. Erez et al. (1979a) in Georgia also confirmed that, when applying Utah Model for Redhaven and Redskin peach, the temperature at 6°C is the most effective for rest completion, while the temperature above or below which may result in extended rest completion and less effective until the maximum temperature reached (12.4 °C) for chilling reversal.

All the classical models were derived from the number of hours of exposure to a given temperatures that were assigned a weighing factors. The weighing functions were mainly determined by laboratory tests and they differ because of tree species and variety (Richardson *et al.*, 1974; Shaultout & Unrath, 1983; Gilreath & Buchanan, 1981). These weighing factors are sensitive to different temperature ranges and estimated the chill unit accumulation in an hourly basis (CU h^{-1}) as a function of temperature and plotted as a discontinuous step function that estimates different values for the model tested (Figure 2).

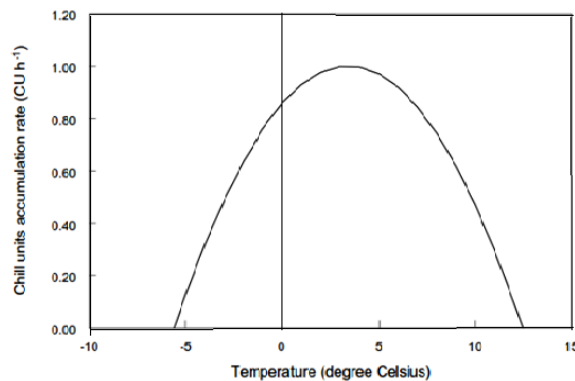


Figure 2. Chill Units accumulation rate (CU h^{-1}) as a function of temperature (Richardson et al., 1974; Shaltout & Unrath, 1983; Gilreath & Buchanan, 1981)

In application, Chill Models all accumulate chill at hourly intervals, require summation of chill to estimate total chill exposure and operate within a defined chilling period. Furthermore, the positive section of the chilling curve becomes difficult to define in warmer locations which do not experience sharp turning points into and out of positive chill accumulation. A classical chilling model approaches can be described as:

(i) Simple temperature accumulation models.

The 0-7.2°C model (Weinberger, 1950) is a simple model first developed over 50 years ago and measures chill hours (CH) according to hourly temperature (T_t). Temperatures within the 0-7.2°C interval are allocated one chill hour, while temperatures outside this interval record zero chill hours (Equ 2 and Figure 3). To determine total chill (CH_{tot}) for a given chill period, chill hours are summed from predetermined start (st) and end (en) times (Equ 2).

$$\text{CH}_{\text{tot}} = \sum_{t=\text{st}}^{\text{en}} \text{CH} \begin{cases} T_t < 0^\circ\text{C} & ; \text{CH}_t = 0 \\ 0^\circ\text{C} \leq T_t \leq 7.2^\circ\text{C} & ; \text{CH}_t = 1 \\ T_t > 7.2^\circ\text{C} & ; \text{CH}_t = 0 \end{cases} \quad \text{Equ.....2}$$

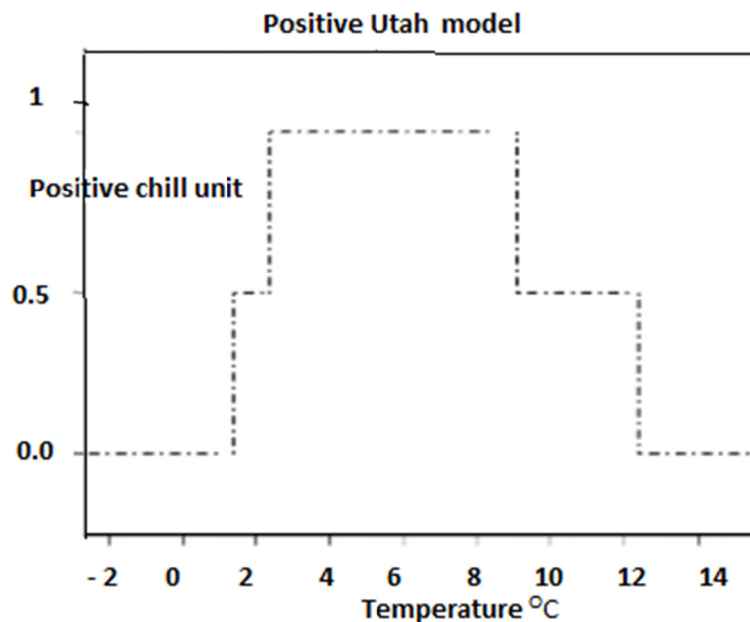


Figure 3. 0-7.2°C model as a function of temperature (Weinberger, 1950)

The attempt to quantify winter chill by Weinberger (1950) revealed that the chill requirements of species would be satisfied after exposure of trees below the threshold of 7.2°C (45°F). This was based on observations of the number of hours of chilling that were required to break dormancy in a number of peach cultivars grown at Fort Valley, Georgia, USA. This enabled the development of a ranking system for the cultivars according to whether they had high or low chilling requirements to fulfill dormancy and promote successful bud break. Further studies, however, demonstrated differential responses of species to chilling temperatures, with the largest effects often occurring above freezing (Erez & Lavee, 1971).

(ii) Simple Temperature weighted models

Alternative to the >7.2°C model, a 0-7.2°C chill model, a number of studies appeared to develop physiologically more appropriate model to estimate dormancy breaking in a number of species grown in particular regions (Byrne & Bacon, 1992). The Utah Model (Richardson et al., 1974) contains weight function assigning different chilling efficiencies to different temperature ranges, including negative contributions by high temperatures (Table 2 and Fig 3). Thus, the chill units (CU), would be considered as a duration of 1 hour period in a temperature range considered optimum (2.5-12.5 °C) to accumulate chill (Richardson et al., 1974). Temperatures < 1.4 °C have zero values and do not contributed to chill accumulation. Temperatures above 12.5 would result in a reversal of the accumulated chilling (Table 2 and Fig 4) (Richardson et al., 1974).

The chill accumulated in the Utah model for an hour at a given temperature is calculated using the weighting system (Table 2). The model takes into account the deterioration in chill accumulation efficiency above and below 6 °C (i.e. optimum chilling efficacy or effective chilling at 6 °C). It also accounts for the deductive effects of short periods of warming during winter, though does not discriminate between the differential behaviour of longer phases of warm weather (Erez & Lavee, 1971).

Table 2. Values of chill units (CU) as a function of hourly temperature for Utah model (Richardson et al., 1974)

Temperature °C	CU
<1.4	0.0
1.5 – 2.4	0.5
2.5 – 9.1	1.0
9.2 – 12.4	0.5
12.5 – 15.9	0.0
16.0 – 18.0	-0.5
>18.0	-1.0

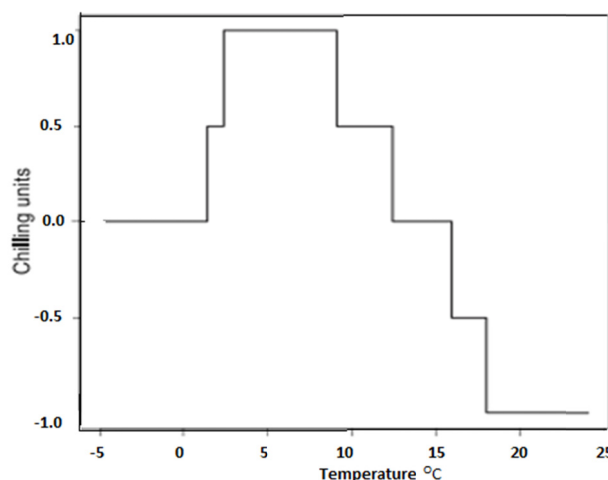


Figure 4. Utah model: Chilling units (CU) as a function of temperature (Richardson et al., 1974)

Though, the Utah model has been employed in studies to characterize the rest requirements of several fruit crops and their cultivars, it has also been used in tandem with another models to calculate growing degree hour accumulation (GDH°C) (Whitworth & Young, 1992; Couvillon, 1985), where a single GDH°C is defined as 1 hour above base temperature (4.5°C). These were applied in tandem to estimate the accumulation of energy required for the development of phenological parameters such as full bloom or fruit set. Other useful contributions made by the application of these models included the demonstration that post-rest chilling bursts beyond the chilling requirements would significantly reduce GDH°C accumulation required for development (Couvillon, 1985).

Other model following similar patterns in application with the Utah chill model is the North Carolina chill model (Shaultout & Unrath, 1983; Gilreath & Buchanan, 1981). This model behaves some minor modification to original Utah, that it accommodates the chill accumulation until the raise in temperature reached at 16.5°C, and above which, the raise in temperature would result in chilling reversal (Table 3). The corresponding temperatures and chill units (CU) values for North Carolina model showed that, because of chilling negation by high temperature, it has a limited applicability in mild winter areas (Table 3 and Figure 5).

