Japanese apricot (Prunus mume Sieb. et Zucc.) is one of the most popular fruit tree species in Japan for producing processed fruits and ornamental flowers (Mega et al., 1988). Most of the japanese apricot produced in Japan comes from Wakayama Prefecture, where the most popular cultivar, Nanko, usually blooms in the middle of February. However, the timing of the blooming stage varies depending on the year, with differences of up to 1 month. This fluctuation is an important factor affecting the synchronization of flowering between the major and pollinator cultivars and the development of early spring frost damage, which can ultimately lead to unstable fruit production.

Flower buds of temperate deciduous fruit tree species enter endodormancy (i.e., suspension of visible growth due to internal factors) in the fall (Faust et al., 1997; Lang, 1987). After endodormant buds are exposed to a certain period of low temperatures, the buds are transferred to the ecodormant state and acquire the ability to resume growth under favorable conditions. Plant responses to low and high temperatures during endo- and ecodormancy, respectively, are critical factors for determining genotype-dependent blooming time. Additionally, recent global climate changes have also affected the timing of the blooming stage in trees, which may soon affect the suitability of certain areas for fruit tree cultivation (Sugii et al., 2012). Thus, characterizing the specific temperature responses in each cultivar and estimating the timing of blooming are needed to achieve stable crop production. Japanese apricot trees ordinarily bloom at relatively low temperatures (Japanese Apricot Laboratory, personal communication), and most cultivars are self-incompatible (Miyake et al., 1995). Therefore, japanese apricot production is closely associated with climate conditions, and accurately predicting the blooming time is especially important.

In previous studies, the number of days transformed to standard temperature (DTS) was used to predict blooming times in several tree species, including Prunus yedoensis ‘Somei-yoshino’ and satsuma mandarin (Citrus unshiu Marcow.) (Hayashida et al., 1998; Omoto and Aono, 1989). In this DTS model, the degree of development is calculated using an Arrhenius equation, and blooming time is predicted by determining the most appropriate values for three parameters (i.e., initiation date, days required for blooming transformed to standard temperature, and temperature sensitivity) based on past measurements. The DTS model is highly accurate, but the predicted values may differ from the actual values depending on location and year (Oono and Konno, 1999). Moreover, flower buds of temperate deciduous trees undergo endodormancy and ecodormancy, and the responses of buds to temperature vary between the two phases. Incorporating these differences into the DTS model may increase its accuracy. The importance of considering the endodormancy release date for the DTS model has been discussed (Aono and Moriya, 2003; Aono and Sato, 1996; Ogata et al., 2012). Thus, characterizing the specific temperature responses in each cultivar and estimating the timing of blooming are needed to achieve stable crop production. Japanese apricot trees ordinarily bloom at relatively low temperatures (Japanese Apricot Laboratory, personal communication), and most cultivars are self-incompatible (Miyake et al., 1995). Therefore, japanese apricot production is closely associated with climate conditions, and accurately predicting the blooming time is especially important.

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There have been several attempts to determine the chilling requirements for endodormancy release, and the following three models have been proposed: chill hour (CH; Weinberger, 1950), chill unit (CU; Richardson et al., 1974), and chill portion (CP; Fishbein et al., 1987a, 1987b). In the CH model, the number of hours plants are exposed to temperatures below 7.2 °C (45 °F) is counted. The CU model involves counting various weighted temperature values, with high temperatures negating the effects of

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Additional index words. endodormancy, ecodormancy, development index, chilling requirement, heat requirement, Prunus mume

