



Review

Declining chilling and its impact on temperate perennial crops

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ABSTRACT

This paper examines the impacts of declining winter chill on the production of temperate perennial crops in the northern hemisphere. Recent studies have linked long-term climate data to key seasonal reproductive events in perennial plants. These studies suggest that the amount of winter chill occurring in the UK has declined and is predicted to continue to do so, based on future climate change scenarios described in the UK Climate Impacts Programme. It is apparent that there is a serious lack of mechanistic understanding of the physiological, molecular and genetical basis of winter chill requirement and dormancy-related environmental factors which affect perennial crop growth and yield. This situation exists despite knowledge of the impacts of climate on perennial plant development and an ability to model its effects, for many temperate fruit crops, on yield. The implications for future reductions in winter chill require recognition as a potential limiting factor on fruit production across Europe, particularly in the south. Within this review we describe the symptoms of lack of winter chill; these include effects on bud break, flower quality and the potential to set fruit, as well as effects on vegetative growth and development. Also included is current knowledge of developmental and physiological events which link flower initiation, anthesis, dormancy, chilling and bud break. Attention is given to what is known about dormancy induction, satisfaction of specific requirements and bud break. Possible strategies are described for mitigation of reduced winter chill, providing long-term solutions to secure perennial fruit supplies in Europe. This 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 low chill.

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1. Introduction

Temperate climates are characterised by a seasonal phase where sub-optimal temperatures restrict or terminate growth. As a consequence, temperate plants have evolved mechanisms to survive low temperature stress during winter (Horvath et al., 2003). This annual rhythm has periods of active meristematic growth separated by periods of dormancy or ‘rest’ which avoids low temperature injury. Dormancy minimises low temperature injury to flowers by delaying bud break and anthesis. Perennial crops, suitable for growing in these seasonally-restricted temperate regions, have to satisfy their chilling requirements to initiate spring bud break, shoot meristematic extension growth and anthesis. Chilling requirements are species- and cultivar-specific and are genetically determined (Samish, 1954). The chilling requirements for native species can be adaptive, for example, in regions with mild winters low chilling requirements are common. Samish (1954) suggests in areas with moderate fluctuating winter temperatures, longer periods of chilling may be required, while plants in continuously cold winters show highly variable ranges of chill requirement. There is however little published support for this notion, beyond late flowering cultivars having greater chilling requirements than early flowering ones and even contrary evidence with *Malus baccata* of cold origin, but no excessive chilling requirement (Swartz and Powell, 1981). Survival post-dormancy requires subsequent environmental conditions appropriate to induce bud break. Failure to receive sufficient chilling reduces bud break, extends anthesis and creates non-uniform flowering. It may also reduce flower ‘quality’, increase flower bud abscission, protract of anthesis (pollination and fertilisation) and reduced fruit set and quality (Abbott, 1962; Jones et al., 2013).

Reproductive development in perennial crops occurs prior to and after winter dormancy and involves an extended sequence of morphological, physiological, metabolic and molecular changes. These events include floral development, dormancy itself, the satisfaction of chilling and bud break, all are linked to the process that induces vegetative meristems to develop into fruits. Most deciduous perennial crops initiate next year’s floral buds in late summer or early autumn, coinciding with final stages of that year’s fruit development (cell expansion) (Abbott, 1977). Once initiated, floral meristems enter dormancy, attaining an inhibited state where they are unable to be stimulated into renewed growth by an increase in temperature the ‘heat requirement’ (sum or forcing, see description of in Cesaraccio et al., 2004), or resource supply (carbohydrate, nutrients, etc.). Subsequently, in spring, after low temperature exposure (‘chilling’), followed by satisfaction of the heat sum, to come out of ectodormancy, bud break is induced and anthesis follows. During these protracted phases the climate is key to determining perennial crop production. Climate is the dominant factor in many temperate *Malus*, *Pyrus*, *Prunus* and *Fragaria* fruit yield models; with variation in temperature, around flowering, showing high statistical significance in explaining year-to-year

differences in yield (Beattie and Folley, 1978; Jackson and Hamer, 1980). For example, Barlow and Cumming (1975) showed, from 31 years of apple (‘Lanes Prince Albert’) yield data, 60 correlations with climate and crop yield, the highest single explanation of yield variation (36%) was “good weather in early May”. Climatic conditions around anthesis also influence yield by altering the effective pollination periods (EPPs), fertilisation and fruit set, as well vegetative meristems and their growth (Williams, 1970). These 31 years of data show little impact of chilling on yield. There may of course have been sufficient chilling during much of the analysis period ensuring little yield influence. The relationship between yield and climate during flower development, and subsequently crop growth, is complex as both influence yields. There is now more evidence that a measured decline in winter chill is apparent in the UK and in other parts of the globe (Atkinson et al., 2004; Sunley et al., 2006; Baldocchi and Simon Wong, 2008; Luedeling et al., 2009, 2011; Schwartz and Hanes, 2010; Darbyshire et al., 2011). Atkinson et al. (2004) hypothesised that some of the recent reductions in UK yields of perennials crops, recorded by growers, was due to a decline in winter chill. They suggested yields had declined due to detrimental impacts on bud break and fruit quality. To test this idea they compared a range of existing chill accumulation models to explain the differences in date of anthesis of *Ribes nigrum* and *Rubus idaeus* over a 50 year period (Sunley et al., 2006). They accessed several long-term UK geographically dispersed data sets on air temperatures and date of anthesis. Of all the chill models used to study chill accumulation only one did not show a statistically significant decline in winter chill over the last three decades. The best fit model explaining the yearly variation in spread of bud break was also used to describe differences in chill accumulation over time using climate change scenarios. This analysis showed a significant decline in winter chill and a reduction in spring frosts, as well as, geographical differences between the UK north and south (Sunley et al., 2006).

Here we are interested in climatic winter warming and its impact on the chilling requirements of perennial fruit. Warm winters are known to impact on the adaptability of deciduous fruit crops to non-temperate regions (Brown, 1958, 1960; Erez and Lavee, 1971; Anderson and Richardson, 1987; Aubert and Bertin, 1987; Darbyshire et al., 2011). In many regions where winter chilling is marginal, the growth of commercial crops of *Malus* and *Fragaria* is achieved through the use dormancy breaking chemicals, or regional transplanting strategies, respectively. These approaches are limited and may not be suitable in the tropics and subtropics (Jackson, 1984). Even in the 1940s, California’s warm winters induced problematic cropping (Brooks and Philp, 1941). Only comparatively recently has the impact of insufficient chilling been suggested as a potential economic problem elsewhere, particularly in temperate regions, for example, USA peach production (Couvillon, 1995). It is therefore surprising that earlier reviews on the impact of climate change on horticultural production, despite awareness of changes in “length of growing season” and

“less severe winters”, have usually failed to indicate that lack of winter chilling could be important (Olesen and Bindi, 2002). Luedeling et al. (2011), however, when evaluating various climate scenarios, indicated even the most conservative greenhouse gas emissions scenario would reduce winter chilling and negatively impact on the productivity of current fruit cultivars in warmer growing regions. Phenological changes, induced by warmer winters and earlier warm springs can also increase the risk of frost damage at anthesis. Such occurrences in tree crops have already been reported in the USA (Gu et al., 2008; Augspurger, 2009), while in Norway frost damage on *R. nigrum* cultivars has increased in recent years following mild winters (Sønsteby, pers. comm.). In contrast, Eccel et al. (2009) examined the risks to apple production in the Trentino area of Italy using simulated climatic projections, and found that the effect of temperature increases could not be mechanistically linked to flowering dates, and that the overall frost risk was unlikely to rise significantly in the future. While for studies carried out in Finland, the risk of frost damage, during flowering, was considered an issue requiring adaption to climate change (Kaukoranta et al., 2010).