Table 3. Values of chill units (CU) as a function of hourly temperature for North Carolina model (Gilreath & Buchanan, 1981; Shaultout & Unrath, 1983)

Temperature °C	CU
-1.1	0.0
1.6	0.5
7.2	1.0
13.0	0.5
16.5	0.0
19.0	-0.5
20.7	-1.0
22.1	-1.5
23.3	-2.0

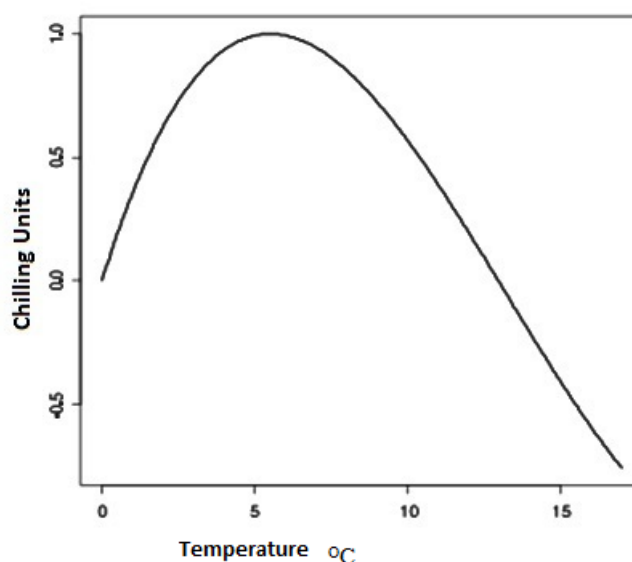


Figure 5. North Carolina chill units (CU) as a function of temperature (Shaultout and Unrath, 1983; Gilreath and Buchanan, 1981)

When considering the original Utah chill unit model (Richardson et al., 1974), it consists of three curves

showing effective bud temperature, air temperature and effective chilling temperatures (Figure 6). The outer curve represents the actual bud temperature that the tree senses and to which it responds. The inner curve is the air temperature as measured in the instrument shelter. The middle curve designated the 'Effective Bud Temperature' is an index relating shelter temperature to bud temperature.

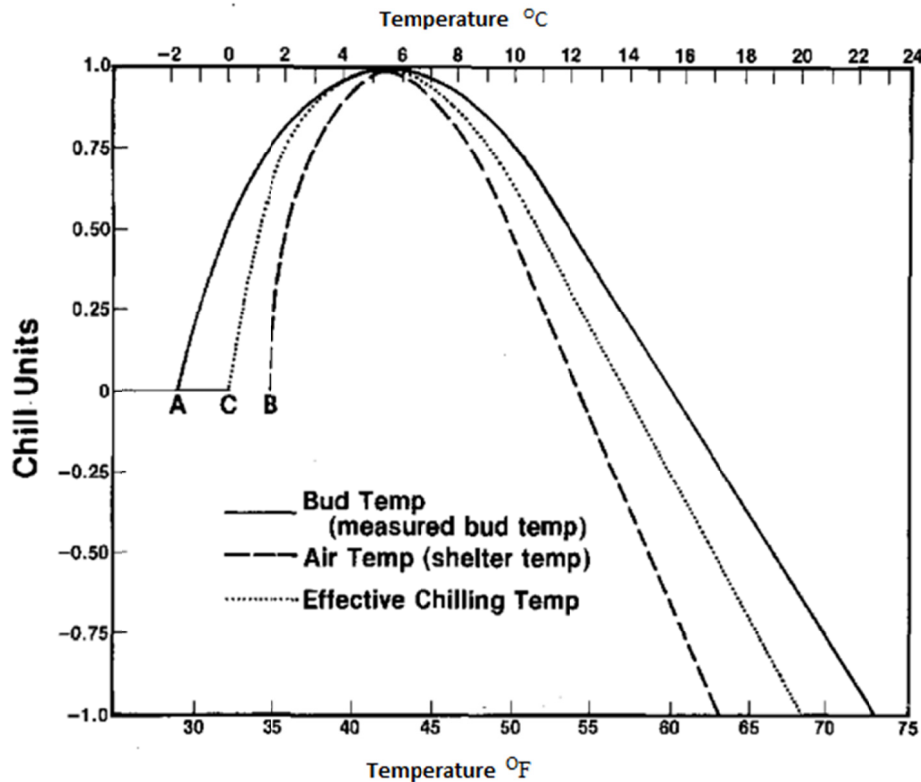


Figure 6. Curves used in estimating Utah chill units (Richardson et al. 1974)

As shown in the curves (Figure 6), the responses of several fruit tree species to their environmental temperatures indicated that, rather than following a true cosine curve, response rates to increasing temperatures often varied, depending on whether the temperature above or below the optimum temperature for the species that can severely affect chill unit accumulation. The calculation process is identical for North Carolina model (Shaultout & Unrath, 1983), because initially the cumulative chill unit curve drops, but later on it starts to increase once positive chill units begin to accumulate (Figure 5).

Gilreath and Buchanan (1981) noted that the widely used Utah model (Richardson et al., 1974) has not proven accurate when tested under climatic conditions that are milder than in the original experiment. Also, the Utah model was developed to predict bud-burst for 'Red-haven' and 'Elberta' peaches, but, in practice, it is widely used for a wide variety of crop species.

Linville (1990) conducted experiments using the Modified Utah model for peach trees to improve accuracy in determining dormancy release. Optimum chilling temperatures ranges from 2.5-9.1°C, with temperature either side of the optimum range declining in ability to accumulate chill. Another important addition was the incorporation of the negation effect that high temperatures (~16°C) can reverse the previously accumulated chill. Thus, the Modified Utah model is more appealing than the original Utah model due to the more gentle response, that is, no solid step boundaries, which is more likely representative of the chill accumulation processes (Figure 7).

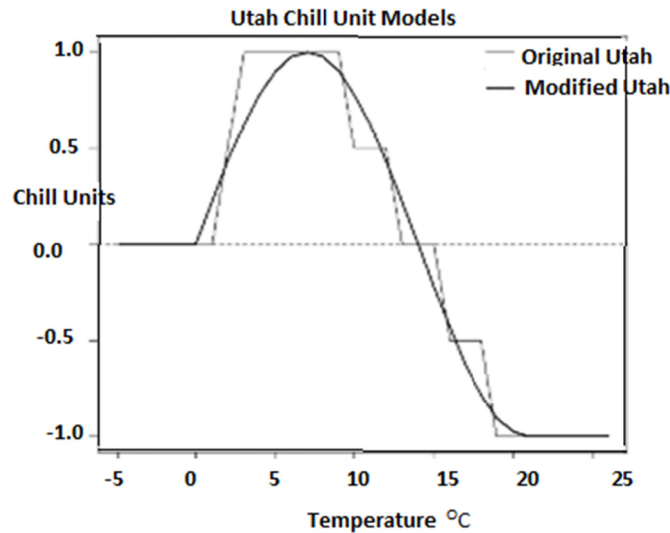


Figure 7. The Modified and original Utah model chill unit allocations for hourly temperature (°C) (Linvill, 1990)

Also, the Modified Utah model allocates chill units (CU) for hourly temperatures (T_t) which are summed over a predetermined chilling period to estimate total chill exposure (CU tot) (Equ 3).

$$PCU_{tot} = \sum_{t=st}^{en} PCU \begin{cases} T_t \leq 1.4^{\circ}\text{C} & ; PCU_t = 0 \\ 1.4^{\circ}\text{C} < T_t \leq 2.4^{\circ}\text{C} & ; PCU_t = 0.5 \\ 2.4^{\circ}\text{C} < T_t \leq 9.1^{\circ}\text{C} & ; PCU_t = 1 \\ 9.1^{\circ}\text{C} < T_t \leq 12.4^{\circ}\text{C} & ; PCU_t = 0.5 \\ T_t > 12.4^{\circ}\text{C} & ; PCU_t = 0 \end{cases} \quad \text{Equ.....3}$$

The Positive Utah model (Linsley-Noakes et al., 1994) is an iteration of the original Utah model however the chilling reversal due to high temperatures is excluded. The model defines optimal chill accumulation between 2.4 and 9.1°C and steps down to nil positive chill units for temperatures less than 1.4°C and greater than 12.4°C (Figure 8 and Equ 4).

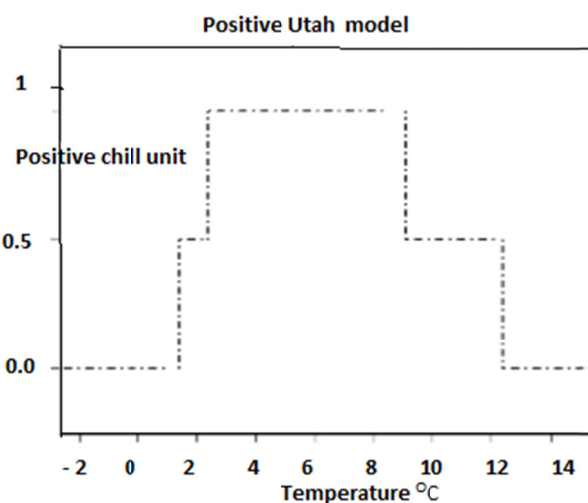


Figure 8. The Positive Utah Model chill allocations for hourly temperature (°C) (Linsley-Noakes et al., 1994)

This model also allocates positive chill units (PCU) for hourly temperatures (T_t) with total chill exposure (PCU tot) determined by summing PCU over a predetermined chilling period (Equ 3).

$$PCU_{tot} = \sum_{t=st}^{en} PCU_t \begin{cases} T_t \leq 1.4^{\circ}\text{C} & ; PCU_t = 0 \\ 1.4^{\circ}\text{C} < T_t \leq 2.4^{\circ}\text{C} & ; PCU_t = 0.5 \\ 2.4^{\circ}\text{C} < T_t \leq 9.1^{\circ}\text{C} & ; PCU_t = 1 \\ 9.1^{\circ}\text{C} < T_t \leq 12.4^{\circ}\text{C} & ; PCU_t = 0.5 \\ T_t > 12.4^{\circ}\text{C} & ; PCU_t = 0 \end{cases} \quad \text{Equ.. 4}$$

The Positive Chill Units model (PCU) as a modified version of the Utah, does not consider the negative values for the chill accumulation (Linsley-Noakes et al., 1995). Following the Dynamic model, its application in tropical and sub-tropical zones has shown improved results. The procedure it follows is the same as original Utah, except that when negative, the chill unit value is set equal to zero (Equ 4). Therefore, the accumulated chill units are equal to zero until the temperatures drop into the effective zone and positive chill units begin to accumulate (Figure 8). The key differences between the original Utah (Richardson et al., 1974) and the Positive Chill Unit model (Linsley-Noakes et al., 1994) were: (i) when predicting chill unit accumulation, an emphasis is given to predict the proportion of bud break rather than time of bud break; (ii) different weighing temperatures for chill accumulation was measured by a fitting procedure to exclude chilling reversal.