Abstract. Flower bud development and the timing of blooming are mainly affected by genotype-dependent chilling requirements (CRs) during endodormancy and subsequent heat requirements (HRs) during ecodormancy. However, little information is available regarding the responses of flower buds to temperatures during endodormancy and ecodormancy in Japanese apricot. We exposed Japanese apricot ‘Nanko’ trees to various temperatures to estimate the CRs and HRs using development index (DVI) models specific for the endormant (DVIendo) and ecodormant (DVIEco) stages. These models were based on the experimentally determined development rate (DVR). The DVRendo value was calculated as the reciprocal of the chilling time required to break endodormancy. The relationship between the DVRendo value and temperature was estimated using a three-dimensional curve. Our results indicated that 5–6 °C was the most effective temperature for breaking endodormancy in ‘Nanko’ flower buds. Additionally, exposure to −3 °C negatively affected endodormancy release, whereas 15 °C had no effect. We also determined that the DVReco values for temperatures between 5 and 20 °C were the reciprocal values of the time required for blooming after endodormancy release. The values outside this range were estimated using linear functions. The DVR was defined as the sum of the DVR values ranging from 0 to 1. Models for predicting the blooming date were constructed using the functions of sequentially combined DVIendo and DVIEco models. The accuracy of each model was assessed by comparing the predicted and actual blooming dates. The prediction of the model in which DVIEco = 1 corresponded to a 40% blooming level and DVIEco = 0 was set to DVIendo = 0.5 had the lowest root mean square error (RMSE) value (i.e., 3.11) for trees in commercial orchards exposed to different climates. Our results suggest that the developed model may have practical applications.

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Blooming Date Predictions Based on Japanese Apricot ‘Nanko’ Flower Bud Responses to Temperatures during Dormancy

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previous exposures to low temperatures. The CP value is calculated using a dynamic model that assumes the chilling effects accumulate in a two-step process. Initially, exposure to low temperatures leads to the formation of a reversible intermediate product. If plants are then exposed to high temperatures, the product cannot be accumulated, whereas a subsequent exposure to low temperatures results in the production of an irreversible CP product.

In this study, we evaluated the responses of Japanese apricot ‘Nanko’ flower buds to different temperature treatments during endodormancy and ecodormancy, and calculated the DVR values for each temperature. We then used two different DVR values (i.e., DVR_{endo} and DVR_{eco}) to predict the blooming date of ‘Nanko’ flower buds. The accuracy of our predicted blooming dates was verified by comparing them with the actual blooming dates in commercial orchards.

**Materials and Methods**

**Evaluation of responses to chilling temperatures during endodormancy.** We conducted three experiments. First, we exposed potted Japanese apricot trees to various temperatures to quantify the chilling requirement (CR) for endodormancy release according to the DVI model. Second, we determined the HR for blooming after endodormancy release based on temperature treatments similar to those used in the first experiment. Finally, we developed a model to predict the blooming date by combining the DVI models for CRs and HRs. We assessed the accuracy of the model by comparing the predicted and actual blooming dates for trees in a commercial orchard.

Three-year-old Japanese apricot ‘Nanko’ trees grown in 25-L pots at the Japanese Apricot Laboratory were analyzed from 2013 to 2015. Trees pruned to maintain one upright trunk with 1-year-old branches were kept at temperatures above 15 °C in a greenhouse until early November of each year to ensure plants were not exposed to low temperatures. Trees were artificially defoliated and individual trees were exposed to the following conditions in darkened phytotrons (i.e., 24 trees were used): 2 °C for 336, 408, 480, 552, or 624 h; 5 °C for 336, 480, 552, 624, or 696 h; 7 °C for 336, 408, or 480 h; 10 °C for 336, 408, 480, 552, or 696 h; 12 °C for 480, 552, 624, or 768 h; or 15 °C for 480 or 720 h. To evaluate the effects of freezing conditions, an additional three trees grown at 5 °C were incubated two to four times in a freezer set at –3 °C for 24 h, with certain intervals between treatments. The trees exposed to chilling temperatures were transferred to a greenhouse and incubated at temperatures above 15 °C. The blooming percentages were recorded for ≤2 months. The relationship between blooming percentage and chilling exposure time for each treated tree was estimated using the following logistic regression curve with threshold and inflection points set to 100% and 50% (i.e., blooming percentage), respectively:

\[
f(d) = \frac{100}{1 + \exp[-\alpha_1(d - \alpha_2)]}
\]

where \(d\), \(f(d)\), \(\alpha_1\), and \(\alpha_2\) correspond to the chilling treatment time, predicted blooming percentage, relative blooming rate, and chilling treatment time at the inflection point (i.e., chilling treatment time required for endodormancy release in 50% of flower buds), respectively. The parameters \(\alpha_1\) and \(\alpha_2\) were determined using a least squares method. Using this equation, the chilling exposure time required to reach an 80% blooming

