# A Review of Dormancy and Chilling Requirements in Raspberries

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## Introduction

In recent years a number of new raspberry varieties have become available in the UK. These include both proprietary varieties and those originating from the Raspberry Breeding Consortium based at the James Hutton Limited (JHL), formerly Mylnefield Research Services, the commercial arm of the James Hutton Institute (JHI). The breeding program, part funded by AHDB-Horticulture, has developed a number of key and historically important floricane varieties, including Glen Ample, Glen Moy and Glen Lyon and more recently Glen Fyne and Glen Ericht. In 2015 it released Glen Dee, which has large conical, pale fruit with a sweet flavour and good shelf life.

Despite the flow of good new varieties, there is lack of understanding of the dormancy and chilling requirements of raspberry. This can delay the rapid uptake of new varieties by the industry as it takes a number of years to 'get varieties to work' effectively and efficiently. Even

the chilling requirements and responses to the environment of long established varieties like Glen Ample are poorly understood.

Understanding a variety's response to the environment enables growers to match varieties to specific commercial needs through more focussed decision-making and manipulation of crop timings and yields. The use of cold storage to manipulate dormancy and chilling requirements underpins key production techniques such as long-cane production. An understanding of the dormancy and chilling requirement also supports breeders in selecting varieties which are more resilient to potential climate change, where increases in global temperatures may reduce the rate of winter chilling (Atkinson et al., 2013).

In this report the key scientific literature describing our current understanding of the dormancy process in raspberry is reviewed and knowledge gaps identified. Key gaps in the understanding of chilling and dormancy in raspberry, include;

- The most effective temperatures to release raspberries from dormancy.
- The number of chilling hours required by different varieties for dormancy release.
- What happens to current varieties if they do not receive enough chilling or do not enter dormancy.

This report also describes a new approach to mathematical modelling of the dormancy response of different floricane raspberry varieties. It also identifies key areas for additional research, which are required to underpin our knowledge of the chilling and dormancy response of raspberries.

## The floricane raspberry lifecycle

Floricane varieties are biennial. They initiate flowers in the autumn and these lead to production of fruit in the subsequent year. Conversely, primocane varieties initiate flowers in July/August and produce fruit in a single season (Carew et al., 2000). This report focuses on floricane varieties as these reflect the new germplasm being developed by the Raspberry Breeding Consortium at James Hutton Limited. The lifecycle of floricane varieties is described in Figure 1, adapted from the approach outlined by Carew et al. (2000, 2005).
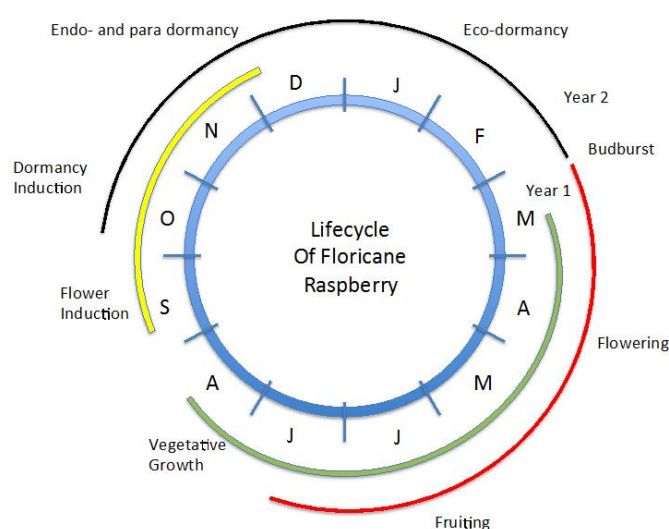


**Figure 1.** The lifecycle of a floricane or biennial raspberry, adapted from Carew et al. (2000, 2005).

The lifecycle of a floricane raspberry can be subdivided into a number of key segments across two years. The lifecycle begins in Year 1 with vegetative growth of the cane through the spring and summer months (often referred to as the primocane or spawn). Flowers are induced and initiated as the temperatures start to cool towards the autumn. The cane goes through a period of dormancy induction promoted by cool temperatures and short days (Williams, 1959b and 1960). Dormancy is released when the buds burst in the spring followed by flowering and fruiting.