(iii). Dynamic Model

The Dynamic model (Fishman et al., 1987; Erez et al., 1990) determines chill exposure differently to the other models. It accumulates chill more interactively and calculates chill portions in a time dynamic two-step process. The creation of an intermediate product, promoted by cold temperatures, is initially determined. This intermediate product can then be destroyed by subsequent warm temperatures. Moderate temperatures are defined to have a positive influence on chill accumulation. Once a threshold amount of the intermediate product is created, it is irreversibly accumulated as a chill portion that cannot be destroyed regardless of subsequent temperatures (Figure 9).

An algorithm for this model was outlined by Darbyshire et al., (2011) in similar procedures with that of the original Dynamic model (Fishman et al., 1987a, b). Chill portions are calculated using hourly temperature ($^{\circ}\text{K}$) input and chill portions are summed over a specified chill period to obtain total chill exposure.

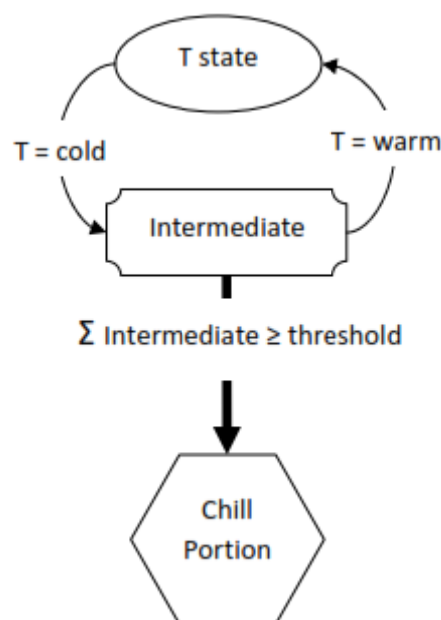


Figure 9. Dynamic model concepts for hourly temperatures, T ($^{\circ}\text{K}$) for initial temperature (T state) followed by subsequent temperatures that can destroy the intermediary after while a threshold amount of the intermediary is amassed a chill portion is irreversibly produced (adapted from Darbyshire et al., 2011)

Fishman et al. (1987a, b) stated that the concept of Dynamic Model encompasses the following elements:

(i) The two-step system concept:

The first step builds an intermediate that is accumulated when exposed to low temperature. The intermediate level depends on following: the bell shape curve effect of chilling, the negating of chilling by high temperatures (effect of level; effect of high temperature duration; effect of cycle and the promotive effect of moderate temperatures. The dynamic curve exhibits a periodic behavior and the model incorporates a second adjustment to correct the effect of the low temperatures with the assumption that the intermediary transformed into a product cannot be reversed (i.e. Chill Portions (CP) once accumulated, cannot be nullified by high temperatures).

(ii) The concept of a fixation effect:

When a critical level of the intermediate is reached, a phase transition occurs, the intermediate level drops to zero and a quantum that is termed 'Chilling Portion' is accumulated.

(iii) The concept of a quantum:

When a portion, the size of which is a physiological measure, is accumulated, it is fixed and conserved. This follows the principle of Arrhenius equation (France & Thornley, 1984) as:

$$k = A x e^{(E/T)} \dots\dots\dots \text{Equ 5}$$

Where T is the absolute temperature expressed in Kelvin degrees (°K), E is the activation energy for the formation and destruction of the intermediary, and A is an independent coefficient of the temperature and (k), the velocity constant.

(iv) The concept of a threshold level:

A critical level of the intermediate has to be reached for effective chilling to accumulate. As long as this threshold is not reached, no matter how close the level of intermediate is to the threshold, no chilling accumulation will occur. Differences among cultivars or species are in the total portions needed for breaking dormancy, not in model parameters.

The equations for calculating chill portions are more complex than the other models (Fishman et al., 1987a, b). Although they are difficult to derive from the original publications, Luedeling et al. (2009c) extracted them from a spread-sheet commonly used by practitioners. The equations for the number of Chill Portions at time t (CPt) are:

$$\begin{aligned} x_t &= \frac{e^{slp \times tetmlt \times (T_t - tetmlt)/T_t}}{1 + e^{slp \times tetmlt \times (T_t - tetmlt)/T_t}} \\ y_t &= \frac{a_0}{a_1} \times e^{(e_1 - e_0)/T_t} \\ ak_t &= a_1 \times e^{(-e_1/T_t)} \\ Inter_{Et} &= y_t - (y_t - Inter_{St}) \times e^{-ak_t} \\ Inter_{st} &= \begin{cases} t = 1, & 0 \\ \text{if } t > 1 \text{ \& } Inter_{Et-1} < 1, & Inter_{Et-1} \\ t > 1 \text{ \& } Inter_{Et-1} \geq 1, & Inter_{Et-1} \times (1 - x_{t-1}) \end{cases} \quad \text{Equ.....6} \\ delt_t &= \begin{cases} t = 1, & 0 \\ \text{if } t > 1 \text{ \& } Inter_{Et-1} < 1, & 0 \\ t > 1 \text{ \& } Inter_{Et-1} \geq 1, & Inter_{Et} \times x_t \end{cases} \\ P_t &= \begin{cases} t = 1, & delt_t \\ \text{if } t > 1, & delt_t + P_{t-1} \end{cases} \\ P_{tot} &= \sum_{t=st}^{en} P_t \end{aligned}$$

The experimentally derived constants slp, tetmlt, a₀, a₁, e₀, and e₁, were set to 1.6, 277, 139,500, 2.567 × 10¹⁸, 4153.5, and 12,888.8, respectively (Erez et al., 1988). T_k is the measured hourly temperature in Kelvin, whereas t denotes the time during the season (in hours) with t₀ being the starting point of chilling accumulation. As a result of the self-limiting effect of the destruction of the intermediate product, this model starts accumulation

automatically.

4.4. The concept of threshold temperatures for chill accumulation

Several factors affect whether or not tree species will accumulate sufficient chilling to release dormancy (Table 4). Threshold temperatures are important because some temperatures contribute to the chilling requirement and others do not. High temperatures do not contribute to meeting chilling requirements and generally temperatures below a lower threshold (0 °C) are not considered effective for chilling. In some models, higher temperatures counteract the positive effects of chilling and negative chill units are applied when temperatures exceed a threshold (Richardson et al., 1974; Gilreath & Buchanan, 1981; Shaltout & Unrath, 1983). In most cases, the temperature weighting factors are based on laboratory studies where plants are exposed to the same temperature for long periods of time and the hours at a specific temperature until bud-burst are observed. Chill factors vary from zero, when the temperature does not contribute to meeting the chilling requirement, to 1.0 when the temperature is the most effective at meeting the requirement (Richardson et al., 1974). Then a chill factor, as a function of temperature, can be developed and used to weight chilling for temperature effectiveness at releasing dormancy.

Table 4. Summary of the major chill models with respect to temperature effects and chill unit accumulation (adapted from E. Luedeling, 2012)

Models and Authors	Basis of Measurement	Differences in temperature weights	Continuity of weights	Negation of chill by heat	Limitation to chill negation	Enhanced by moderate temperatures	Two-step chilling
Chilling Hours Model (Bennett 1949; Weinberger, 1950)	h	-	-	-	-	-	-
Utah Model (Chili Units; Richardson et al., 1974)	h	†	-	-	-	-	-
North Carolina Model (Shaltout and Unrath, (1983)	h	†	-	†	-	-	-
Anderson and Richardson, 1987	h	†	†	†	-	-	-
+ve Utah Model (Linsley-Noakes and Allan, (1994)	h	†	-	†	†	-	-
Modified Utah Model (Linville, 1990)	h	†	†	†	-	-	-
Dynamic model (Chill portions); Fishman <i>et al.</i> , 1987a; 1987b)	h	†	†	†	†	†	†
Other models applied on regional basis							
Chmielewski et al. (2011)	d	-	-	-	-	-	-
Legave et al. (2008)	d	±	±	-	-	-	-
Cesaraccio et al. (2004)	d	†	†	-	-	-	-

N.B. † (plus) indicates that the characters included in the model; - (minus) indicates these characters not included; ± means different characters exists, but, include few characters; h - hourly; d - monthly; weighting - refers to different temperature ranges; continuity for continuous weighting; chilling negation indicates the reversal of chilling; limit to chill negation means how much chill can be negated by moderate temperature; two step process for chill portions and its irreversibility.

4.5 Alternative Approaches to Classical and Dynamic Models

(i) The Mean Temperature Model

The mean temperature model is one of the alternative approaches for the area requiring low-chill under tropical conditions. The Mean Temperature Model uses mean winter (October to January and/or February) monthly temperatures to estimate accumulated chilling. The model also estimates the relationship between the mean monthly temperature of the coldest month(s) and total chill unit accumulation for specific location (Linville, 1990; Shaltout & Unrath, 1983; Gilreath & Buchanan, 1981).