**Table 1. Evaluation of DVR_{endo} values at –3 °C.**

| Time (h) | Blooming percentage | DVR at only 5 °C | Back calculated DVR | Value of decreased DVR | DVR at –3 °C (h⁻¹) |
|----------|---------------------|-----------------|---------------------|-----------------------|---------------------|
| 48       | 408                 | 53.4            | 0.8703              | 0.7998                | 0.1605              | -0.0033             |
| 72       | 480                 | 66.3            | 1.0239              | 0.8354                | 0.1884              | -0.0026             |
| 96       | 576                 | 77.7            | 1.2287              | 0.9690                | 0.2597              | -0.0027             |

Mean ± SE: -0.0029 ± 0.00023

DVR_{endo} = endodormant development rate; DVR = development index.

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**Fig. 1.** Schedule of exposures to –3 °C during incubations at 5 °C. Total number of hours exposed to –3 and 5 °C were 48 and 408 h for sample 1, 72 and 480 h for sample 2, and 96 and 576 h for sample 3, respectively.

**Fig. 2.** Relationship between chilling exposure time and blooming percentage in Japanese apricot ‘Nanko’ trees. The relationships were estimated using logistic regression curves. For 2 °C, \(f(d) = 100/(1 + \exp[-0.012(d - 496.8)])\), \(r^2 = 0.922\); for 5 °C, \(f(d) = 100/(1 + \exp[-0.009(d - 317.9)])\), \(r^2 = 0.810\); for 7 °C, \(f(d) = 100/(1 + \exp[-0.018(d - 444.6)])\), \(r^2 = 0.865\); for 10 °C, \(f(d) = 100/(1 + \exp[-0.010(d - 549.6)])\), \(r^2 = 0.903\); and for 12 °C, \(f(d) = 100/(1 + \exp[-0.006(d - 779.7)])\), \(r^2 = 0.372\).
level for each temperature was calculated and defined as the CR. The DVR\textsubscript{endo} value for each temperature was calculated as the reciprocal of the CR value.

The DVR\textsubscript{endo} value at \(-3^\circ\text{C}\) was determined based on the decreased DVR\textsubscript{endo} accumulated values (DVR\textsubscript{endo}) resulting from the freezing treatment. First, the DVR\textsubscript{endo} value was back-calculated from the recorded blooming percentage using the DVR\textsubscript{endo} function at \(5^\circ\text{C}\). We then compared the assumed DVR\textsubscript{endo} value and the DVR\textsubscript{endo} value for trees continuously exposed to \(5^\circ\text{C}\) to calculate the decreased DVR\textsubscript{endo} value caused by exposure to \(-3^\circ\text{C}\). Finally, the DVR\textsubscript{endo} value per unit time at \(-3^\circ\text{C}\) was determined by dividing the decreased DVR\textsubscript{endo} value by the exposure time. The DVR\textsubscript{endo} value for each temperature was estimated according to the regression curve function.

**Evaluation of responses to high temperatures during endodormancy.** We analyzed 3-year-old ‘Nanko’ trees grown as described above. After trees were exposed to \(5^\circ\text{C}\) for \(\approx500\) h in early November to break the endodormancy, they were incubated at 5, 10, 15, or 20 \(^\circ\text{C}\) in phytotrons. We recorded the blooming percentages until all flower buds bloomed. We used three trees for each temperature treatment. The relationship between bloom release and blooming percentage was estimated using the following logistic regression curve with threshold and inflection points set to 100% and 50% (i.e., blooming percentage), respectively:

\[
f(d_h) = 100\left[1 + \exp\left(-\beta_1(d_h - \beta_2)\right)\right]
\]

where \(d_h\), \(f(d_h)\), \(\beta_1\), and \(\beta_2\) correspond to the temperature, blooming percentage, relative blooming rate, and time after endodormancy release at the inflection point (i.e., treatment time required for a 50% blooming rate), respectively. The parameters were determined as described above. The heating time required to reach a 30%, 40%, or 50% blooming level at each temperature after endodormancy release was calculated and defined as the HR. The DVR\textsubscript{eco} value for each temperature was calculated as the reciprocal of the HR value. The DVR\textsubscript{eco} value at each temperature was estimated using the polygonal regression line function.