## The induction of dormancy

For plants of all species the dormancy process is complex and has been subdivided into a number of key categories, endo, para and eco-dormancy (Lang et al., 1987). These reflect the different physiological processes which control dormancy within plants. They can act separately or concurrently within a plant at any one time.

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*Endo, para and eco-dormancy*

There are three different types of dormancy:

**Endo-dormancy** is dormancy controlled within an individual bud per se. typically a period of cold (c. 1 to 4°C) temperature is required to break this process.

**Para-dormancy** occurs where dormancy is controlled from outside the bud. White et al. (1998) found that in raspberry, signals from the apex can prevent the breaking of buds further down the cane. Removing apical meristems can help stimulate the breaking of buds. Para-dormancy is also broken by extended periods of cold temperatures. The optimum temperature for chilling and duration are not well known. However, by precedent, scientific experiments to test the chilling mechanism are typically run at 4°C.

**Eco-dormancy** occurs once the bud has been chilled. Effectively the bud is primed but now needs improved environmental conditions, typically warm temperatures, in order to grow and for the leaves to burst.

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The induction of dormancy can be a prolonged period. Normally in the UK, canes achieve a fully dormant state (endo and para-dormancy) during November and this state can only be broken after the buds have received cold temperatures for an extended period (White, 1999). The process of endo-dormancy is controlled by mechanisms only within a bud. In the UK endo-dormancy typically ends towards the end of December through to January. Prolonged periods of cold are required for all the buds on a cane to break dormancy (White et al., 1998).

Extended periods of cold, beyond that necessary to break endo-dormancy, also help to remove the additional state of para-dormancy (White et al., 1998). This occurs simultaneously with endo-dormancy. Once endo and para-dormancy have been broken, warm temperatures are required to enable the leaves to burst (eco-dormancy, see Figure 1). Following bud break, warm temperatures (c. January onwards) promote flowering and fruit development in Year 2.

## Entering dormancy

Despite the critical importance of dormancy in the lifecycle of the raspberry, the phenomenon has received relatively little research attention. Key early studies showed that floricane raspberries enter dormancy as the temperatures cool and day length shortens in the autumn

(Williams, 1959). Williams (1959) demonstrated that young plants required at least 8 to 10 weeks of cool (10°C) temperatures before plants became dormant. Cool temperatures (10°C) also promoted the formation of flower primorida (Williams, 1960). This typically occurs from September in the UK crop; first in the terminal buds, followed by auxillary buds 5-10 nodes below the apex and progressively down the stem by the end of January (Williams, 1959b). White (1999) showed that Glen Moy had fully entered endo-dormancy by the beginning of November. However, if plants do not receive cool temperatures they can keep growing vegetatively (Williams, 1960); Malling Promise grew continuously at high temperatures (21°C) in 9 hour and 14 hour daylengths initiating leaves for 19 months after which they formed a terminal inflorescence.

Sønsteby and Heide (2008) also demonstrated that Glen Ample was very sensitive to environmental conditions as it entered the pre-dormant state. They showed that if plants received a combination of warm temperatures and long days (20°C, 18 hour day lengths) then after only 2 to 4 weeks of cool (9°C under short 10 hour days) the plants would resume normal growth and continue initiating leaves. Dormancy was only fixed in Glen Ample after the plant had received at least 5 weeks at 9°C and 10 hour day lengths.

Therefore in floricane raspberry, it is clear that an extended period of cool temperatures (9°C) and short days (10 hour day lengths) are required for a plant to enter dormancy and that this process can be disrupted by warm temperatures (20°C) and long days (18 hour day lengths). Sønsteby and Heide (2008) showed that temperatures below 15°C are critical for the induction of dormancy in short days in Glen Ample.

Sønsteby and Heide (2008) also managed to create 'tip flowering' behaviour in the floricane Glen Ample, where flowers grew from the tip in the first year of cane growth. They showed that a short drop (3-4 weeks) in temperature to 9°C followed by warm temperatures (20°C) made plants flower and fruit in a single year. During the short cold temperature period the canes initiated flowers. The return to warm temperatures (20°C) then enabled two thirds of the plants to produce some flowers, (around 9 per plant), in short day conditions. This demonstrates that temperature conditions can change the flowering behaviour of typical floricane varieties.