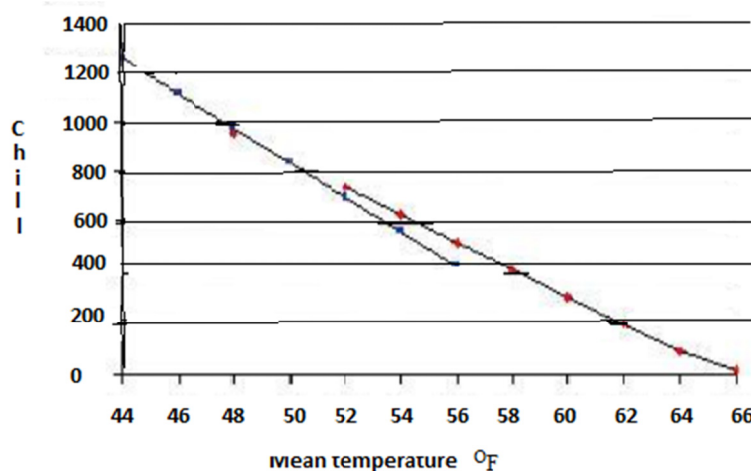


Figure 10. Total chill unit accumulation based on mean winter temperature (Linville, 1990)

The accuracy and the simplicity of calculating chill accumulation with mean temperatures will aid fruit researchers and growers in several ways. Mean temperature data is routinely kept by cities and state climatologists and is usually easily accessible for tracking chill accumulation for a specific area over long periods of time (Shaulout & Unrath, 1983; Linville, 1990). This will make it easy for a researcher, extension agent, or grower to more accurately match cultivars to a given locale.

(ii) Growing Degree Hour (GDH) Model

Another method useful for tropical and sub-tropical climate to estimate the chilling accumulation is the Growing Degree Hour (GDH) Model (Linkosalo, 2000; Hänninen, 1990; Cannell & Smith, 1983). The model uses degree day calculations to determine chill days (units for chilling) and anti-chill days (units for heating). The Chill days (Cd) represents a sequential accumulation of chill to break rest, while the anti-chill days (Ca) to overcoming the quiescence (i.e. occurrence of dormancy due to unfavorable environmental conditions) that contribute to chilling reversal. Rest is broken when the Cd curve falls to the chilling requirement (CR) and quiescence is overcome when the Ca curve reaches zero (Figure 11) (Linkosalo, 2000; Snyder et al., 1999; Zalom et al., 1983).

Chill days and anti-chill days are calculated from daily maximum (T_x) and minimum (T_n) temperature data and threshold temperature (T_c) Table 5. Chill days are calculated by first calculating the degree days above a 0°C threshold temperature (T_c) and then the anti-chill days (or degree days above T_c) are subtracted (Snyder et al., 1999; Zalom et al., 1983). The sign of the difference is changed to make Cd a negative number, and the negative (Cd) values are accumulated until they reach a pre-selected value that is identified as the chilling requirement (CR) (Figure 11 and Table 5).

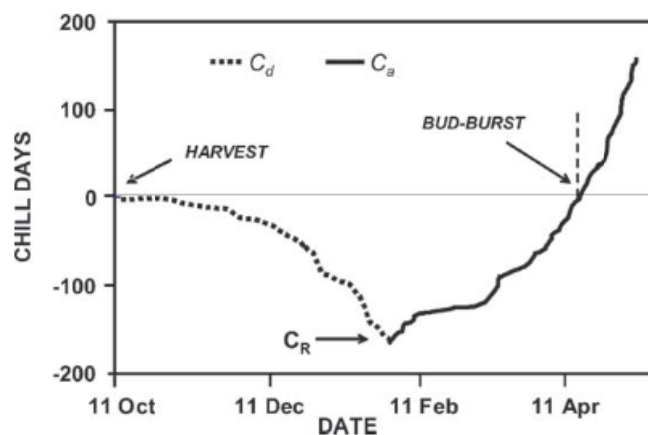


Figure 11. The single triangle degree day method showing the Chill days (Cd) and anti-chill days (Ca) accumulation from harvest, leaf fall, or fully fruit ripe to bud-burst (Zalom et al., 1983; Snyder et al., 1999)

Rest is broken when the Cd curve falls to the chilling requirement (CR) and quiescence is overcome when the Ca curve reaches zero (Figure 11). The chilling requirement is met on the day when the $\sum Cd \leq Cr$ which corresponds to breaking rest. On the following day, the model begins to add anti-chill days on each day starting at $CR + \sum Ca \geq 0$ at the predicted bud-burst (Linkosalo, 2000). The chill days and anti-chill days both depend on the selection of a temperature threshold (T_C) and CR so these parameters are iterated to find the combination that best predicts the bud-burst dates. Thus, the most important features of the Growing Degree Hour (GDH) model is a sequential dormancy model with an abrupt change from chilling to temperature forcing when the cumulative Cd reaches CR, that can potentially avoid chilling negation.

For calculating Cd and Ca, there are five possible cases, based on the single triangle degree day computation method, which depends on the relationship between T_x and T_n relative to T_C and 0°C (Table 5) (Snyder et al., 1999; Zalom et al., 1983).

Table 5. Chill days (Cd) and anti-chill days (Ca) equations that relates the maximum (T_x) and minimum (T_n) temperature to the threshold temperatures T_C and 0°C (Snyder et al., 1999; Zalom et al., 1983)

Temperature cases	Chill days	Anti-chill days
$0 \leq T_C \leq T_n \leq T_x$	$C_d = 0$	$C_a = T_M - T_C$
$0 \leq T_n \leq T_C < T_x$	$C_d = -\left[(T_M - T_n) - \left(\frac{(T_x - T_C)}{2}\right)\right]$	$C_a = \frac{T_x - T_C}{2}$
$0 \leq T_n \leq T_x \leq T_C$	$C_d = -(T_M - T_n)$	$C_a = 0$
$T_n < 0 < T_x \leq T_C$	$C_d = -\left(\frac{T_x}{T_x - T_n}\right)\left(\frac{T_x}{2}\right)$	$C_a = 0$
$T_n < 0 < T_C < T_x$	$C_d = -\left[\left(\frac{T_x}{T_x - T_n}\right)\left(\frac{T_x}{2}\right) - \left(\frac{T_x - T_C}{2}\right)\right]$	$C_a = \frac{T_x - T_C}{2}$

(iii) Exponential temperature response function

Lantin (1973, 1977) proposed an alternative approach for chill estimation based on an exponential cold action function, first described in Bidabe, (1963), summed over the period of time for which chill accumulation is being studied:

$$Af = Q_{10}^{-tm/10} + Q_{10}^{-tM/10} \dots \dots \dots (\text{Equ 7})$$

Where:

Af = daily chill units accumulated

tm, tM = minimum and maximum temperatures for day

Q_{10} = temperature coefficient (expressed as the ratio of the effect at T divided by the effect at $(T-10)$).

Lantin (1977) selected a value of 1.4 as the one that gave the best fit to his data for a range of blackcurrant cultivars grown in UK. By raising daily max/min temperatures to a negative power function in this calculation, higher temperatures give rise to less chill-unit accumulation than do lower temperatures. The nonlinear response weights lower temperature periods, and especially extreme cold spells, even more than does the $>7.2^\circ\text{C}$ model. A problem with this model, however, is the fact that accumulation occurs even for temperatures well above the threshold for physiological chill effects, so that larger values of $\sum Af$ may simply reflect longer periods of accumulation, rather than more chill. Alternative ways to use this principle could be to accumulate only daily values greater than 1.57 (equivalent to a threshold of 7.2°C), or possibly to express the chill units as a daily average over the period concerned. A second and equally important problem is that this model gives increasing weightings to lower temperatures with no lower threshold for action, even though much physiological evidence suggests that this is unrealistic.

4.6 Comparison of the Predictive Performance of Chill Models

Many studies revealed that multiple chill models are used by researchers with no consensus reached for a 'best' chill model. However, several studies have been conducted investigating chill model skill. For instance, Alburquerque et al. (2008) used the 0-7.2°C, Utah and Dynamic models to test chill model ability to predict flowering dates in seven sweet cherry varieties in Spain across several locations over two seasons. The Dynamic and Utah models were found to perform equally well but results from the 0-7.2°C model were poor in comparison. They concluded the use of the 0-7.2°C model for sweet cherry in their locations was no longer appropriate.

Viti et al. (2010) compared the skill of the Utah and Dynamic models in determining the chill requirement for apricot species in Spain and Tuscany. They found that the Dynamic model was less sensitive to temperature changes and was slightly more accurate than the Utah model. However, the author's highlight that improvement in accuracy in both models was needed. Perez et al. (2008) investigated the application of four chill models in two climatically different regions in Chile. The analysis over two seasons concluded that the 0-7.2°C model was ineffective at differentiating subtropical and temperate climates. Further, this model was not able to account for inadequate chill observations in Thompson Seedless grapes at the subtropical site. The Utah model was found to better distinguish the sites, with the Dynamic model best able to explain the regional differences.

Ruiz et al. (2007) tested the suitability of the 0-7.2°C, Utah and Dynamic models in predicting flowering in 10 apricot varieties over three years. The 0-7.2°C model was inconsistent, with the difference in recorded chill requirement between seasons as great as 30%. They found both the Utah and Dynamic models reported homogeneous chill requirements and found strong correlations between the two models. Ruiz et al. (2007) summarized that either the Utah or Dynamic model could be reliably used.