**Construction and verification of a DVR model to predict the blooming date.** During the 2013–14 and 2015–16 growing seasons, we selected one conventionally managed adult ‘Nanko’ tree planted at the Japanese Apricot Laboratory (Minabe, Hidaka, Wakayama, Japan) as the standard model for the analyzed trees. The DVR\textsubscript{endo} value at each temperature was estimated using a three-dimensional curve (Fig. 3). The DVR\textsubscript{endo} value at each temperature was calculated assuming that endodormancy was 100% at \(-3^\circ\text{C}\) (Table 2).

| Definition of endodormancy release (%)\(^a\) | Coefficients of DVR\textsubscript{endo} curves\(^b\) | DVR\textsubscript{endo} = endodormant development rate; DVR\textsubscript{endo} = endodormant development index. |
|---|---|---|
| a | b | c | d | \(r^2\) |
| 40 | 4.99e-06 | -1.61e-04 | 1.29e-03 | 1.77e-04 | 0.986 |
| 50 | 4.25e-06 | -1.57e-04 | 1.08e-03 | 3.61e-04 | 0.992 |
| 60 | 3.58e-06 | -1.18e-04 | 9.32e-04 | 4.31e-04 | 0.995 |
| 70 | 3.09e-06 | -1.03e-04 | 8.20e-04 | 4.56e-04 | 0.997 |
| 80 | 2.62e-06 | -9.12e-05 | 7.62e-04 | 3.17e-04 | 0.997 |
| 90 | 2.95e-06 | -8.32e-05 | 7.32e-04 | 3.01e-04 | 0.998 |
| 100 | 3.52e-06 | -7.87e-05 | 6.96e-04 | 2.95e-04 | 0.999 |

\(a\)Bloom percentage under forcing conditions.

\(b\)Coefficients of the estimating function: DVR\textsubscript{endo} = \(a^t + b + c + d\), where \(t\) refers to temperature.

**Results and Discussion**

Responses to low temperatures during endodormancy and development of the DVR\textsubscript{endo} model. The blooming levels for 3-year-old Japanese apricot ‘Nanko’ trees reached 91.9%, 85.4%, 60.0%, and 76.6% following treatments at 2 \(^\circ\text{C}\) for 624 h, 5 \(^\circ\text{C}\) for 480 h, 7 \(^\circ\text{C}\) for 480 h, and 10 \(^\circ\text{C}\) for 552 h, respectively. Less than 50% of the flower buds in trees treated at 12 \(^\circ\text{C}\) for 624 h bloomed. No flower buds bloomed in trees incubated at 15 \(^\circ\text{C}\). The relationship between treatment temperature and blooming percentage at each temperature was estimated using logistic regression curves (Fig. 2). We determined that incubations of 613.7, 468.8, 523.3, 687.8, and 1003.5 h were required for a blooming level of 80% at 2, 5, 7, 10, and 12 \(^\circ\text{C}\), respectively. Therefore, the reciprocal of these times (i.e., 0.00163, 0.00213, 0.00191, 0.00145, and 0.001) corresponded to the DVR\textsubscript{endo} values at each temperature.

Bloom percentages were 53.4% for trees incubated at 5 \(^\circ\text{C}\) for 408 h and –3 \(^\circ\text{C}\) for 48 h (24 h \times 2), 66.3% for trees incubated at 5 \(^\circ\text{C}\) for 480 h and –3 \(^\circ\text{C}\) for 72 h (24 h \times 3), and 77.8% for trees incubated at 5 \(^\circ\text{C}\) for 576 h and –3 \(^\circ\text{C}\) for 96 h (24 h \times 4). The DVR\textsubscript{endo} values were back-calculated from these percentages using the regression curve at 5 \(^\circ\text{C}\). The sum of the DVR\textsubscript{endo} values for trees continuously incubated at 5 \(^\circ\text{C}\) was subtracted from the back-calculated DVR\textsubscript{endo} values to calculate the decreased DVR\textsubscript{endo} values resulting from the freezing conditions (–3 \(^\circ\text{C}\)) (Table 1). The decreased DVR\textsubscript{endo} values divided by exposure time at –3 \(^\circ\text{C}\) for three different treatments had relatively small s.s. Therefore, the mean value (i.e., –0.0029) was used to represent the DVR\textsubscript{endo} value at –3 \(^\circ\text{C}\). Because no flower buds bloomed in trees incubated at 15 \(^\circ\text{C}\), the DVR\textsubscript{endo} value was considered to be 0 at 15 \(^\circ\text{C}\).