## The breaking of dormancy

Both endo and para-dormancy are broken by extended periods of cold temperatures.

***Describing and measuring periods of cold***

Periods of cold can be described by 'chilling', 'chilling hours' or 'thermal time'.

**Chilling** - is the process whereby the accumulation of cold temperatures promotes the breaking of dormancy. The mechanism is found in many temperate crop species. It effectively helps plants measure when winter is over so that they can burst buds in the spring and avoid winter frosts. Buds burst after plants have received a cumulated number of 'chilling hours'.

**Chilling hours** are often considered to be a fixed number of hours at a standard temperature, often 4°C. However, it is well known that the number of chilling hours required by plants can vary with temperature. In raspberry, our models suggest that the fastest rate of chilling accumulation occurs at around 1°C and as temperatures increase they become gradually less effective. This means at higher temperatures longer durations in real time (hours) may be required to break dormancy.

**Thermal time** - Many other plant developmental responses are also a function of temperature. Plants are considered to measure time by accumulating a set amount of thermal time. This is the temperature summed from between one phenological event to another (e.g. sowing of a seed to flowering). Thus development progresses at a faster rate at higher temperatures compared to lower ones. It is measured in day degrees. The number of day degrees accumulated is equivalent to the average temperature above a given base temperature on any day. Thus if the average daily temperature was 12°C this would be equivalent to 12 day degrees if the base temperature is 0°C.

*Requirements to break dormancy*

Williams (1959a) demonstrated that young plants of Malling Promise broke dormancy (judged by the ability of plants to recommence elongation growth) after they had received 1,008 hours (6 weeks) at 3.3°C. Gillespie et al. (1999 and 2000) found that 6 weeks at 4°C fulfilled the chilling requirements of the upper buds of Glen Moy.  White et al. (1998) showed that intact canes of Glen Moy would break 50% of their upper and mid cane buds after they had received 951 hours (just under 6 weeks) at 4°C. Buds on the lower third of the cane required 1,510 hours at 4°C to achieve 50% bud break.  White et al. (1998) concluded that the lower parts of a cane require a longer duration of chilling than the upper parts.

More recently, Mazzitelli et al. (2007) showed that Glen Ample required c.1,300 hours at 4°C for 50% of the buds to break. Similar to White et al.'s (1998) findings on Glen Moy, the lower parts of the canes required a longer duration of chilling than the buds on the upper parts of the canes. However, Mazzitelli et al. (2007) demonstrated that if canes were dissected and buds from the upper, mid and lower parts of the canes were chilled in isolation from each other, all the buds broke dormancy at similar times, regardless of whether they were from the upper, mid or lower part of the cane.  This confirmed that raspberry shows both endo and para-dormancy. Where buds were separated from each other they all responded identically to chilling (endo-dormancy) and where canes were left intact lower parts of the cane required more chilling (para-dormancy).

Longer durations of chilling have also been shown to correlate with berry yield, partly due to an increase in the number of laterals. For instance, Gillespie et al. (2000) showed that berry yield of Glen Moy and Glen Ample was c. 200g per cane when chilled at 912 hours compared to c. 500 to 600g after canes had received 3,432 hours of chilling.

It has been suggested that para-dormancy control is imposed by the terminal meristem and therefore that tipping may help stimulate more even bud release (White et al., 1999). However, detailed studies by Gillespie et al. (1999 and 2000) found little impact of tipping under semi-commercial conditions with the varieties Glen Moy, Glen Clova and Glen Ample, which showed similar levels of bud break. However, tipping did seem to lead to increases in individual berry weight in some varieties, notably Glen Moy and Glen Ample; untipped berry weight of Glen Ample was c. 5g compared to 6.9g for September tipped canes.