Zhang and Taylor (2011) conducted a 5 year study to estimate chill requirements of Sirora pistachio in Australia. They used the 0-7.2°C, Utah and Dynamic models to estimate chill requirements by forcing the cuttings grown in growth chambers. They found it difficult to determine a chill threshold using either the 0-7.2°C or the Utah model due to large variability in calculated chill thresholds between the seasons. The Dynamic model was found more consistent in determining threshold chilling requirement as reported in this study.

Many studies outline that the Dynamic model consistently performs similarly or better than the other chill models. The positive findings in favor of the Dynamic model are most likely due to the structure of the model. The model incorporates many observations of temperature effects on chill; including optimum chilling temperatures, and negation effects of high temperatures and the positive influence of moderate temperatures on chill accumulation. Further, the model is non-static in nature which would be expected to better reflect biological processes. The Modified Utah model similarly contains optimum chilling temperatures and negative influence of high temperatures. However, when using this model, chill that is accumulated early in the season can be negated some time later by late season high temperatures. The Positive Utah model is a derivative of the Utah model which does not include the negation aspects of high temperatures. It has been found to perform better than the original Utah model in mild locations: For example, in South Africa (Linsley-Noakes et al., 1994) and in California (Luedeling et al., 2009) in their study of walnut phenology.

The Dynamic model only considers the impact of high temperatures in influencing the production of an intermediate product, which is linked to time. Once a sufficient amount of the intermediate product is formed a chill portion is irreversibly created, and cannot be reversed by high temperatures later in the season.

The 0-7.2°C model is very simplistic and does not incorporate many of the observed effects of temperature on chill accumulation, such as the negative effect of high temperatures. The step-change structure of the model forces solid boundaries to chill accumulation, for example, 7.3°C will accumulate nil chill hours while 7.2°C will be allocated a full chill hour. Given the restricted knowledge on the chilling process this level of accuracy is unlikely to be defensible.

The 0-7.2°C model is dated and many studies have found it to perform poorly in predicting observed changes (Zhang & Taylor, 2011; Alburquerque et al., 2008; Perez et al., 2008; Ruiz et al., 2007). Nonetheless, this model has been extensively used in research and continues to be with a recent study in California using only this model to investigate future chilling conditions (Baldocchi & Wong, 2008).

Aron, (1975) compared the differences between chill models, using meteorological data recorded at HRI-East Malling research station, UK. The temperatures were extracted for the winter months over some 50 years and functions were applied to produce accumulated chill units for each of the chill models. Accordingly, <7.2°C,

0-7.2 °C and the Lantini models showed generally strong associations with the correlation coefficients between these variables being greater than 0.5. Only the Utah model was irregular and being poorly correlated with the other chill measures.

Aron (1975) also noted that the main limitation of the Utah Model resides in its specificity i.e. based on peach cultivars grown in North America. As a generic chill model it certainly conflicts with large amounts of literature that demonstrate, for example, that some species can accumulate chill below 0°C, whereas such temperatures in other species contribute negatively towards chill units (Aron, 1975). Effectively, the limitations of the Utah model varied with species, cultivar and environmental specificity. Although the Lantini, the <7.2°C and the 0-7.2 °C models all agree reasonably well and are all simple calculations that can be extracted from daily or hourly temperature data to give general assessments to the local chill conditions.

Luedeling and Brown (2010) compared chill models globally to confirm the differences among them across multiple climates using the 0-7.2°C, Utah and Dynamic models in their analysis. It was found that the chill models are not proportional and conversion factors could not be established. This global assessment was further confirmed by Darbyshire et al., (2011) in Australia who reported historical trends in chill accumulation using four different chill models.

They found that in Australian setting, trends differed in magnitude and/or direction between the chill models, with contradictory interpretation between chill models across locations. These suggesting further physiological research that is required to tailor chill models in terms of species specificity; Such tailoring is still needed for a given location where a more specific model is still required, particularly one that incorporates a more realistic model of the chill-physiology.

5. Effect of Lack of winter chilling on reproductive and vegetative development

5.1 Influence on Floral Bud and Flower Development / Reproductive Growth/

The symptoms of inadequate chilling are many, and vary with fruit species. Generally, they are recognized as a delay in flower and vegetative bud break (often described as 'delayed foliation'), which is frequently evident as an extended period of bud break (Jacobs et al., 2002; Cook & Jacobs, 2000; Couvillon, 1995; Jacobs et al., 1981). In pear (*Pyrus communis*), autumnal warming has been shown to dramatically delay flowering time (Atkinson & Taylor, 1994; Atkinson & Lucas, 1996). This response is greater in earlier flowering cultivars than later ones. This implies that there may be two phenomena occurring, a delay in foliation and an increase in flowering irregularity. Extension of the bloom period may itself impact on the potential to crop; it may also cause large variations in crop development rate, fruit size and picking date.

The symptoms associated with lack of chilling also include the death of flower bud initials and the abscission of flowers prior to opening. Stone and pome fruit appear to generally differ in their response to lack of chilling. The stone fruit, which include almonds, apricots, peaches, plum and cherries, frequently abort entire flower buds. There are, however, studies that report anatomical abnormalities in flower buds of various apricot cultivars which could not be related to lack of chilling (Viti & Monteleone, 1991). On the other hand, pome fruits, which include apples and pears, may show dead flower clusters but vegetative buds can survive (Brown, 1952). Exposure to low temperatures has been shown to be necessary for the initiation of pistillate flowers (i.e. female and fruit bearing) in pecan (Amling & Amling, 1983).

Conversely, when chilling is inadequate, for example with peach, normal flowers are produced but they can lack stigmas and styles. Flowers of *Prunus avium* have been shown to be smaller in response to limited chilling (Mahmood et al., 2000a). Developing flowers may also fail to set fruit, and when fruits do set they may be of poor quality due to short pedicel length or insufficient leaf area development (Mahmood et al., 2000a).

Insufficiently chilled trees may not only show sparse bud break, but also maturing fruit and flowers on the same shoots. In a study carried out by Abbott (1962), trees subject to mild winters produced a larger number of flowers relative to trees exposed to average winter temperatures. However, these buds failed to break due to the sub-optimal chilling treatments so fruit bud number and yield were reduced. In years experiencing mild winters, Weinberger (1954) described "prolonged dormancy" in North American peach cultivars, characterized by irregular bud break and delayed asynchronous flowering, leading to a prolonged blossoming phase. Buds on older wood near the centre of the trees apparently had lower chill requirements, resulting in foliage clusters developing in the centre and large sections of bare stems on the newer, outer wood.

In a recent study of apple blossom development, cultivars subject to shallow dormancy conditions were observed to be highly apically dominant and deficient in reproductive spur density (Oukabli et al., 2003). At the differentiation stage the buds form vegetative buds rather than flower buds, resulting in poor flower indexes.

Closer anatomical investigations further showed that the flower tissues develop abnormalities that are carried on to anthesis, which is characterised by pistil abortion. Additionally, vascular disorganisation results in a failure in the establishment of the connection of the xylem vessel elements to the base of the flower buds. In raspberry, poor bud break is generally found in the lower cane, whereas the apices appear to have the lower chill requirements (White et al., 1999, 1998). Delayed bud break has been commonly observed in both raspberry and blackberry germplasm following mild winters in Californian coastal regions (Fear & Meyer, 1993).

Using the raspberry cultivar ‘Autumn Bliss’ as an experimental model, Carew et al., (2001) described an increase in vegetative growth and simultaneous decline in time to flowering that occurred with increasing chilling, either natural or artificial. The researchers pointed out the likely distinction between the two responses, providing experimental evidence to support the observation that cold treatment on flowering appeared to be a distinct vernalization effect. In blackcurrant, there are many symptoms associated with lack of winter chill. These include erratic or uneven bud break, leading to loss of yield and a reduction in fruit quality due to uneven ripening, delayed and protracted growth and flowering, a tendency for flower formation to precede leaf formation, and increased fruit ‘run-off’.

Winter chill requirements varied with tree species and show diverse indications if it becomes inadequate in mild winter areas (Table 6). Its manifestations include a delay in vegetative bud-break and time of anthesis (Cook & Jacobs, 2000; Couvillon, 1995; Jacobs et al., 1981). For example, In *P. communis*, Atkinson and Lucas (1996) reported that autumnal warming delayed anthesis in early flowering cultivars than late flowering which showed two separate effects (i.e. a delay in bud break and an increase in irregularity of date of anthesis). They indicate that extended period in the time of anthesis causes variation in fruit development, fruit size, and harvest date and fruit quality. This was in conformity with the report of Mahmood et al. (2000) on *P. avium* flowers that inadequate chilling would result in failure of flower cluster to set fruit, and even when fruits do set, it may be of low quality due to short pedicel length or insufficient supportive leaf area for full fruit development.

Table 6. Summaries of the different aspects of perennial fruit crop growth, development, and production impacted by low winter chill (Atkinson et al., 2013)

Fruit trees	Aspects which are affected by low winter chilling									
	Vegetative bud break ^a	Floral bud break ^a	Bud abscission ^b	Flower abscission ^c	Flower quality ^d	Reproductive morphology ^e	Fruit set ^f	Vegetative growth ^g	Crop yield ^h	Product quality ⁱ
Apple	†	†		†	†			†	†	†
Pear				†		†			†	
Cherry			†		†	†	†			
Plum			†							
Peach		†	†		†	†		†		
Nectarine			†		†					
Apricots			†		†					
Almond			†					†		
Raspberry	†	†								
Blackberry	†									
Blackcurrant	†	†					†		†	†
Strawberry	†						†	†	†	†

^a Delayed, erratic or uneven bud break (column 1 vegetative and column 2 floral); ^b Abscission of entire flower buds; ^c Abscission of single flowers within a cluster; ^d Reduction in flower quality; ^e Changes in reproductive morphology; ^f Reduction in fruit set or increased run-off; ^g Changes in vegetative growth, apical dominance, etc.; ^h Reduction in crop yield; and ⁱ Changes in crop/product quality.