Determining the impact of reduced winter chilling is not easily understood without knowledge of the processes which influence flower bud development prior to chilling and those which occur during release from dormancy. For example, recent emphasis has been given to the environmental cues that *Malus* buds must receive prior to entering dormancy (Cook and Jacobs, 2000). In their absence, during mild winters, increases in chilling did not reduce time to bud break, suggesting standard chilling models are inadequate (Richardson et al., 1974; Shaltout and Unrath, 1983b). Not only where chilling temperatures important but those evident during post-chilling and bud break had an interactive impact on reproductive performance. A *Prunus avium* study showed when chilling was limited (360 h at 4 °C), trees exposed to cooler post-chilling temperatures had greater fruit set (Mahmood et al., 2000). To achieve the same degree of fruit set as that at the lower post-chilling treatment, required a much longer period of chilling. *Pyrus communis* shows a similar relationship between chilling and the heat sum requirements for renewed growth and bud break (Spiegel-Roy and Alston, 1979).

Our objectives are to outline why winter chill is important biologically and how it impacts on the production of perennial fruit crops. We briefly discuss the approach and the experimental models used to conclude that, at least in the UK, winter chill has already declined, and from future likely climate scenarios, it will continue to do so. The likely impacts of a decline in winter chill on perennial fruit crops are also described. We conclude with cultural and breeding approaches which are suggested as possible ways to adapt to reductions in winter chill.

2. Impacts of reduced winter chill

Symptoms of inadequate chilling are many, and vary with species (Table 1). Generally, they appear as a delay in anthesis and vegetative bud break, apparent as extended periods of bud break and anthesis (Black, 1953; Samish, 1954; Brown, 1952; Couvillon, 1995; Jacobs et al., 1981, 2002; Cook and Jacobs, 2000). In *P. communis*, autumnal warming delayed anthesis, with the response being greater for early flowering cultivars compared to later ones (Atkinson and Taylor, 1994; Atkinson and Lucas, 1996). This implies that there are two separate effects, a delay in bud break and an increase in irregularity of date of anthesis (Brown, 1952). Extension of the anthesis period causes variation in crop development rate, fruit size, harvest date and fruit ‘quality’. Exposure to low temperatures is necessary for the initiation of pistillate flowers (i.e. female and fruit bearing) in *Carya* (Amling and Amling, 1983). Conversely, when chilling is inadequate *Prunus persica* flowers can lack

stigmas and styles. *P. avium* flowers can be smaller due to limited chilling (Mahmood et al., 2000). Developing flowers may also fail to set fruit, and when fruits do set they may be of low quality due to short pedicel length or insufficient supportive leaf area for full fruit development (Mahmood et al., 2000).

In mild winters, Weinberger (1954) described “prolonged dormancy” in North American *Prunus persica* cultivars, characterised by irregular bud break and delayed asynchronous anthesis, leading to prolonged anthesis. Buds on older wood at the centre of the tree had lower chill requirements, resulting in clustering of flowers and large sections of stem devoid of flowers. Flower development in *Malus x domestica*, cultivars subject to limited dormancy, can not only have reduced floral buds but may also show high apically dominance (Oukabli et al., 2003). Anthesis is delayed due to a failure in the development of protoxylem establishing bud to stem connectivity. Hoyle (1960) found 12–15 weeks at 2 °C satisfied the chilling requirement of dormant *R. nigrum* although there are cultivar differences (Stone, 1989; Plancher and Dördrechter, 1983). Insufficient chilling in *R. nigrum*, often results in non-synchronous bud break and flowering, and variable ripeness at harvest, which is an issue during processing (Jones et al., 2013). The problem of a lack of winter chill causing crop variability is relevant to other machine-harvested processed crops. Inadequate chilling of *Fragaria x ananassa* is known to result in a lack of plant vigour, reduced vegetative growth (Voth and Bringham, 1970) and yield (Craig and Brown, 1977). In France where the cultivation *F. x ananassa* is predominantly under plastic tunnels, their use too early in spring can result in inadequate chilling and a reduction in vegetative vigour (Robert et al., 1997). Plants with low vegetative vigour flower intensely and produce small fruit (Bringham and Galleta, 1990).

2.1. Flower bud abscission

In pome fruits, with their mixture of bud types, all or part of the flower primordial may abscise during warm winters (Brown, 1952), leaving flower bud clusters reduced in size which look like leafy spurs. Many stone fruits grown in California also abscise flower buds following warm winters (Brooks and Philp, 1941; Brown, 1958). These losses, relative to total flower number, are often small and can be beneficial because flower ‘thinning’ can improve fruit quality (mainly fruit size). Mild winters affect *P. communis* with some embryonic flowers dying, but unlike some *Prunus* spp., entire shedding of buds does not occur (Brown, 1952). Analysis of a number of *P. persica* cultivars show two distinct peaks of flower abscission, with abscission being less for cultivars with lower chilling requirements (Samish, 1954). The yields of *P. persica* from 280 (peach) and 58 (nectarines) cultivars in California were compared after the winter of 1941, when orchard temperatures were higher than the previous 12 winters (Brooks, 1942; Brooks and Philp, 1941). Ranking cultivars relative to the amount of flower bud abscission, showed at the extremes, 21 cultivars of *P. persica* with no abscission and 78 where abscission ranged from 100 to 85%. The abscission and loss of flowers with *Prunus armeniaca* (119 apricot cultivars) and *Prunus domestica* (53 plum cultivars) was more extreme with only one cultivar of each found to have no abscission, most *P. armeniaca* (62) and *P. domestica* (27) cultivars showed extensive bud abscission (Brooks, 1942). Mild-winters in California in 1950–51 provided further evidence of the negative impacts of a warm climate on fruit yields, with less than 25% of the required chill (Brown, 1952). *M. x domestica* crops also show extended anthesis when chill is low. Not all these flower bud losses can be attributed to mild winters; the decline in *P. persica* flower bud quality can occur in mid-September, suggesting factors other than winter chill can influence bud development (Brown, 1958). There is also evidence from *Ribes rubrum* that a proportion of the

Table 1

A summary of the different aspects of perennial fruit crop growth, development, and production impacted by low winter chill.

Commodity	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.ⁱ Changes in crop/product quality.

total number of floral initials abscised during dormancy was not linked to winter temperatures, but branch orientation (Palonen and Voipio, 1994).

2.2. Flower quality

Limitations in the amount of chilling can influence flower morphology. *P. avium* (cv. 'Stella') subject to low chill shows reduced flower size and pedicel lengths (Mahmood et al., 1999). The pattern shown with respect to flower size was similar to that at fruit set, with chilling promoting set to an optimum. These data also show when post-chilling temperatures were high, 25 °C compared to 19 °C, fruit set was much reduced and did not increase with further chilling (Mahmood et al., 1999). This has implications for determining climate change responses where scenarios for reduced winter chill are linked to warmer forcing temperatures prior to bud break.