In terms of the eco-dormancy process, there have been few if any studies attempting to quantify the duration of this process. Mazzitelli et al. (2007) showed that bud burst occurred in Glen Ample after the plants had received just 14 days at 20°C post endo-dormancy. The temperature response of eco-dormancy is exploited in long-cane production. During eco-dormancy warm temperatures promote bud burst, but conversely low temperatures inhibit the process. This underpins the process of cold storage of long-canes. For example, Gillespie et al. (1998) showed that Glen Ample could be stored for 10 months at 1°C but that Glen Lyon buds burst in cold storage after 4 months at 4°C in the dark.

Once canes are removed from cold storage they progress rapidly to bud burst and this process is temperature dependent. However, the impact of the temperature on the time from bud burst to flowering and fruiting has not been quantified for raspberry.

## Long-cane production

Understanding dormancy and chilling responses is crucial for out-of-season 'long-cane production', where the crop is manipulated via the cold storage of canes to extend the UK season and manipulate crop timings and yield of summer fruiting varieties.

Long-cane production involves producing one year old shoots in field spawn beds and lifting them with roots intact in the autumn when they are dormant. They are subsequently placed in cold stores, typically below 4°C, until they have received adequate chilling (Gillespie et al. 1999). The duration of chilling is typically thought to be 6 weeks but this is not well defined for

different varieties. The plants are then brought out of cold storage and planted into a variety of production systems, including pots, raised beds, under tunnels or glass. Planting dates are manipulated so production either precedes the main season or is delayed. After fruiting, new primocane can be grown and either retained or lifted and cold stored to repeat the process.

Gillespie et al. (1999 and 2000) investigated different elements of long-cane production with a view to optimising the system. Their experiments on cane production in the field showed that cane density in commercial spawn beds affected the quality of the cane, its morphological development and thus its fruiting performance. They found that canes of Glen Moy attained a diameter of 11mm when grown at 25 canes m$^2$ compared to 15mm at a density of 5 to 6 canes m$^2$. Canes within a dense canopy initiated flowers two weeks later than those on the outside of the bed (Brennan et al., 1999).

The time of lifting was critical. Brennan et al. (1999) found that canes lifted too early (late August/early September) had poor survival in cold storage whereas those lifted late were considered at risk of frost injury. Optimal lifting dates in Scotland, to maximise subsequent bud break, were found to be from mid-October until late November. Moreover, the lifting date affected cane survival in cold storage. Material lifted between mid-October and late November showed 80% survival (Gillespie et al., 2000). However, canes lifted in early December only showed a survival rate of around 60% (Gillespie et al., 2000).

Gillespie et al. (1999) also investigated cane storage and found that high quality, healthy cane was essential for survival in cold storage and good subsequent fruit production. They made recommendations to help maintain fruiting potential, minimise desiccation and *Botytris* infection in cold storage. These included leaf removal to reduce disease incidence and wrapping bundles of canes in breathable fleece to maintain humidity. They also recommended that cold storage temperatures of around 1$^o$C were necessary to prevent bud break during long term storage.

## A model of the dormancy response

This review has shown some of the key environmental triggers driving the dormancy process in raspberry. However, there are significant knowledge gaps, including the dormancy response to temperature, which have not been fully quantified. To explain these gaps, a mathematical model was constructed to predict the date of first bud break and flowering for raspberry. By developing a biologically meaningful model it will be possible to accurately predict the date of first bud burst and flowering for a range of floricane raspberry varieties. Models can also help to identify knowledge gaps and often help provide a basis for further experimental work.

The model was calibrated using phenological records of the date of first bud burst and flowering recorded from 2005 to 2014 at James Hutton Ltd for the raspberry varieties; Glen Ample (10 years data), Glen Moy (9 years), Glen Lyon (5 years), Glen Dee (5 years) and two new trial selections from the Raspberry Breeding Consortium at James Hutton Ltd including 0435D-3 (5 years) and 0485K-1 (5 years). The data was recorded from 2 x 5 plant replicate trial plots of each variety. Daily maximum and minimum temperatures recorded at James Hutton Ltd were used to construct the models.