The DVR\textsubscript{endo} value at each temperature was estimated using a three-dimensional curve (Fig. 3, dashed line). However, the curve was calculated assuming that endodormancy was broken when 80% of the flower buds had bloomed. Because regression curve coefficients can vary depending on how endodormancy release is defined (i.e., what blooming level is used), the DVR\textsubscript{endo} values at each temperature were affected by the blooming level used to determine the endodormancy release date (Table 2). In the CU model for peach, the maximum CU value (i.e., 1) occurred at 2.4–9.1 \(^\circ\text{C}\) (Richardson et al., 1974). The highest DVR values for endodormant flower buds of peach, Japanese pear, and Japanese chestnut were observed at 6 \(^\circ\text{C}\) (Sakamoto et al., 2015;
Sugiura et al., 2010; Sugiura and Honjo, 1997). The highest DVR\textsubscript{endo} value for Japanese apricot occurred at 5–6 °C, which likely corresponds to the most effective temperature for breaking endodormancy in temperate deciduous fruit tree species. However, the DVR value was determined to be 0 at temperatures above 12 °C in Japanese pear (Sugiura and Honjo, 1997). We observed that temperatures greater than 15 °C produced a DVR value of 0 in Japanese apricot, which was consistent with the results for peach (Sugiura et al., 2010). These observations suggest the effects of high temperatures on endodormancy release vary depending on species. Our data indicate that exposure to −3 °C negatively affects endodormancy release in Japanese apricot, which is in contrast with the findings for peach, which has a positive DVR value at −3 °C (Sugiura et al., 2010). These results imply that Japanese apricot trees have adapted to warmer climates and are more susceptible to the effects of cold stress than other fruit tree species. In other words, decreased blooming percentages are simply a consequence of CI due to exposure to −3 °C. The effects of temperatures below −3 °C are unclear, but the accuracy of predictions based on our regression curve (Fig. 3; Table 2) would likely not be affected because of the infrequency of temperatures below −3 °C in Wakayama Prefecture, even during winter in the open-field production sites. However, overestimating the negative effects of freezing temperatures on endodormancy release can affect the estimated endodormancy release date, especially in cold regions. Additionally, there are no reports suggesting that freezing temperature is associated with a negative DVR value in any other species. Therefore, when developing a model to predict the blooming date, we set negative DVR\textsubscript{endo} values estimated by the regression curve to 0 (Fig. 3, solid line).

Responses to high temperatures during ecodormancy and development of the DVR\textsubscript{eco} model. Because exposure to 5 °C for ≈470 h induced an 80% bloom and resulted in endodormancy release, we considered ‘Nanko’ trees incubated at 5 °C for 500 h to have shifted to the ecodormant stage. We observed that the higher the incubation temperature, the earlier the flower buds bloomed. The relationship between incubation time and blooming percentage at each temperature was estimated using logistic regression curves (Fig. 4). Based on the regression curves, incubations for 550.1, 667.3, 1316.2, and 2888.4 h at 20, 15, and 10 °C, respectively, were necessary to produce a 50% blooming level. Therefore, the reciprocals of these times (i.e., 0.00182, 0.00150, 0.00176, and 0.00035) represented the DVR\textsubscript{eco} value at each temperature. The DVR\textsubscript{eco} value varied depending on which blooming percentage corresponded to the blooming date (Fig. 5). The DVR\textsubscript{eco} model consists of three linear functions associated with temperature ranges (i.e., <10 °C, 10–15 °C, or >15 °C) (Fig. 5).

Previous studies on Japanese pear adopted two linear regression functions using 20 °C as a boundary to estimate the relationship between DVR values during ecodormancy and temperature (Oya, 2006; Sugiura et al., 1991). We were unable to obtain reliable blooming data for plants incubated at temperatures above 25 °C because many of the flower buds died (data not shown). Therefore, the function used for 15–20 °C was used for temperatures above 20 °C. Ecodormant Japanese apricot flower buds may be sensitive to high temperatures because flower buds continue to develop throughout winter, and flowers bloom while it is still cold. Further research is required to evaluate the effects of high temperatures on flowering. Additionally, when the regression function for 5–10 °C was used for temperatures below 5 °C, the DVR\textsubscript{eco} value was negative at ≈0 °C. However, negative DVR\textsubscript{eco} values at a given temperature are considered equivalent to 0 when the DVR\textsubscript{eco} model is used to predict the blooming date.