2.3. Fruit set

Observations after the mild Californian winter of 1950–51 show that despite *P. armeniaca* flowers being aborted early in their development, yield was not limited by floral abscission but as a result of low fruit set (Brown, 1952). Even with flower bud abscission rates in *Prunus* as high as 70–90% there was little effect on yield providing fruit set was favourable (Brown, 1952). The annual production of a large number of flowers, relative to the final number of fruit which set and contribute to the harvestable yield, is considerable. This behaviour is apparent with many species within the Rosaceae and a number of explanations have been put forward to explain it (see Guitian, 1993). Commercial production of fruit frequently relies on reducing the number of fruit (thinning) which set to ensure the remaining fruits are of a large size and quality to maximise their storage-life. *P. avium* exposed to increasing levels of chill results in an increased number of flowers per tree and an enhancement in the remaining flowers ability to set fruit (Mahmood et al., 1999). It is suggested that 'forcing' *Fragaria*, after a short period of dormancy, not only influences vegetative growth but also floral capacity (Piringer and Scott, 1964; Kronenberg and Wassenaar, 1972). Although flower number per plant was not influenced by chilling or cold-storage temperature in the cultivar 'Elsanta', fruit

set appears to be (Tehrani et al., 1998). The interaction between vegetative vigour and fruit production suggests that fruit set is modified.

2.4. Fruit quality (size)

The variation in size of *M. x domestica* fruits when grown in regions where adequate chilling varies suggests that pre-anthesis differences in fruit cell number are important (Grebeye and Berg, 2000). Growth of the cultivar Royal Gala in South Africa, where small fruit can occur, shows that the number of cells within reproductive buds relates to winter chilling, but the influence of limited winter chilling was modified if yields per tree were reduced (Grebeye and Berg, 2000). Moderate chilling of *F. x ananassa* has considerable influence on fruit quality with respect to size and shape (Larson, *pers comm.*). Similarly *R. nigrum* crops that have not flowered synchronously can show uneven ripening and variable fruit size.

2.5. Vegetative growth and development

Chilling requirements differ with respect to bud type and position (Hauagge and Cummins, 1991). Vegetative shoots on terminal buds can open prior to lateral buds; this can induce strong apical dominance due to the prevention of lateral shoot growth. Branching in *M. x domestica*, for example, is primarily via distal buds (acrotinic) with little development of proximal buds (basitonic). Similarly, with *R. idaeus* variation in bud break along canes shows a consistent pattern and is linked to the presence of the apical bud (White et al., 1998). This inhibition occurs via correlative influences (apical dominance) on the distal shoot (paradormancy) and can be reduced by phloem girdling (Champagnat, 1983). This suggests development is controlled by auxin transport (Faust et al., 1995). Removal of distal portions of dormant shoots 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 (Shaltout and Unrath, 1983a; Steffens and Stutte, 1989). The apical dominance responses in *P. persica*, with its terminal vegetative buds having the lowest chill requirements, when subject to low chill it produces 'long shoots' devoid of lateral side shoots capable

of developing fruit bearing spurs (Scalabrelli and Couvillon, 1986). Given that buds at different positions on shoots and canes can behave in a predictably different way with respect to their dormancy breaking requirements, see the work of White et al. (1998), caution is required in interpreting forcing experiments when endodormancy and paradormancy effects may be interacting.

3. Developmental and physiological events linked with flower initiation, dormancy induction, chilling and bud break

Effects of winter chilling on dormancy in many perennial fruit crops have been understood, at least descriptively, for some time (e.g. Coville, 1920) and similarity to the processes of vernalisation and germination of seeds are recognised (Erez and Lavee, 1971). Here we are primarily interested in low temperature dormancy effects, often described as vernalisation, while this term has been used to describe other environmental factors which induce/promote flowering (see Chouard, 1960). Species and cultivars have chilling requirements that are distinct and genetically defined. Chill acquisition is cumulative and the range of temperature that contribute to this accumulation is species-specific (e.g. Eggert, 1950). Early reviews of dormancy defined 'rest' as having three distinct phases: 'early-rest', 'main' or 'middle-rest', and 'after rest' (Samish, 1954). Early-rest is the autumnal phase when dormancy induction begins; 'middle-rest' the main period of chilling accumulation; and 'after-rest' when dormancy is effectively completed. The latter phase is when growth becomes responsive to effective growing degree hours (GDH), or the forcing heat sum. These phases are in part equivalent to the types of dormancy classified by Lang (1987): ecodormancy, where growth inactivity is environmentally imposed until conditions become favourable; and endodormancy, which is caused by factors within the bud itself, and where the effects of chilling accumulation are crucial. The physiological processes involved during dormancy are not however fully understood, but it is possible to hypothesise about a number of likely mechanisms. Key factors affecting the different dormancy sub processes include temperature, light, drought and hormones such as abscisic acid and the gibberellins (Rohde et al., 2000).

3.1. Floral initiation

The processes involved in anthesis are described by Oukabli et al. (2003). Induction of flower buds involves signalling processes within floral tissues and the whole plant (see Faust, 1989; Westwood, 1993). Long-distance control of developmental/dormancy events can be induced in non-dormant tissue even across graft unions (Chandler, 1960). Floral initiation varies with crop; in *M. x domestica* it requires the production of around 20 growth nodes or 'plastochrons' (Landsberg, 1974; Abbott, 1977; Luckwill and Silva, 1979). Increases in apical meristem diameter are followed by the differentiation and development of floral organs acropetally (Diaz et al., 1981) during late summer around the time shoot extension, meristematic activity terminates (Landsberg, 1974). Abbott (1970) suggested the rate of *M. x domestica* primordia initiation influences the fate of the bud (reproductive versus vegetative), along with its 'quality' and fruit setting potential. Rapid growth to node 20 promotes flower initiation; slower production produces vegetative buds. Abbott (1977) also showed that the longer floral primordia had been initiated the more morphologically and physiologically developed they were at the onset of dormancy. Primordia age, when entering dormancy, has implications for subsequent development and performance. Variation in time of flower initiation does not however directly influence flower setting quality (Abbott, 1977). Reproductive bud

scales begin forming in early May, but remain dormant due to correlative inhibition. Cessation of vegetative growth and terminal bud formation can be delayed, but normally terminates in late summer. Other factors such as rootstocks that are dwarfing, high yields and drought stress can all induce early cessation of meristematic shoot growth and the production of 'resting' buds in *M. x domestica*. Evidence with *Prunus cerasis*, during dormancy induction, shows starch accumulation and changes in nuclear structure, while bud development continues, and cellular differentiation of flower parts slows (Felker et al., 1983). Differentiation of ovules and pollen sacs in *M. x domestica* occurs at the end of the winter (Bergh, 1985); with bud xylem maturation and a more direct connection to the subtending stem in some *Prunus* species, not occurring until around anthesis (Hanson and Breen, 1985). There are reports that nitrogen, irrigation, radiation and temperature all influence floral initiation (see review Sedgley, 1990). In *F. x ananassa*, flower initiation also takes place in autumn followed by dormancy (Gutteridge, 1958).

Flower induction is driven by environmental changes and occurs in short-day plants as day length and temperature decline (Darrow and Waldo, 1934; Darrow, 1936; Piringer and Scott, 1964; Battey et al., 1998). Despite *F. x ananassa* being a facultative short-day plant, its photoperiodic response is modified by temperature (Ito and Saito, 1962; Nishizawa and Hori, 1993a; Le Miere et al., 1996). It appears that flower induction is primarily induced by photoperiodic reduction, rather than low night temperatures (Arney, 1956). However, Brown and Wareing (1965) showed with *Fragaria vesca* (wild strawberry) temperature was more important than photoperiod. Increases in autumn temperatures in Scotland enhance flower number (Mason, 1967) but once dormancy is complete initiation of flowers and leaves declines (Arney, 1956). *F. x ananassa* 'everbearers' show flower induction irrespective of daylength, or temperature (Downs and Piringer, 1955; Smeets, 1980). Williams (1959a) described the formation of floral initials in *R. idaeus* with differentiation occurring from autumn to spring. Changes in apical meristems from vegetative to reproductive are stimulated by shortening day length and falling temperatures, with the initiation and development of dormancy co-occurring but independently (Williams, 1959b). Sønsteby and Heide (2008) show for *R. idaeus* a critical photoperiod linked to air temperature, for growth cessation and floral initiation. While warm autumns promote flowering, up to an optimum, in *R. nigrum* (Sonsteby and Heide, 2010).