In North American mild winter conditions, Weinberger (1954) stated that in *Prunus persica* cultivars, prolonged dormancy due to lack of adequate chilling would result in irregular bud break and delayed anthesis, leading to poor fruit set and unproportional fruit development with inferior quality fruit. Accordingly, buds on older wood at the centre of the tree had lower chill requirements, resulting in a small clustering of flowers and large sections of stem devoid of flowers. Oukabli et al. (2003) also reported that when flower development in *Malus x domestica* cultivars subject to limited dormancy, it can not only have reduced floral buds but may also show high apically dominance. Inadequate chilling of *Fragaria x ananassa* is known to result in a lack of plant vigour, reduced vegetative growth and yield (Craig & Brown, 1977; Voth & Bringham, 1970). Thus, plants with low vegetative vigour flower intensely and produce small fruit (Bringham & Galleta, 1990).

Generally, the reproductive performance of perennial trees are influenced not only by chilling temperatures based on the species requirement, but also, the post chilling cooler temperature in the area had a great impact on vegetative growth, flower bud development, pollination, fruit setting and development. This was clearly indicated by a *Prunus avium* study, Mahmood et al. (2000) showed when chilling was limited (360 h at 4°C), trees exposed to cooler post-chilling temperatures had greater fruit set. They also reported that, to achieve the same degree of fruit set as that at the lower post-chilling treatment, it required a much longer period of chilling especially in late flowering cultivars. Similar observation was made in *Pyrus communis* (Spiegel-Roy & Alston, 1979) showed that there was a strong relationship between chilling and the heat requirements for renewed growth and bud break. Climatic conditions during and around the time of anthesis influence crop yield by promoting or inhibiting the effective pollination periods, fertilization and fruit set, as well vegetative meristems and their growth (Williams, 1970).

5.1.1 Floral Bud Abscission and Flower Quality

In pome fruits, with their mixture of bud types, all or part of the primordial flower may abscise (Brown, 1952). This may leave flower bud clusters which are reduced in size, or they may open only as a leafy spur. Many cultivars of stone fruit grown in California are well known to shed flower buds following warm winters (Brown, 1958; Brooks & Philp, 1941). However, when these losses are small they can be beneficial because they induce a level of flower thinning which benefits subsequent fruit quality. The effect of mild winters on pears is typical of pome fruits, in that one or more of the embryonic flowers within the bud die. However, unlike the stone fruits, the entire shedding of the bud does not take place (Brown, 1952). Pear flower bud abscission has been shown to be highest shortly before bud swell and when higher temperatures are followed by sudden declines. There is also evidence of abnormalities being induced when meiosis had taken place at higher temperatures (Whelan et al., 1968).

Analysis of a wide range of different cultivars supports the notion of two distinct peaks of peach flower abscission, which can be correlated with maximum temperature values. It should also be noted that floral bud abscission and delayed bud break are more prevalent after warm winters, but bud abscission is not clearly correlated with relative chilling requirement (Brookes, 1942). Evidence with French prune and some peach cultivars shows that bud drop was less intense with cultivars with lower chilling requirements (Samish, 1954). A study carried out in California showed that in 1941 the winter orchard temperatures were higher than they had been at any time during the previous twelve winters (Brooks 1942; Brooks & Philp, 1941). The extensive descriptive study of 280 peach and 58 nectarine cultivars ranked them relative to the amount of flower bud drop. They found some 21 cultivars of peach that showed no flower bud abscission (class 1) and 78 that incurred heavy bud drop (class 4, only 0 to 15% of original numbers of flowers were left). The trees within their 'class 2' had sufficient flowers (50 to 85%) to enable full crops (optimal crop loads) to develop. About half the cultivars within the study lost no more flowers after the first recording date in mid-February (Brooks & Philp, 1941). In a similar survey carried out with apricots (119 cultivars) and plums (53 cultivars) after the mild winter of 1940-41, only one cultivar of each was found to show no bud drop (class 1). While 62 apricot and 27 plum cultivars were in the heavy bud drop, class 4, and showed correspondingly poor crops (Brooks, 1942).

The mild-winter temperatures in California in 1950-51 provided a further opportunity to describe the impacts of low chilling on fruit production. In the early 1950s, the winter of 1950-51 was described as the ninth winter out of the past 22 where it was mild enough to cause "flower bud deterioration" (Brown, 1952). Comparing climatic records, however, showed that the winter of 1950-51 was not as mild as that in 1940-41.

Despite this, records with California almonds that have low chill requirements were not considered to be influenced by warm winters. Heavy bud drop of unopened almond flowers was apparent in early December. Apricots described in the same study were shown to be less negatively influenced than expected from previous knowledge of their vulnerability to sub-optimal chilling. The chilling received during 1950-51 was around 25%

less than the predicted requirement. Only one cultivar consistently showed severe flower abscission. There was not only site-to-site variation with data collected from the same cultivar, but also tree-to-tree and block-to-block variability. It was equally true with apples within the same geographical region, with their higher chill requirements, that they showed only an extended bloom period, but the set level was normal (Brown, 1952). Not all of these losses of flower bud can be easily attributed to mild winters; evidence exists that the decline peach flower bud quality and health can occur as early as mid-September (Brown, 1958). This implies factors other than winter chilling influence bud development.

Limitations in the amount of chilling have been shown to influence flower morphology. When the sweet cherry cultivar 'Stella' received insufficient chilling, flower size and pedicel lengths were dramatically reduced (Mahmood et al., 1999). Once a threshold value (30 days at 4 °C) had been reached there was no further change in flower size. The pattern shown with respect to flower size was very similar to that of fruit set, with chilling promoting set to an optimum after which no further increase was apparent. When the post chilling treatment was at a higher temperature, 25°C compared to 19°C, the amount of fruit set was much reduced and did not increase with further chilling (Mahmood et al., 1999). This has important implications for determining climate change responses where scenarios for reduced winter chilling may be linked to warmer forcing temperatures prior to bud break.

5.1.2 Fruit set and quality (size)

Observations made after a very mild winter in California in 1950-51 suggested that despite flowers of almond having aborted early in their development, subsequent cropping was, not however, limited by floral abscission but as a result of low fruit set (Brown, 1952).

Equally, it has been suggested that flower bud abscission rates in stone fruit as high as 70 to even 90% can be tolerated, providing the subsequent conditions for fruit set are favourable (Brown, 1952). Work with *Prunus avium* has shown that when plants were chilled at 4°C for 360 hours, only very low levels of fruit set were achieved compared to those chilled for up to 1440 hours (Mahmood et al., 2000a). Recent work with the sweet cherry cultivar 'Stella' showed that extension of the chilling period to around 50 days (number of days at 4°C) resulted in an increased number of flowers per tree. The ability of these flowers to set fruit also increased over this chilling period (Mahmood et al., 1999). Further chilling did not have any additional benefits to flower number or fruit set.

It has been suggested that forcing strawberries after short periods of dormancy can not only have an impact on the plant's vegetative growth habit, but it can also influence floral capabilities (Kronenberg & Wassenaar, 1972; Piringer & Scott, 1964). Although flower number per plant is not influenced by chilling or cold-storage temperature in cv. 'Elsanta', fruit set may well be (Tehraniifar et al., 1998). The interaction between vegetative vigour and fruit production suggests that fruit set is modified.

The smaller size of apples grown in regions where adequate chilling may vary has been suggested to be due to pre-anthesis differences in fruit cell number (Grebeye & Berg, 2000). The implications of this were apparent in the production of Royal Gala in the Western Cape, where small fruit size was a recurring issue compared with other fruit producing regions in South Africa. Examination of the number of cells within reproductive buds was related to winter chilling. The influence of winter chilling can be modified if cropping loads induce reduce or biennial bearing (Grebeye & Berg, 2000).

5.2 Vegetative Development

Responses can be carried over from one winter and expressed at the start of the second subsequent growing season. These symptoms include poor or late start to extension and lateral shoot growth and abnormally dominant apical shoot growth. Hoyle (1960) found that a period of 12-15 weeks at 2°C was sufficient to satisfy the chilling requirement of dormant blackcurrant buds in Western Europe.

Accordingly, initial data from cultivar trials of blackcurrant in eastern England suggest that the presently available cultivars and breeding germplasm cover a wide range of chilling requirements and those cultivars can be placed in broad groupings according to the amount of chill units required for uneven bud break. Lantin (1973) suggested that differences exist between the chilling requirements of buds on the same blackcurrant plant, and that this can lead to uneven bud break, when the chilling requirement of some, but not all, buds is satisfied. Lantin (1973) also predicted that this unevenness within the bud break of a single plant was exacerbated by a high chilling requirement. Inadequate chilling of strawberry is known to result in lack of vigour, reduced vegetative growth (Voth & Bringham, 1970) and reduced yield (Craig & Brown, 1977). However, experiment to

induce early cropping dates of some cultivars suggests that reducing chilling exposure speeds up the initiation of fruiting in the spring (Gutteridge & Anderson, 1975).