The model developed was a two-step model. The first step of the model predicted when the plant has been sufficiently chilled to complete endo-dormancy. The second step then predicted the date of bud burst assuming that it was a function of warm temperatures starting from the end of endo-dormancy. The key temperature responses are shown in Figure 2.
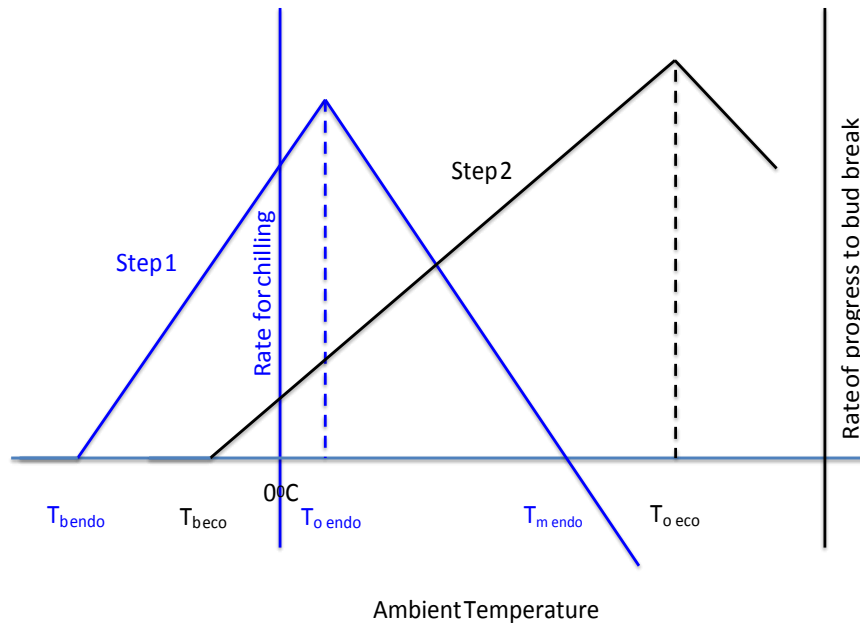
**Figure 2.** The two indicative temperature responses used in the floricane raspberry dormancy model. Step 1 represents the endo-dormancy temperature response and eco-dormancy is shown in Step 2 - see text for full explanation.

The model assumed the endo-dormancy response to temperature (Step 1, Figure 2) was triangular as a triangular approximation of the endo-dormancy response is widely used to model other species (see Fu et al., 2012). The optimum rate of chilling occurred at $T_{o\ endo}$. Based on the raspberry literature, the optimum temperature to break endo-dormancy was anticipated to be around 0 to 4°C. The model quantified the impact of temperatures above or below the optimum ($T_{o\ endo}$) on the rate of chilling. This model had an additional function in that as temperatures increased above a maximum, $T_{m\ endo}$, the chilling accumulation became negative and thus the model simulated de-chilling impact of warm temperatures. De-chilling, defined as the short term impacts of high temperature reversing dormancy progression, has been shown for a number of woody plants (see Fishman et al., 1987a and b).

The model simulated hourly temperatures (using the approach of DeWitt et al., 1978) from actual maximum and minimum data recorded on site at James Hutton Ltd. For each hour, it determined the number of effective chilling units received. Effective chilling units were calculated by weighting them according to the triangular response function (Step 1, Figure 2). Endo-dormancy was assumed to be broken when the raspberry had accumulated a set number of effective chilling day degrees ($\Theta_{endo}$). It was assumed that the chilling clock started on the 1st November, the peak time of endo-dormancy (White, 1999).

The higher temperature eco-dormancy began response (Step 2; Figure 2) once the endo-dormancy process had completed. The eco-dormancy response was also assumed to be triangular. The shape of this response has been used to approximate the temperature response function of a wide number of species (see Pearson et al., 1993). In this instance, the base temperature (the point at which development begins) was described as $T_{b\ eco}$ and the optimum was $T_{o\ eco}$. Again the model was run using hourly temperature data. Bud burst was assumed to occur after a set amount of thermal time ($\Theta_{eco}$, day degrees) had been accumulated.