3.2. Genetic control of anthesis

Flowering studies with *Arabidopsis* have identified over 80 genes which can be placed in different pathways according to their genetic and physiological function (Putterill, 2001). These groupings effectively separate genes involved in daylength perception and transduction, genes controlling perception and response to cold temperatures (vernalisation pathway), genes responding to internal factors such as plant hormones, and finally genes involved in light quality perception and transduction. Srikanth and Schmid (2011) added a further pathway, based on plant age. These pathways are all involved with the floral meristem identity genes needed for development (Koorneef et al., 1998).

Genetic analysis using *Arabidopsis* has shown that two genes, *FLOWERING LOCUS C* and *FRIGIDA*, are mainly responsible for the vernalisation requirement in flowering mutants (Johanson et al., 2000; Michaels and Amasino, 1999, 2001). Additionally, Rédei (1962), describing mutants of *Arabidopsis* insensitive to inductive day lengths, identified the *CONSTANS (CO)* gene, which acts as a central regulator of other flowering genes, including the floral integrator *FLOWERING LOCUS T (FT)* (Yoo et al., 2005). Horvath (2009) suggested that some FT orthologues have a role in the induction and maintenance of endodormancy.

The relevance of *Arabidopsis* work to the elucidation of the mechanisms in fruit species remains unclear, despite the existence of some homologues found in *F. vesca*. This model does however agree with what we know about winter chilling, as a cumulative phenomenon over time and, as a mechanism, can prevent floral transition from occurring too early in otherwise favourable conditions, e.g. an unusually warm spring/winter period. Transformation experiments with *FT* from *Populus* sp. and orthologues e.g. BpMADS4 from *Betula* sp., produced earlier flowering in plum (Srinivasan et al., 2012) and apple (Flachowsky et al., 2007), and may be of interest in the development of germplasm adapted to different climatic regions in the future.

Plant hormones, including auxins, gibberellic acids (GAs) and cytokinins, are also associated with controlling time of anthesis (Bernier, 1988). Molecular studies involving plant hormones are limited to what is known about GA on *Arabidopsis* (e.g. Blazquez et al., 2002). GA signalling or GA synthesis mutants show delayed anthesis. GAs are also implicated in defoliation and dormancy with autumn applications of GA delaying autumnal changes in leaf colour, leaf abscission, and subsequent emergence from dormancy and bud break (e.g. Brian et al., 1959; Walser et al., 1981). It is highly likely that the systems present *Arabidopsis* are similar in perennial crops, and Måge (1976) reported that in raspberry application of gibberellins influenced both the timing of the onset of bud dormancy and the depth of dormancy. The levels of bud break were also reduced by increasing concentrations of GA. Olsen et al. (1997) overexpressed the *PhyA* gene, the major photoreceptor for short days, in transgenic *Populus* trees, and found that these trees had a significantly altered response to daylength for growth cessation. These changes were also associated with down-regulation of GA levels, suggesting that reduction in GA levels is part of the growth cessation, and therefore dormancy, processes.

3.3. Dormancy induction

Flower initiation and development in late summer and autumn is followed winter dormancy. Dormancy is defined as a state where visible growth is not apparent (see reviews by Samish, 1954; Saure, 1985; also Lang, 1987), this lack of growth does not mean that tissue differentiation is not occurring. During dormancy cellular differentiation occurs along with increases in bud weight (Chandler and Tufts, 1934; Brown and Kotob, 1957). Primordial development in *M. x domestica* continues throughout the northern hemisphere winter, with growth greatest during February to March (Buban and Faust, 1995). Growth curves of *P. armeniaca* flowers within buds show three phases of growth, the last being very rapid and associated with bud break (Brown, 1960). There is also synthesis of RNA and protein during dormancy in *P. communis* (Zimmerman and Faust, 1969), *P. persica* (Bagni et al., 1977) and *M. x domestica* (Li et al., 1989) with the amount of protein maximising when close to reaching the chill requirement (Arnold and Young, 1990). Differences in dormancy state and the progression of it is regulatory factors have been reviewed by Horvath et al. (2003). Paradormancy occurs when factors outside the bud but within the plant affect growth and determine activity (Lang, 1987). This type of dormancy is synonymous with apical dominance and correlative inhibition, as occurs with lateral buds; both are overcome by physical (terminal bud removal) and chemical (growth regulators) treatments (Hillman, 1984). Winter-dormancy (endodormancy or 'rest') is where bud growth is inhibited within the bud and occurs after autumn leaf abscission. Removing bud scales or leaves does not remove endodormancy, and growth cannot proceed even with favourable environmental conditions, until endodormancy is broken by sufficient chilling. Imposed dormancy occurs when growth is prevented directly by external environmental factors and is reversible (ecodormancy). The latter occurs mainly in late winter

when meristems and buds are able to grow in response to increasing temperatures as evident during 'forcing' (see Cesaraccio et al., 2004). Ecodormancy can be induced in *F. x ananassa* by short days and low temperatures (Darrow and Waldo, 1934; Darrow, 1936; Gutteridge, 1985).

The stage at which a bud enters endodormancy is determined by the prevailing climatic conditions, and until dormancy is broken the bud is unable to grow, even under favourable conditions (Jonkers, 1979). Dormancy begins as growth ceases, which itself is triggered by a range of environmental cues, such as, declining day length and temperature. Signalling of the short day cue in *Populus* sp. is regulated by the *FT* and *CONSTANS* genes (Böhlenius et al., 2006), which also controls flowering. Common mechanisms regulating flowering and dormancy are postulated by several authors, including Horvath (2009) and Rohde and Bhalerao (2007). Some Rosaceous species such as *M. x domestica* and *P. communis* are however insensitive to photoperiod in the context of growth cessation and dormancy induction (Nitsch, 1957), and temperatures below 12 °C can induce both processes regardless of photoperiod (Heide and Prestrud, 2005). Similarly, a lack of photoperiodic control is known for other Rosaceae (e.g. *Sorbus* Heide, 2011); although work with *P. persica* found the opposite, where growth cessation and dormancy were induced primarily by photoperiod but enhanced by low temperatures (Heide, 2008). From this it was concluded where there was no effective photoperiodic regulation of dormancy, there was a greater likelihood of vulnerability to global warming, since an alternative low temperature-based regulation of anthesis may prove less reliable.