In climatic regions, such as Kenya, where chilling is not possible and runner plants are required for plant propagation, applications of GA3 are used (Kahangi et al., 1992). Considerable development has taken place throughout the world over the last few years with the development of protected strawberry production. In France and the UK, for example, much of the cultivation occurs under plastic tunnels. It appears from work in France that, if tunnels are used too early during the winter, the inadequate chilling reduces plant vigour (Robert et al., 1997). Plants which show low vigour flower intensely and produce small fruit (Bringhurst & Galleta, 1990). It is apparent that chilling requirements differ with respect to bud type and position (Hauagge & Cummins, 1991). On vegetative shoots, the terminal bud can open prior to lateral buds, which induces strong apical dominance due to the prevention of lateral shoot growth. Branching in apple, for example, is mainly from distal buds (acrotinic) with little development of proximal buds (basitonic). This inhibition occurs via correlative influences (apical dominance) of the distal shoot (paradormancy) and can be reduced by phloem girdling (Champagnat, 1983). This suggests that developmental control is mediated via the transport of auxin (Faust et al., 1995). It is equally true that removal of distal portions of dormant shoot prior to forcing appears to remove paradormancy, allowing lateral buds to develop (Cook et al., 1998).

Application of cytokinins can also overcome the inhibition of these lateral buds from over-wintered shoots (Steffens & Stutte, 1989; Shaltout & Unrath, 1983a). The apical dominance response is well documented with peach (*Prunus persica*), which has terminal vegetative buds with the lowest chill requirements (Scalabrelli & Couvillon, 1986). This can have the effect of producing long shoots devoid of lateral side shoots capable of developing into fruit bearing spurs. Differences in bud type responses can also be detected around the point of adequate chilling when the temperature warms. Respiration rate appears to increase in relation to the switch to carbohydrate utilization and rates are higher in buds closer to the shoot apex than the shoot base (Young et al., 1995). This correlates with increased dormancy of lateral buds moving away from the apex. A quantitative study of the ontogenetic development of pear buds from a range of cultivars grown in South Africa revealed a relative high proportion reverting to a non-growing state (the 'latent phase') after being initially determined as within the growing phase (du Plooy et al., 2002). This developmental reversion has been recorded in apple, but at a much lower level (<2%) than evident with pear (Lauri et al., 1995). It is suggested that the increase in reversion (11 to 21%) was due to inadequate chilling and generally greater with the higher chill requirements of cultivars such as 'Beurre D'Anjou' and 'Golden Russet Bosc' (du Plooy et al., 2002).

6. Regional reports on winter chilling decline

Baldocchi and Wong (2008) reported that nut production in California was highly threatened by winter chill losses. They detected historic decline of winter chill for the majority of growing locations, using the chill hour model. Accordingly, the decline in winter chill ranges from 50 and 260 Chilling Hour per decade, and projected further losses in future at the rate of around 40 Chilling Hours per decade. This was further confirmed by Luedeling et al. (2009c) that the long term daily records from all weather stations in California revealed that changes in historic Safe Winter Chill by 2000 of up to -30%, compared to the 1950s baseline, according to the Chilling Hours Model. It indicates that in the 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.

Luedeling et al. (2013) reported responses of three different tree species (chestnut, cherry and walnut) to temperature variation during the chilling period at different locations, using the Dynamic Model. The result (Table 7) revealed that Chestnut bloom in the cold-winter climate of Beijing was found to depend primarily on the rate of heat accumulation, while cherry bloom in the temperate climate of Germany showed dependence on both chill and heat accumulation rates. The timing of walnut leaf emergence in the mild-winter climate of California depended much more strongly on chill accumulation rates. Accordingly, spring phases of cherry in Klein-Altendorf (Germany) and especially chestnut in Beijing will likely continue to advance in response to global warming, while for walnut in California, inadequate chilling may cause delays in flowering and leaf emergence (Table 7). Such delays could serve as an early-warning indicator that future productivity may be threatened by climate change.

Table 7. Estimated start and end dates of the chill and heat accumulation periods of chestnuts (*Castanea spp.*), cherry (*Prunus avium*) and walnut (*Juglans regia*) at different ecological zones (Luedeling et al., 2013)

Specific location	Chill period			Forcing period		
	Start	End	Requirement	Start	End	Requirement
Chestnut/ Beijing	23 rd Sept	2 nd Mar	79.8 ± 5.3 CP	5 th Jan	11 th May	13466 ± 1918 GDH
Cherry-Klein-Alterndorf	16 th Sept	4 th Mar	104 ± 8.9 CP	13 th Feb	13 th Apr	2698 ± 1183 GDH
Walnut/ Davis	25 th Oct	2 nd Jan	37.5 ± 5.0 CP	18 th Jan	5 th Apr	12245 ± 1697 GDH

Atkinson et al. (2013) reported that the amount of winter chill occurring in UK has declined and is predicted to continue to do so, as described in the UK Climate Assessment Program. This happens because of the projected climate change scenarios that are always in dynamism. They evaluated long term climatic data and linked it with the key seasonal reproductive events to describe the symptoms of lack of winter chill; these include vegetative growth and development that affects bud break, flowering and fruit setting potential of tree species. Also, the decline in chilling affects the developmental and physiological events which mainly linked with flower initiation, anthesis, dormancy and bud break.

Atkinson et al. (2013) also indicates that there is a serious lack of phenological modeling and mechanistic understanding of the physiological, molecular and genetic basis of winter chill requirement and dormancy-related environmental factors which affect tree growth and yield. This indicates future reductions in winter chill that require recognition as a potential limiting factor on fruit production in many European countries, especially in the southern parts where winter chill reduces. Possible strategies suggested for long term solutions to secure perennial fruit industries in Europe includes exploiting genotypic variability within several perennial crops, through plant breeding to develop low chill-cultivars, together with opportunities to change crop management practices and growing systems to tolerate the decline in chilling. At present a lot of evidences indicate that there is a measured decline in winter chill in UK and in other parts of the world (Baldocchi & Wong, 2008; Luedeling et al., 2009, 2011; Darbyshire et al., 2011) hypothesized that some of the recent reductions of winter chill in UK resulted in low yields of perennials crops as recorded by scientists and growers. Sunley et al. (2006) compared a range of existing chill accumulation models (data not shown) to explain the differences in date of anthesis of different fruit trees over a 50 year period. They also accessed several long-term UK geographically dispersed data sets on air temperatures and date of anthesis. Accordingly, all the chill models used to study chill accumulation show a statistically significant decline in winter chill over the last three decades.

Hennessy and Clayton-Greene (1995) used the Modified Utah Model for quantifying winter chill in Australia. The study revealed that that warm sites, and sites with wide diurnal temperature ranges, were more strongly affected by chilling decline than cooler sites with more similar temperature records. Regarding climate change scenarios, Hennessy and Clayton-Greene stated chilling declines for all sites, and for the stronger warming scenarios, they suggested that these losses have a greater impact on fruit industry. Thus, the situation requires different orchard management skills such as the use of artificial dormancy breaking, developing low chill requiring cultivars and other routine orchard management practices that can manipulate the microclimate of the area.

Darbyshire et al. (2011) in Australia evaluated four winter chill models; namely the Chilling Hours Model, the Modified Utah Model, the Positive Utah Model and the Dynamic Model for 13 locations by considering historic winter chill trends of the country from (1911-2009). Accordingly, for all 13 locations the result differs substantially and indicating that there was a limitation for all models in accuracy of estimating the chilling trends mainly for warmest locations (Figure 10). They found that the models rank the locations differently in terms of mean chill (1911-2009), with the 0-7.2°C model showing the greatest deviation (Figure 10 and Table 8). This study clearly indicates that chill model choice is important that it affects conclusions and the models are notably different when applied to multiple climates.

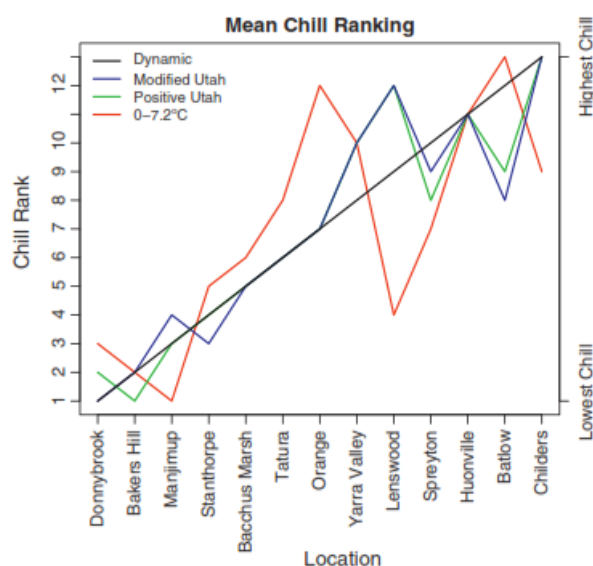


Figure 10. Chill model ranking of the 13 Australian locations from lowest to highest chill, relative to the dynamic model ordering (Darbyshire et al., 2011)

Although, the declining winter chill trends was inconsistent for almost all locations (Darbyshire et al., 2011), which varied strongly according to the model chosen (Table 8), through comparing trends at each location especially recent trends, location sensitivity to climate changes have already occurred, but many of the trends were not found to be statistically significant (Table 8), with the data showing high season-to season variability at all locations, regardless of model choice.