The model had six key parameters which described the entire response of raspberry bud break to temperature ($T_{b\ endo}$, $T_{o\ endo}$, $\Theta_{endo}$, $T_{b\ eco}$, $T_{o\ eco}$ $\Theta_{eco}$). To solve the model, each of the key parameters was varied until it adequately described the known data on time to first bud break of raspberries over a number of years. In this instance, the parameter values were determined using a genetic algorithm provided within the 'Solver Add In' of Microsoft Excel.

## Chilling requirement by variety

Figure 3 shows the relationship between actual and predicted time to first bud break for all varieties and years. For all the varieties, the model provided a good fit to the data.
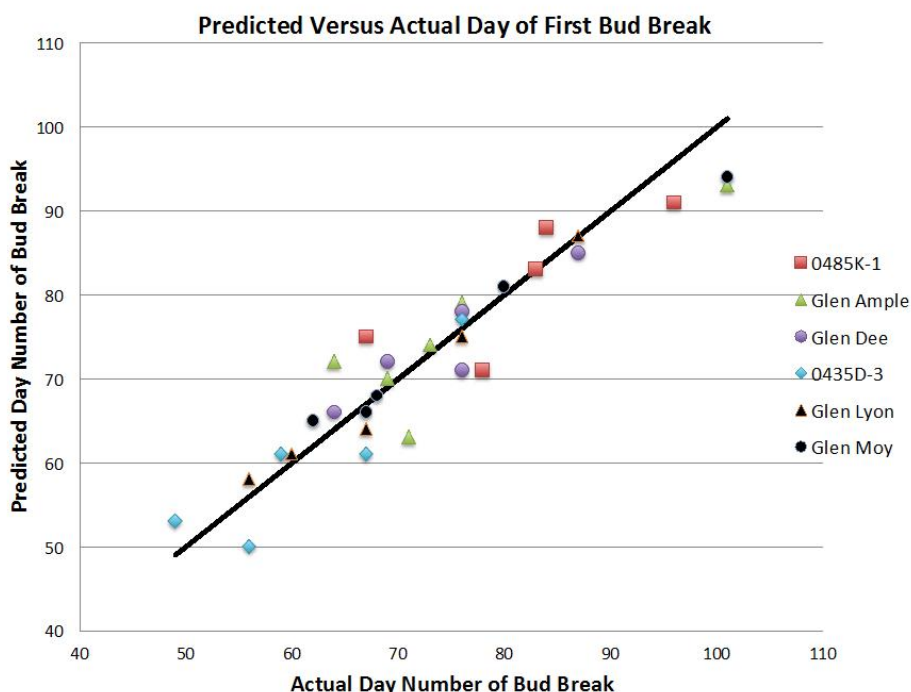


**Figure 3.** The predicted versus actual time in terms of day number (where 1st January = day 1) to first bud break of 6 raspberry varieties recorded between 2008 and 2014 at James Hutton Ltd.

The combined coefficient of determination ($r^2$), i.e. the proportion of variation explained by the model, was 84%. The model predicted the date of first bud break to +/- 4.2 days averaged across all years and varieties. The high $r^2$ suggested that the model provided a good description of the underlying mechanisms controlling bud break in raspberry. The model was able to predict over a wide number of first bud break dates ranging from the earliest break by 0435D-3 on 19th February in 2013 to the latest by Glen Ample breaking on 12th April in 2010.

The parameter values determined by the model are shown in Table 1. For all varieties the model fitted the data with $r^2$ varying between 65% (0485K-1) to 97% (Glen Lyon). The model showed small differences in optimum chilling temperatures between varieties, with Glen Ample having an optimum chilling temperature of -1.6°C compared to 0485K-1 at 2.5°C. The optimum temperatures for eco-dormancy were between 20°C to 25°C depending upon variety.

For ease of comparison and validation with previous experimental data, Table 1 shows the predicted number of chilling hours at a set 4°C which are required to break dormancy for each of the varieties. It showed some important differences. Glen Lyon was predicted to require 944 hours at 4°C and Glen Moy 975 hours at 4°C to break dormancy compared 1,210 hours at 4°C for 0435D-3 and to 1,215 hours at 4°C for Glen Ample. Glen Dee and 0485K-1 were modelled to have very long endo-dormancy phases.