Dormancy induction appears to involve the conversion of a 'product' from the unchilled to chilled state by exposure to low temperatures. The breakdown of the product permits the effects of corresponding warm forcing temperatures to modulate or negate chilling. Product accumulation to a certain level results in dormancy completion (Erez and Couvillon, 1987; Erez, 1995; Rowland and Arora, 1997). Changes in protein concentrations of *P. persica* flower buds and those of *Populus tremula*, during chilling have been linked to the requirements to satisfy chill (Lang and Tao, 1990, 1991; Renault et al., 2003). The decline of a 61 kD protein, as chilling requirements are met, is difficult to mechanistically separate from protein changes due to concomitant processes, such as the loss of bud cold hardness. Lang (1994) also observed a decline in a similar protein in *P. persica* which was related to changes in dormancy level induced by dormancy-breaking compounds like GA and hydrogen cyanamide. These proteins have highly conserved regions which are lysine-rich, as with dehydrin proteins which link to cold acclimation rather than degree of dormancy (Rowland and Arora, 1997). Induction of dormancy in *F. x ananassa* is related to short days and declining temperatures, which induces a decline in leaf size and petiole length (Durner and Poling, 1987). The situation is different with *M. x domestica* where starch concentration declines during dormancy (Whitworth and Young, 1992) and sucrose increases with chilling until around 50% bud break. These changes, as with protein, are a likely reflection of carbohydrate utilisation, particularly with respect to metabolism and respiratory consumption during both chill accumulation and protection against low temperature injury (Raese et al., 1978; Hansen and Grauslund, 1973). There is no evidence to mechanistically link changes in carbohydrate status with tissue dormancy; they are much more likely descriptors of dormancy, effects and release, rather than its cause. As is the case with chilling and bud break in *Fraxinus excelsior* (Atkinson and Denne, 1988). Variability in the chilling requirements of *M. x domestica* rootstocks shows that scion bud break chilling responses are influenced by the roots (Couvillon et al., 1984; Young and Werner, 1985). This may occur via a phloem-mobile element (or chemical 'signal'), originating in the roots. Root cooling of *F. x ananassa* is a prerequisite for effective bud break (Nishizawa and Hori, 1993b).

3.4. Dormancy fulfilment

Once floral buds are initiated anthesis does not occur until sufficient chilling is received. Time to anthesis is therefore dependent on temperature, which can be quantified from the average daily temperature and the number of days at a species-specific temperature (Landsberg, 1974). Empirical statistical models estimate, using meteorological data and the amount of chill required by perennials (Cesaraccio et al., 2004). Attempts to quantify winter chill 'hours of chilling' below a threshold of 7.2 °C, based of observation made with a cultivar ranking system of *P. persica* and *P. armeniaca* cultivars grown in the USA (Ruiz et al., 2007). Subsequently, optimal chilling temperatures have been shown to vary markedly with species. Hoyle (1960) found 12–15 weeks at 2 °C satisfied the chilling requirement of dormant *R. nigrum*, although cultivar differences existed across Europe (Stone, 1989; Plancher and Dördrechter, 1983). Richardson et al. (1974) model ('Utah' model) proposed a more sophisticated variable temperature weighting scheme, while further refinements were based on exponential "cold action" functions summed over time (Bidabé, 1967) and empirically selected weighting for specific crop species (Lantin, 1977). Successful applications of this approach include those of Jackson and Hamer (1980) who developed a model that accounted for c. 80% of national annual yield variation in 'Cox's' apples (*M. x domestica*), Goldwin (1982) also for *M. x domestica*, Browning and Miller (1992) for pears (*P. communis*), Young and Jones (2002) for *R. idaeus* and Jones et al. (2013) for *R. nigrum*.

Whitworth and Young (1992) showed changes in carbohydrate composition during dormancy where evident with a decline in the starch: total carbohydrate ratio following the onset of winter. This is probably a preparatory step in low temperature response with the accumulation of sucrose and sorbitol for low temperature tolerance. *M. x domestica* rootstocks show marked changes in hexose sugars and sucrose which are important in early spring growth. Some variation in the pattern of carbohydrate status, once chilling is completed, may depend on the amount of chill received. Similarly in *R. idaeus*, variation in root and stem (cane) carbohydrate composition can be linked to dormancy onset (Jennings and Carmichael, 1975). Changes in respiration rate the Q_{10} and the 'energy of activation' have been used to track bud development through endo- to ectodormancy and bud break (Young et al., 1995). The respiratory quotient (RQ) during early dormancy for *M. x domestica* indicates consumption of lipids as the primary substrate, while an RQ increase after 990 chilling units, suggests a switch to a carbohydrate substrate (Young et al., 1995). *M. x domestica* cultivars with known differences in chilling requirements show a decline in bud primordia abscisic acid (ABA) concentration in spring compared to mid-winter (Swartz and Powell, 1981). The rate of decline in ABA was more rapid with low chill compared to high chill cultivars, it is however unclear if ABA acts as a causal agent, or if changes in ABA are a response to chill accumulation. ABA concentration declines in *P. cerasis* buds under both cold and warm conditions (Mielke and Dennis, 1978), while bud GAs increase during chilling (Frankland and Wareing, 1962; Eagles and Wareing, 1964).

Recent developments in transcriptome analysis have facilitated the identification of changes in expression and activity of a number of dormancy-specific RNAs, proteins and enzymes. Currently dormancy proteins are characterised into two groups, either 'bark storage proteins' or dehydrins (Rowland and Arora, 1997). The concentration of bark storage proteins increases in the autumn (by 200% in *M. x domestica*), and declines during spring growth (Taylor and May, 1967). In poplar (*Populus deltoids*), the gene (*bsp*) associated with bark storage protein is expressed during shortening of the photoperiod, high nitrogen tissue concentrations and low temperature (Coleman et al., 1992; van Cleve and Apel, 1993). The latter may have interactive/modulative effects on the expression

of *bsp*. The decline or breakdown of bark storage proteins is likely controlled by plant hormones such as GA, cytokinins and auxin (Rowland and Arora, 1997). However, neither bark storage proteins, nor dehydrins have been mechanistically linked with the regulation of endodormancy, although Balk et al. (2004) showed dehydrins to be up regulated in dormant forest trees.

Several quantitative trait loci (QTL) have been identified for ecotypes of poplar with different dormancy induction thresholds and linked to chromosome regions that encode for a phytochrome gene (Frewen et al., 2000). Senescence has also been linked to the induction of endodormancy, and with ethylene and ABA having inducing roles, suggesting a commonality of action or hormonal linkage (see Horvath et al., 2003). Dormancy breaking results in the up-regulation of several genes early in cell cycle growth phase, including cyclins and histones (Freeman et al., 2003). The transition to 'S phase' in the cycle, in which DNA replication takes place, is modulated by several plant hormones, i.e. GAs, cytokinins and brassinosteroids (see Horvath et al., 2003). It appears that growth inhibitors accumulate inducing bud dormancy (Eagles and Wareing, 1963), while others report the depletion of a growth-promoting substance, such as a cytokinin (Abbott, 1970). *M. x domestica* dormancy can be broken by cytokinin applications (Williams and Stahley, 1968). In *P. persica*, IAA bud concentration declines during chilling, while high ABA declines at bud break, at which time cytokinin (zeatin riboside) increases (Mielke and Dennis, 1975; Powell, 1986; Ramina et al., 1995). Despite these correlations, the direct role of ABA in dormancy regulation is unclear (Powell, 1987).