Verification of the predicted blooming date. The flower buds of the ‘Nanko’ trees started to bloom at the Japanese Apricot Laboratory on 4 Feb. 2014, 17 Feb. 2015, and 4 Feb. 2016. The blooming initiation dates at commercial orchards in the coastal, moderately elevated, and mountainous areas in 2016 were 4 Feb., 11 Feb., and 11 Feb., respectively (Table 3).

Because the endodormancy of flower buds was gradually broken during exposures to low temperatures, the accumulation of heat during endodormancy, which is necessary for blooming, likely begins before the endodormancy release date. Moreover, the functions of the DVR\textsubscript{endo} and DVR\textsubscript{eco} models vary depending on how the endodormancy release and blooming dates are defined. Therefore, the initial DVR\textsubscript{endo} value was set to DVR\textsubscript{endo} = 0.4–0.7, and the endodormancy release date (DVR\textsubscript{endo} = 1) and blooming date (DVR\textsubscript{eco} = 1) were set to 40% to 80% and 40% to 60% blooming levels, respectively. Additionally, we verified the blooming date prediction for each model developed by sequentially combining the DVR\textsubscript{endo} and DVR\textsubscript{eco} models.
The differences between the predicted and actual blooming dates for several orchards located in Wakayama are provided in Table 3 (except for clearly incorrect predictions). Preliminary validations of the models suggest that an 80% blooming level is the most suitable value for $DVI_{endo} = 0.5$ (data not shown). The RMSE values, which correspond to the accuracy of the models, were low when $DVI_{eco} = 1$ was set to a 40% blooming level and the initial $DVI_{eco}$ value was set to $DVI_{endo} = 0.5$. With this combination, the differences between the predicted and actual blooming dates in 2014–15 and 2015–16 were up to 3 d, whereas the difference in 2013–14 was 6 d. Unfortunately, the RMSE values in 2015–16 tended to be higher than those of the other years. Our model is based on data from a relatively small number of treatments because of the limited number of trees and availability of treatment space. Additionally, the treatments consisted of continuous exposures to low or high temperatures. A relatively mild winter in 2015–16 likely delayed endodormancy release, which may have resulted in increased error values.

The start of the blooming stage was accurately predicted for each analyzed year when the initial $DVI_{eco}$ value was set to $DVI_{endo} = 0.5$, likely because the temperature effects during the late stages of endodormancy were excluded from the model (Table 3). Oya (2006) developed a model to predict the blooming date of Japanese pear by considerably adjusting the initial $DVI_{eco}$ value after trees transitioned to the ecodormancy stage. This was done to minimize inaccurate predictions. The most suitable initial $DVI_{eco}$ value was determined to be $DVI_{endo} = 2.2$. The differences between the models for Japanese apricot and Japanese pear suggest that the Japanese apricot blooming date is affected more by the HR during ecodormancy than the CR of endodormancy, whereas both HR and CR have crucial effects on the blooming date of Japanese pear.

For blooming date predictions, the DTS model requires data from several previous years, but data from new experiments are unnecessary. The CH, CU, and CP models were originally modified to be applicable for peach. Therefore, it is unclear whether these models can be used to analyze Japanese apricot under changing climate conditions (e.g., global warming). Alternatively, although the DVI model requires the completion of complex experiments using many plants, DVI values can be used to represent developmental stages based on plant physiological reactions regardless of climate conditions. Our DVI model was verified in Japanese apricot production sites in Japan. The predicted and actual blooming dates differed by only a few days, indicating the developed model may have practical value. However, we generated limited experimental data for the temperatures during endodormancy ($-3 \degree C$ to $15 \degree C$) and ecodormancy ($5 \degree C$ to $20 \degree C$). It is possible that the negative effects of temperatures below $-3 \degree C$ on endodormancy observed in this study are overestimated. To apply this model for other production sites or for climates affected by global warming, analyses involving a wider temperature range will be necessary.

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