The model predicts the first bud break day, which is effectively the end of endo-dormancy. Additional chilling hours will be required to fully break para-dormancy, which will release all the buds on the stem.

By comparison Glen Dee was predicted to have a short eco-dormancy phase (183 day degrees compared to 497 day degrees for Glen Ample). This suggests that Glen Dee may have a prolonged chilling requirement but that bud burst can thereafter proceed quite rapidly.

Table 1. Key parameter values for different varieties determined by the model and the derived number of chilling hours, at a standard 4°C, required to break dormancy.

| Parameters | Glen Ample | Glen Moy | Glen Lyon | Glen Dee | 0435D-3 | 0485K-1 |
|---|---|---|---|---|---|---|
| Optimum chilling temperature ($T_{o\ endo}$) °C | -1.6 | 1.3 | 1.4 | 1.8 | 1.0 | 2.5 |
| Thermal time to bud break post endo-dormancy ($\Theta_{eco}$) day degrees | 497 | 435 | 412 | 183 | 358 | 334 |
| Optimum eco-dormancy temperature ($T_{o\ eco}$) °C | 23 | 20 | 25 | 20 | 20 | 25 |
| Base temperature for eco-dormancy ($T_{b\ eco}$) °C | -3 | -2.1 | -2.3 | -2.0 | -3.0 | -2.9 |
| $r^2$ | 77% | 94% | 97% | 84% | 79% | 65% |
| **Chilling Units** (hours at 4°C required to break endo-dormancy) | **1,215** | **975** | **944** | **1,845** | **1,210** | **1,688** |

The derived chilling hours for each variety were broadly consistent with known data. White (1999) demonstrated by using cold stores that Glen Moy required 951 chilling units at 4°C for 50% bud break. Similarly, Mazzitelli et al. (2007) showed Glen Ample required c. 1,300 chilling units at 4°C. Glen Lyon is also considered to have a low chilling requirement and as such is widely used in Spain for cold stored long cane production. Glen Dee and 0485K-1 seemed to require larger quantities of chilling to break dormancy. However, there is no independent data from cold storage experiments to verify these values. Such trials would be useful to underpin the model as well as to show important genetic differences in chilling requirements between varieties and allow improvements to agronomic practices in the cultivation of different varieties.

In summary, the model provided a reasonable framework to describe the chilling response of raspberries. The model was biologically simple and can be easily tested. Experiments to validate the number of chilling hours needed by each variety are required. This work will be conducted by James Hutton Ltd in the winter of 2015 / 2016 where raspberry canes from different varieties will be removed from the field at different dates during the winter. After field removal they will be grown on under warm temperatures to see if they break buds and have therefore completed dormancy. The data should demonstrate any varietal differences in time to fulfil dormancy chilling requirements under field conditions.

## Summary and main conclusions

This report presents a review of our understanding of the dormancy of raspberries:

- The literature has been reviewed, demonstrating the processes of endo, para and eco-dormancy controlling bud burst in raspberry.

- It indicates that raspberries take a prolonged period of cool temperatures and short days to fully enter dormancy. This process can be disrupted by warm temperatures

and short days such that raspberries can regrow if they are exposed to warm temperatures.

- The literature suggests the critical temperature for dormancy induction must be below 15°C.

- Raspberries need a minimum of 6 weeks of cold (c. 4°C) to break first buds. However, longer periods of chilling are required for even bud break down the length of the cane.

- Here a model of the dormancy process has been constructed. This showed key differences by variety in the duration of their cold requirements, with Glen Lyon requiring 944 chilling hours for first bud break compared to 1,215 chilling hours for first bud break in Glen Ample. These differences now need experimental verification. However, the approach may enable selection of variety by dormancy response; a key response that underpins the linkage between raspberry growth and the environment.

- The model suggests that fastest chilling under field conditions occurs at c -1.6 to +2.5°C.

- Selections for warm countries might require a low chilling requirement.

- Further investigation of the genetic differences in dormancy response will help the industry manipulate varieties to maximise production as well as enable future breeding strategies to select varieties which show a high degree of resilience to environmental change.

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