Different temperature combinations during dormancy, and the duration of the chilling period, can satisfy the plant's chilling requirements (Jacobs et al., 2002). The optimum combination of temperature and duration, to achieve adequate chilling, is however species specific, with optimum temperatures ranging from below zero for many *Ribes* (Bidabé, 1967; Lantin, 1973; Jones et al., 2013), to between 4 and 8 °C for *P. persica* (Richardson et al., 1974). For *F. vesca* a varied optimum chilling requirement exists between –1 and 10 °C depending on cultivar (Gutteridge, 1985), while for *F. x ananassa* increased chilling leads to stimulation of vegetative growth, stolon production and floral capability (Gutteridge, 1958; Smeets, 1982; Battey et al., 1998). It is however debatable if *Fragaria* actually has true dormancy as seen with most members of the Rosaceae, but it does show an optimum requirement after which flower initiation does not occur (Arney, 1956). While short-day cultivars, adapted to cooler winters, will grow in more tropical regions, but require chilling to achieve full production. Large variation in chilling requirement exist for *F. x ananassa* adapted to different climatic regions, e.g. 'Tioga' requires between 2 and 4 weeks, while 'Glasa', 'Elsanta', 'Gorella' and 'Sequoia' need 5–8 weeks, with 'Redgaunlet' needing 8 weeks (Darrow, 1955; Kronenberg and Wassenaar, 1972). The way chilling is achieved may also influence its effectiveness; work with 'Elsanta', suggests field chilling was more effective than cold storage (Tehraniifar et al., 1998). The latter, presumably, was carried out in the dark.

Within *R. nigrum* substantial differences in genotype chilling requirement are documented; most cultivars require up to 1600 h below 7.2 °C, although some of northern origin require over 2000 h (Brennan, 2008). While in New Zealand cultivars have been bred adapted to a low-chill environment, with requirements of 1300 h or less (Snelling and Langford, 2002). Accumulation of chilling may be reversed by warm breaks in some cases (Jones et al., 2013; Rose and Cameron, 2009), while there is also evidence that excessive chilling inhibits the satisfaction of dormancy in low chill requiring cultivars (Jones et al., 2013). Genetic differences in chill with *M. x domestica* are apparent with late flowering cultivars having a greater requirement than early flowering cultivars (Swartz and Powell, 1981). Genes linked to low chilling requirement are known

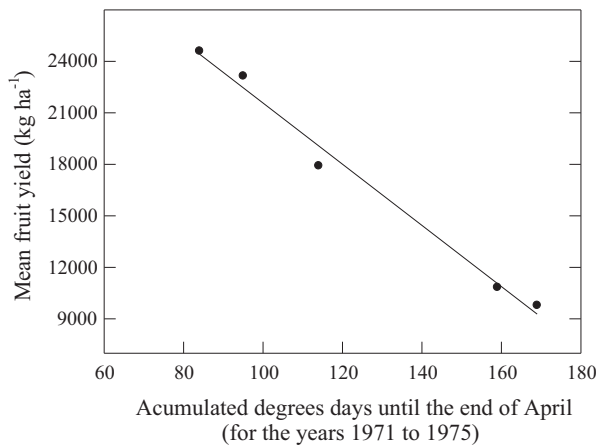


Fig. 1. The relationship between mean yields of 'Cox's Orange Pippin' from selected orchards in Kent and Sussex and the accumulated degree-days over 5 °C for the period February to April for each year.

Source: Data drawn from Beattie and Folley (1977).

for several cultivars of *R. idaeus* (Rodriguez and Avitia, 1989). Wild populations of *R. idaeus*, *R. occidentalis* and *R. strigosus* are a source of new genes linked to low chill requirement (Daubeny, 1996). While other *Rubus* species possess genes for low winter chilling, including *R. trivialis*, *R. cuneifolius*, *R. frondosus* and *R. rubrisetus* (Sherman and Sharpe, 1971; Jennings, 1988). The role of the *VIN3* gene has been identified in the measurement of cold exposure; its expression is not, however, induced during short periods of cold, which cause other temperature acclimation responses (Sung and Amasino, 2004). Studies involving gene silencing suggest that *VIN3* works by modification of histones within *FLC* chromatin (Bastow et al., 2004). The repression of *FLC* does not occur until after the induction of *VIN3* with the level of *VIN3* correlating with cold duration and *FLC* repression.

Chilling requirements also vary with bud type and rootstock (Couvillon and Werner, 1985). Vegetative terminal buds of *P. persica* and *M. x domestica* have low chill requirements, while lateral bud requirements are higher, with floral buds generally in-between (Scalabrelli and Couvillon, 1986; Faust et al., 1995). Autumn leaf retention in *M. x domestica*, due to a conducive climate, increases the chill requirement (Chandler, 1950, 1960). Milder autumns and winters are therefore potentially important if effective chilling is delayed (Walser et al., 1981). Leaf abscission can be correlated with the duration and intensity of rest in *P. persica* terminal vegetative buds (Walser et al., 1981). Orchard management practices, which influence leaf abscission, can therefore delay anthesis. Application of autumn foliar nitrogen slows leaf abscission and anthesis in *P. persica* (Reeder and Bowen, 1981) as does treatment with GA (Walser et al., 1981).

Leaf-derived GA is a likely candidate for delaying bud break and anthesis, as its application temporally delays leaf senescence. Removal of a source of such a signal molecule, through premature leaf removal, induces early bud break (Walser et al., 1981; Atkinson, unpublished). There are also interactions between chill requirements and the subsequent heating (forcing) to achieve bud break. Partially chilled *M. x domestica* requires a greater heat sum, to achieve anthesis, than fully chilled trees (Swartz and Powell, 1981). In years where winter temperatures were above average apple yields can be reduced. Beattie and Folley's (1977) analysis of UK 'Cox's Orange Pippin' yields from 1971 to 1975 showed a close correlation between fruit yield and temperature accumulation from February to April (Fig. 1). They also showed a similar response using *M. x domestica* data from northern Europe. This correlative approach using UK *P. communis* yields showed a negative effect of

warm air temperatures during February on fruit yield (Browning and Miller, 1992). There was also a large negative effect of November temperatures (0–10 °C) on yield, which was not related to increased bud dormancy. These results suggests, prior to achieving full dormancy, chilling (in November) may adversely influence yields and this has been confirmed experimentally with warm autumn temperatures delaying anthesis (Atkinson and Taylor, 1994; Atkinson and Lucas, 1996). Failure to acquire sufficient chilling has been an issue with several *Prunus* species when grown in semi-temperate locations, such as southern California, and more recently during the expansion of perennial fruit cultivation into sub-tropical and tropical regions (Brown, 1958; Ruck, 1975; Cook and Jacobs, 1999). Advances have now been made in breeding cultivars with low-chill and the development of chemical and orchard management practices to induce bud break (Sedgley, 1990). Under tropical conditions, low-chill *P. persica* crops biannually if defoliated after the first crop (Sherman and Lyrene, 1984) as is the case with *M. x domestica* where a second crop is induced (Janick, 1974). Seasonal timing is also important, in that early chilling is less effective, compared to chilling in later winter (Thompson et al., 1975). This may explain why Beattie and Folley's (1977) correlative analysis of *M. x domestica* yields and climate showed a negative influence of February to April cumulated temperatures on yield. Variation in effective chilling, for a range of crops, can also change if chilling is continuous. When chilling is interrupted by warmer periods, even over a short-term diurnal change, chill accumulation can be nullified and bud break slowed (Erez and Lavee, 1971). This has important implications if winter weather patterns become more erratic with warm autumn and spring extreme events.