Table 8. Mean chill and standard deviation (in brackets) at each location for the period of 1911 – 2009 (Darbyshire et al., 2011)

	Dynamic (CP)	Modified (CU)	Utah Positive (PCU)	Utah 0-7.2 °C (CH)
Donnybrook	57 (6)	929(146)	1285(104)	576(115)
Bakers Hill	58 (7)	1011(172)	1274(128)	522(127)
Manjimup	67(6)	1247(179)	1369(134)	489(117)
Stanthorpe	72(5)	1235(141)	1443(101)	937(107)
Bacchus Marsh	78(3)	1525(94)	1690(64)	988(89)
Tatura	79(4)	1585(124)	1731(92)	1068(95)
Orange	85(3)	1671(142)	1801(137)	1395(124)
Yarra Valley	86(3)	1843(94)	1916(81)	1139(102)
Lenswood	86(4)	1978(138)	1956(117)	841(134)
Spreyton	87(3)	1840(83)	1837(78)	1016(108)
Huonville	88(2)	1882(133)	1948(81)	1377(108)
Batlow	89(2)	1785(131)	1914(144)	1624(137)
Childers	89(2)	2032(86)	2047(77)	1130(115)

Guo et al. (2013) studied the chilling and heat requirements for flowering time in two temperate fruit trees (chestnut and jujube) in Beijing, China, with daily chill and heat accumulation between 1963 and 2008. The data collected over the past fifty years was subjected to the Dynamic Model and the Growing Degree Hour Model to convert daily records of minimum and maximum temperature into physiologically meaningful metrics. The result revealed that (Table 9) over the past 50 years, heat accumulation during tree dormancy increased

significantly, while chill accumulation remained relatively stable for both species. Accordingly, heat accumulation was the main driver of bloom timing, with effects of variation in chill accumulation.

Table 9. Chilling and heat requirements estimation of Chinese chestnut (*Castanea mollissima*) and jujube (*Ziziphus jujube*) at Beijing, using the Dynamic and Growing Degree Hour (GDH) Models

Species	Chill period			Forcing period		
	Start	End	Requirement	Start	End	Requirement
Chestnut	14 Sept.	24 Mar	93±6 CP	4 Jan	23 May	17,481±1,983 GDH
Jujube	17 Sept.	19 Mar	89± 6 CP	9 Jan	13 May	13, 619±2,033 GDH

Observations on the phenology of two local peach genotypes (early and late) maturing were also conducted in Tanzania, using Utah, Dynamic and Mean Temperature models in 2010 and 2011 (Scalisi et al., 2014). The result (Table 10) showed that both Utah and Mean temperature models indicated low chilling accumulation and inconsistent with the actual phenology, suggesting that both models show some limitations under East and Central African highland conditions. This is mainly influenced by the climatic variables such as seasonal rain fall that play a role in temperature fluctuation that contribute positively or negatively for chilling accumulation. Also, chilling estimation by the Dynamic model at this location yielded a relatively low amount of Chill Portions (CP), which was not associated to CU obtained with the other two models (Table 10)

Table 10. Accumulation of Chilling Units According to the Utah and the Mean Temperature Models at Pomerini Tanzania

Year	Utah ^Z	Mean temperature ^Z	Dynamic ^Y
2001	105	303	2.02
2002	36	322	3.02
2003	118	318	3.02
2004	36	367	4.01
2005	-	-	-
2006	143	367	6.05
2007	91	472	6.04
2008	83	456	11.05
2009	131	410	4.03
2010	116	518	4.03
2011	121	462	5.05
Median	110.6	388.6	4.03
75th Percentile	85.2	333.4	3.27

Z = Chill Units (CU)

Y = Chill Portions (CP) ; 1 CP = aprx. 20 CU

This study showed that insufficient chilling is a major limiting factor in peach adaptation at the uplands of Tanzania. To further develop peach cultivation in the area, research should focus on selection of low chill cultivars and adopting the use of artificial rest breaking agents (Scalisi et al., 2014).

Luedeling et al. (2009) reported the effects of climate change to cause winter chill decline in Arabian Peninsula as they indicated in their case studies of four mountain oases of Oman. They used high-resolution record from Saiq to calibrate the long-term record of daily temperatures, especially the daily mean temperature records (Table 11). Also, in some places where the high-resolution measurements was absent, they used the mean daily

temperatures (0 – 7°C) on hour basis and/ or they are based on point measurements at a certain time of day to calculate the mean between minimum and maximum temperatures.

Table 11. Trends in monthly mean of daily minimum and maximum temperatures observed in Sayq (Oman), between 1979 and 2008, adjusted coefficient of determination (R^2) of the linear regression.

Month	Minimum temperature			Maximum temperature		
	Slope ($^{\circ}\text{C a}^{-1}$)	R^2 adjusted	P value	Slope ($^{\circ}\text{C a}^{-1}$)	R^2 adjusted	P value
January	+0.07	0.13	0.04 ^a	+0.02	-0.03	0.58
February	+0.09	0.24	0.01 ^a	+0.08	0.17	0.03 ^a
March	+0.02	-0.02	0.50	+0.03	-0.01	0.40
April	+0.07	0.08	0.09	+0.08	0.07	0.11
May	+0.04	-0.01	0.39	+0.05	0.07	0.12
June	+0.03	-0.02	0.50	-0.01	-0.04	0.80
July	+0.05	0.17	0.03 ^a	+0.03	0.02	0.25
August	+0.04	0.09	0.09	+0.07	0.22	0.01 ^a
September	+0.05	0.07	0.11	+0.03	0.03	0.21
October	+0.05	0.10	0.08	+0.04	0.05	0.17
November	+0.09	0.30	0.00 ^a	+0.02	-0.03	0.52
December	+0.05	0.02	0.24	-0.03	-0.01	0.42

N.B. Trends is statistically significant at $P \leq 0.05$.

Also, a historic temperature record was made between 1983 and 2008, as well as for three sets of 100-year synthetic weather records generated to represent historic conditions. A variety of temperate fruit tree crops requiring low chilling temperatures were considered in this study. These include pomegranates (*Punica granatum* L.), peaches (*Prunus persica* L.), apricots (*Prunus armeniaca* L.), walnuts (*Juglans regia* L.), and even apples (*Malus domestica* Borkh.), pears (*Pyrus communis* L.) and plums (*Prunus domestica* L.), all of which have minimum chilling requirements (Low chill) between 100 and 400 h, and unable to be cultivated in the lowlands.

The result indicates that climatic changes likely to occur within the next 30 years (temperatures elevated by 1°C and 2°C). Accordingly, in the studied areas of Northern Oman, a decrease in the numbers of chilling hours in high-elevation oases by an average of 1.2-9.5 h/year between 1983 and 2008, during this period winter chill was sufficient for most the species grown in the oasis according to the scenario analysis. For temperate fruit trees grown in oasis, a place where marginalized winter chilling, production might become impossible in the near future.

7. Adaptation Strategy Perspectives

Orchard establishment is expensive, time taking and require a lot of care and attention throughout the orchard existence. This requires special attention of scientists and growers in understanding climatic elements in a given location for successful orchard. It appears that cultivar placement in a locality must be based on the chilling requirement (Low, medium or high) as was required by the species. Accordingly, careful selection of cultivars to the particular climatic condition to meet the chilling demands against climatic scenarios is the most useful tools in areas where high temperature fluctuations happen irregularly. Inadequate chilling requirements in tropical climates forced the growers to forcedly defoliate trees after harvest to artificially induce dormancy (Edwards, 1987; Griesbach, 2007). If this is practiced, trees appear to be able to resume their annual cycle without requiring chill. This management has enabled the production of temperate fruits in the tropics and sub-tropics where the chilling requirement is incomplete, but it cannot be recommended at colder regions with pronounced seasonal cycles.

Molecular technique is another important approach in the modern breeding program to develop adaptable cultivars to a particular situation with special focus on chilling requirements. In respect of this, the past experience indicates that many low chill temperate fruit cultivars are developed for warmer regions and the present situation of climate change demands similar patterns of technology generation. Also, the use of rest breaking chemicals or growth regulator has been found to promote bud-break where the chilling requirement is insufficient especially in tropics and sub-tropical regions. 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), Southern United States (Dozier et al., 1990) and Italy (de Salvador and di Tommaso, 2003). However, this chemical has shown phytotoxic and to cause strong yield reductions (George et al., 1992; Siller-Cepeda et al., 1992), that it has been banned in several countries. Alternative chemicals, such as plant growth regulators containing thidiazuron (Campoy et al., 2010) have a positive effect in rest breaking and less toxicity for human health as suggested by many reports.

8. Summary and Conclusion

Given the present knowledge, and the lack of conclusive evidence for any particular theory of dormancy regulation, chilling requirements and chill models used to estimate chill accumulation, it is certainly not possible to propose a general correspondence between all these phases due to diverse environmental factors that seriously influence the processes and the endogenous mechanisms of control. It is possible that observations of empirical behavior will allow one to decide between likely proposals. That is, any promising candidate among models must at least be amenable to such tests. These situations always demand exhaustive work to reconcile environmental influences across geographical regions with respect to the changing climate. Studies indicated that major chilling losses in all warm growing regions of temperate fruits, both in the past, at present 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 at present. Cold growing regions, in contrast, may experience little change, or even increases in winter chill, as increasing numbers of days become frost-free.

Many authors also 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 temperate fruit trees. This is the case predominantly in warm growing regions, while growers in colder locations have traditionally paid little attention to winter chill. As stated in this reviews from many 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 mild winter climates than other approaches. A lot of experimentation is still needed to come to a consensus of which approach to modeling 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.

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