3.5. Dormancy release

Timing of bud break, in perennials, is highly heritable and often ecotypically adapted (see Cannell, 1989). Bud break follows fulfilment of the chilling requirements and is normally initiated during ecodormancy as the temperature increases forcing. Low temperatures during ecodormancy keep buds dormant. Most deciduous species have a 'heat sum' requirement, which has to be met before bud break (Ashcroft et al., 1977; Eisensmith et al., 1980; Couvillon and Erez, 1985). The heat sum can be combined with the chilling requirement to derive 'chilling and forcing' models which predict date of bud burst in relation to climate (Cesaraccio et al., 2004, 2006). 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 (Campbell and Sugand, 1979; Sparks, 1993; Spiegel-Roy and Alston, 1979; Swartz and Powell, 1981; Couvillon and Erez, 1985). In *M. x domestica*, differences in the timing of anthesis of cultivars described as early or late blooming is due to different heat sum requirements, with late blooming cultivars having the higher heat accumulation requirements (Swartz and Powell, 1981). *P. communis* artificially warmed in the autumn, shows delayed bud break and anthesis (Atkinson and Taylor, 1994; Atkinson and Lucas, 1996). In *P. avium*, dormancy breaking is accompanied by increases in bud nucleic acids, proteins and polyamines (Wang et al., 1985; Young et al., 1995). Resumption of growth is associated with an increase in maintenance respiration rate, fatty acid saturation and a decline in membrane sterol content (Young et al., 1995; Wang and Faust, 1994a,b). Dormant to non-dormant buds show a change in respiratory metabolism from reducing power (pentose-phosphate cycle) to energy production for growth (glycolytic pathway and the TCA cycle). This change occurs in early spring and reverts back in autumn (Sagisaka, 1972, 1974).

There are differences in the timing and efficiency of bud break for buds from different shoot positions (Chandler, 1960; Jacobs et al., 1981) and this is linked to their different chill requirements

(see above). Poor bud break in *R. idaeus* can be found with basal buds, whereas apical buds appear to have a lower chill requirement (Fear and Meyer, 1993; White et al., 1998, 1999). High chilling requirements of many cultivars can be correlated with their strong apical dominance (Faust et al., 1995). These positional effects are lost once buds are excised (Borkowska and Powell, 1979). Endogenous cytokinins increase in terminal buds in spring prior to and during bud break (Cutting et al., 1991; Young, 1989; Cook and Bellstedt, 2001). As with chilling, temperatures models have been developed to use growing-degree-hours (GDH) as a measure of time to induce bud break (Richardson et al., 1974). These models use hourly temperatures estimated from daily maximum and minimum temperatures (Landsberg, 1974). Warmer winters will likely impact not only on the rate of chilling, but also on the shape of the growth model response curve, with respect to the absolute date of anthesis (Landsberg, 1974). Analyses of *M. x domestica* yields ('Bramley's Seedling' from 1936 to 1971 and 'Cox's Orange Pippin' from 1949 to 1975), showed that 75% of the variation in date of anthesis was explained by differences in day-degree accumulation from February to April (Pearce and Preston, 1954; Jackson, 1975; Jackson and Hamer, 1980). However anthesis in *M. x domestica* may be more dependent upon bud growth temperatures and heat sum requirement, than the cultivars chilling requirement (Gianfagna and Mehlenbacher, 1985). Differences in cumulative temperatures for *M. x domestica* 'Delicious' between February and April above a day-degree value of 371 °C showed earlier anthesis, and a smaller variation in flowering date, compared to values at or below 149 °C (Sisler and Overholser, 1943). The base temperature requirements for heat accumulation vary with species, ranging from 2.5 °C for *P. persica* to 4.5 °C for *P. communis* (Spiegel-Roy and Alston, 1979) and *P. dulcis* (Rattigan and Hill, 1986). Heat sum requirements also vary considerably with species, from 680 h in *Vaccinium vitis-idaea* (lingonberry), to 3420 for some *P. communis* and 8900 h for *P. dulcis*. Studies of *M. x domestica* bud phenology have identified major and population-specific genomic regions which influence bud break and have a strong interaction with chilling requirement (Celton et al., 2011). In other woody species, several genes including those coding for calmodulin-binding protein, beta tubulin and acetyl CoA carboxylase were found to co-localise with bud break QTLs in *R. nigrum* (Hedley et al., 2010). Genes involved with dormancy break in *R. idaeus* have also been identified by Mazzitelli et al. (2007), and certain categories of genes appear to be common to several woody species. Flowering dates, over the last 100 years, are available for a wide range of species and cultivars (Hatton and Grubb, 1925; Beakbane et al., 1935; MAFF, 1973; Atkinson, unpublished). Combined with meteorological data recommendations about geographical cropping strategies can be proposed (Hogg, 1967). Much of the geographical suitability of growing regions is based on temperature derived determination of the length of growing season. However, cropping patterns change and will likely continue to do so as a result of climate change. There is already substantial evidence that climate change has induced longer growing seasons in Europe (Menzel and Fabian, 1999; Penuelas et al., 2002; Sunley et al., 2006). Studies show that bud break in northern Europe has advanced by 6 days, while autumn leaf abscission has been delayed by around 5 days.

4. Adapting to climate change

4.1. Genotypic variation in chilling-requirements and opportunities for breeding

4.1.1. *Rubus*

Only recently have breeding strategies been altered for *R. idaeus* due to problems with winter chill in Europe. Adaptability of new

cultivars to a range of climatic conditions is now an important consideration in the development of new cultivars (Daubeny, 1996). For new cultivars to be suitable to the low winter temperatures, now found across much of the USA and Europe, requires them to rapidly acclimate during autumn and late bud break (Brierly and Landon, 1946; Jennings, 1988). In regions with low winter chilling, e.g. Australia and New Zealand, poor bud break and the consequential reduction in yield due to insufficient chilling (Jennings et al., 1986; Hall and Brewer, 1989), needs to be considered along with adaptation to higher summer temperatures (Jennings, 1980). Many existing breeding lines have a potential low chill requirement derived from the inclusion of several Asiatic species, i.e. *Rubus biflorus*, *Rubus kuntzeanus* and *Rubus parvifolius*, in their background (Jennings et al., 1991). Early-fruiting cultivars are considered to have lower chilling requirements than later fruiting cultivars (Jennings et al., 1986), with phenotypic variation in response to differences in chilling (Daubeny, 1996). Crossing of *R. idaeus* by Fear and Meyer (1993) produced low chill cultivars using parent material with robust bud break characteristics under low chill. While, in Mexico, two cultivars of *R. idaeus* 'Anita' and 'Gina' required as little as 500 units of chilling or less for adequate bud break (Rodriguez and Avitia, 1989).

4.1.2. *Ribes*

Within UK-grown *Ribes* cultivars there is variation in chilling requirements (Stone, 1989; Atwood, 2003), as there is in Europe (Plancher and Dördrechter, 1983). One of the main limitations to commercial production has been spring frost damage and this has led to the introduction of frost-tolerant late-flowering cultivars which has improved European cropping consistency. It may not however be entirely appropriate to select new cultivars based on their chilling requirements and prevailing climatic conditions (Plancher, 1982). Low chilling requiring germplasm may increase the risk of frost damage at anthesis (Lantin, 1973; Brennan, 1996, 1991; Brennan et al., 2012). Cultivars, such as 'Ben Hope', have proved more adaptable in terms of chilling requirement in the UK and are also of use for growing in the low-chill environment of New Zealand. HortResearch has released several low chill cultivars ('McWhite', 'Torlesse', 'Murchison' and 'Owen') with good commercial fruiting characteristics (Snelling and Langford, 2002). The genetic base available to breeders includes older cultivars with a low chilling requirement, such as 'Baldwin', 'Blackdown' and 'Cotswold Cross', as well as some Russian types including 'Altayskaya Desertnaja' and 'Zoja' (Lantin, 1977; Plancher and Dördrechter, 1983).

4.1.3. Other crops

There has been limited effort to select perennial tree fruit cultivars solely on the basis of their chill-requirement, with few exceptions (Oppenheimer and Slor, 1968; Spiegel-Roy and Alston, 1979); the situation is now changing (de Souza et al., 2000; Labuschagne et al., 2002; Lyrene, 2005). Nevertheless it is clear that chilling requirement is a genetically determined heritable trait; as is apparent from our ability to manipulate it using traditional breeding methods (Hancock et al., 1995). There is wide variation between and within species with respect to their chilling requirements, for example, species of *M. baccata* originates from a cold climate despite not having an excessive chill requirement. Evidence from breeding a *P. armeniaca* 'sport' shows it possesses a dominant mutation for requiring low chill (Lammerts, 1941). Early work suggested that chilling requirements depended on multiple genes some of which were intermediate in character (Lesley, 1944). More recent studies with the low chill *Malus* cultivar ('Anna') show at least one major dominant gene, along with minor genes modulate chilling requirements (Hauagge and Cummins, 1991a). For tree

fruits, management approaches have generally been emphasised in adaptation of crops to low-chill environments.

5. Opportunities for change in management

Successful temperate fruit industries flourish in parts of the world where traditionally these regions would have been considered as only suitable for semi-tropical or tropical crops due to lack of winter chilling. To overcome a lack of winter chill two main approaches have been used. In regions where temperatures are high enough for yearlong growth the key has been to avoid dormancy onset. In areas where the cool period is insufficient to meet chill requirements, physical management or chemical methods are used to break dormancy. There are limitations in the use of dormancy-breaking chemicals; most frequently they do not fully substitute for the chilling requirement and may only work effectively during specific phases of dormancy (Saure, 1985; Erez, 1987). There are also issues with the phytotoxicity of these chemicals.

5.1. Plant and environment management

Chilling requirements can be overcome, in warmer climatic conditions, by evaporative cooling generated from overhead irrigation sprinklers, which reduces bud temperature (Erez, 1995). This increases bud break and enhances uniformity of leafing (Erez and Couvillon, 1983). Evaporative cooling is also used in combination with other physical methods, such as orchard/tree management practices which reduce bud chill requirement. These methods include reducing tree vigour by orientating branches to a horizontal angle, preventing vegetative growth late in the season, and delaying dormant season pruning. Tree vigour associated with apically dominant upright branches, induces deeper dormancy (Erez, 1995). Limited winter chill in warm lowland regions, such as in California, has been overcome by moving material (e.g. *Fragaria* and *Rubus* plants) to high elevations (>1000 m) to chill during dormancy.

5.2. Dormancy breaking chemicals

Chemical breaking of dormancy depends much on the cultivar (see review by Subhadrabandhu, 1995). The initial use of simple plant and animal oils has been replaced with mineral oils. These act by coating tissues and inducing oxygen starvation with the products of anaerobic respiration breaking dormancy (Samish, 1945). Modification of these mineral oils with the addition of phenolic substances increases their efficacy when chilling is low. Other chemicals such as oil-DNOC act as respiration uncouplers, where electron transport proceeds unchecked in the absence of ATP synthesis producing heat. This can induce anaerobic conditions and the production of ethanol in buds (Erez, 1995). The calcium salt of cyanamide can break dormancy in *Malus*, *Pyrus*, *Prunus* and *Rubus* with high chill requirements (Erez, 1987; see Erez, 1995; Snir and Erez, 1988; Snir, 1986; Linsley-Noakes, 1989; Rantanen and Palonen, 2010). Successful use of cyanamides relies on appropriate chemical application, which is determined by the state of bud dormancy and the amount of chilling received. There are however huge disadvantages in that these chemicals are toxic to mammals and can show phytotoxicity. Thiourea is a very effective dormancy breaker in combination with KNO_3 and oil-DNOC, but is toxic to humans (Erez, 1987). The effective use of S-containing compounds, such as allyl mercaptan and methyl disulfide in inducing bud break is linked with the ascorbate-glutathione cycle and free radical reduction (Wang and Faust, 1994a,b). It is not however clear if these changes actually cause bud break. Plant growth regulators like gibberellic acid (GA) and cytokinins can also break dormancy, but only at high endogenous concentrations (Stembridge and LaRue, 1969;

Erez, 1987; Wang et al., 1986; Lloyd and Firth, 1993). Gibberellic acid reduces radial shoot growth; with responses to GA_3 vary depending on time of application and extent of chilling (Stembridge and LaRue, 1969; Couvillon and Hendershott, 1974; Måge, 1986). The use of adjuvants to enhance cuticular penetration reduces the concentration of active ingredient required for dormancy breaking (Erez, 1995). Chemical defoliants, such as maleic hydrazide are also used to stimulate and synchronise anthesis in fruit crops in tropical regions.

5.3. Crop management

Use of chemical control methods are unlikely to be widely acceptable for many reasons, not least, the environmental damage they may cause. Crop management practices such as excessive irrigation and/or fertiliser application along with climatically extended warm autumns can prolong growth, and in consequence increase the required chilling hours, delaying anthesis (see Walser et al., 1981). Soil drying and restrictive use of fertilisers may offer ways to regulate bud break. There are also reports for soft fruit (e.g. Spiers and Draper, 1974) and perennial tree fruit (Hill and Campbell, 1949; Jones, 1987) that premature leaf removal, either artificially or induced by drought, can reduce dormancy, synchronise anthesis, and stimulate bud break. Pruning has the potential to manipulate anthesis; experiments with *R. idaeus* show increases in bud break when exposed to limiting winter chill (White et al., 1998, 1999). This may be due to pruning reducing apical dominance. Manipulation of the dormancy cycle of *R. idaeus* via 'long-cane' production, outside main fruiting season, can be achieved by cane cold storage (Brennan et al., 1999; Carew et al., 2000; Oliveira et al., 2002). Treating *M. x domestica* shoots with hot water, at an optimum temperature, will induce bud break (Wang and Faust, 1994a,b). Similarly, 'dormancy stage dependent' studies with *Populus nigra* show elevating bud temperature, on isolated shoots, increases endodormancy release (Wisniewski et al., 1997). It is also suggested as a means to overcome uneven bud break in *R. idaeus* in warm winter climates and when grown under a protected cropping systems (Rantanen and Palonen, 2010). It is challenging however to see how heating approaches could be achieved practically, or economically. As with the use of chemicals it is not entirely clear how heating breaks dormancy. Changes occur in heat shock proteins (HSP), such as ubiquitin, and acquiring thermotolerance are apparent combined with mediation of protein breakdown by ubiquitin (Wisniewski et al., 1997). *R. idaeus* studies link bud dormancy changes to candidate genes encoding for HSP production and parts of the ascorbate-glutathione detoxification cycle (Mazzitelli et al., 2007). The capacity of microarray technology used by these authors provides an opportunity for looking at mechanisms and understanding the interactive behaviour, in real time, of tissues during and on release from dormancy.

6. Conclusions

A number of studies demonstrate that there is good evidence of climate warming and winters that have become warmer reducing winter chill accumulation. The impacts on perennial crops of insufficient winter chilling, to optimise reproductive development and crop yield, are described. Evidence is presented that insufficiency of chill is already happening in several global locations not just the UK. The complex interactive nature of the processes involved in acquiring and release from winter dormancy are also presented. Developing our understanding of these processes is vital and critically important if production systems and approaches to the intensification of agriculture are going to deliver more food in a warming world. Opportunities are discussed by which adaptation to declining winter temperatures could be undertaken, but

urgency is required given the often long-term nature of some of these more sustainable strategies, such as, the development of germplasm more appropriate to predicted future winter climate scenarios.

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