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Is winter coming? Minor effect of the onset of chilling accumulation on the prediction of endodormancy release and budbreak

Guillaume Charrier

Université Clermont Auvergne, INRAE, PIAF, Clermont-Ferrand, France

Correspondence
Guillaume Charrier, Université Clermont Auvergne, INRAE, PIAF, 63000 Clermont-Ferrand, France.
Email: guillaume.charrier@inrae.fr

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Abstract
The buds of perennial plants become dormant in autumn and must integrate the information related to chilling and forcing temperatures to resume their growth in spring. In many studies, the initial date for chilling accumulation ($D_{CA}$) is set arbitrarily using various rules resulting in high variability across studies and sites. To test the relevancy of different rules to set $D_{CA}$, sequential models (taking into account or not the negative effect of warm temperature) were optimized by minimizing the sums of squares between observed and predicted values for 34 endodormancy release and 77 budbreak dates for the walnut *Juglans regia* L. cv Franquette across France. Optimization of these different models highlighted that many of the $D_{CA}$ rules, incorporating a photoperiod signal on endodormancy induction, were effective (predicted root mean square standard error less than 10 and 8 days for endodormancy onset and bud break, respectively). Furthermore, the use of functions that compute negative chilling accumulation did not improve the performance of the models. Among the different rules, the projections of the best models were explored under different climates (current climate and Representative Concentration Pathways RCP scenarios). The projections revealed a tipping point at a mean annual temperature between 13 and 15°C, beyond which the advance in ontogenic development during ecodormancy does not compensate for the delay in endodormancy release. Although the physiological mechanisms driving the onset of endodormancy may be profoundly altered by global change, they appear to have minimal impact on the way current models predict dormancy and budbreak dates in walnut.

1 | INTRODUCTION

In frost-exposed environments, deciduous trees must timely adjust their phenology to anticipate unfavorable conditions during the winter period. To avoid exposure to frost events, meristems switch from an apparently active period to a “dormant” period, characterized by the inability to grow even under favorable conditions (Charrier et al., 2015). In temperate species, bud dormancy is divided into three stages depending on the inhibiting factor (Lang et al., 1987). During paradormancy, in late summer, other organs such as apical bud or leaves inhibit meristem growth. During endodormancy, in autumn, growth is inhibited by factors intrinsic to the bud (“endo”), whereas during ecodormancy, in late winter-early spring, growth is limited by environmental factors (“eco”). Different phenological stages are visible during the transition from growth to dormancy (e.g. growth cessation, leaf fall, lignification, or bud set), whereas others are cryptic (e.g. endodormancy induction and release). Observation of the succession of phenological stages is therefore difficult, which makes prediction in a changing environmental context even more challenging.
Various factors control dormancy, including its depth (Faust et al., 1997): metabolic activity, morphological changes, and hormonal balance (e.g., auxine during paradormancy, abscisic acid during endodormancy; Beauvieux et al., 2018; Horvath et al., 2003). The interaction between these factors and environmental cues triggers the transition between dormancy stages. In late summer, the induction of endodormancy is mainly triggered by the decreasing photoperiod and low nighttime temperature (Maurya & Bhalerao, 2017). The deposition of callose on plasmodesmata within the shoot apical meristem has been suggested to block the coordination of these cells to resume growth (Rinne et al., 2001). In autumn, endodormancy release is under the control of decreasing temperature (Arora et al., 2003; Welling et al., 2002). Low temperature would promote the 1,3β-D-glucanase activity that would hydrolyze callose deposits (Rinne et al., 2001). After the release of endodormancy, cryptic growth of ecodormant buds progresses under the control of warm temperature, in most species, eventually modulated by photoperiod in photosensitive species, such as late successional species (Basler & Kömer, 2012).

In the context of global change, temperature would be expected to change at a given location, whereas photoperiod signals would remain similar, thus jeopardizing the regulation of phenological stages. Phenological processes would be affected in a complex manner (e.g., budbreak may be either delayed, due to the effect of warmer temperature during the endodormancy induction or release, or hastened, if warming occurs during the ecodormancy stage; Beil et al., 2021). The induction of endodormancy, under the dual control of cold temperature and short photoperiod could be particularly disturbed.

Since the first empirical model describing the relationship between temperature and plant development, through the concept of thermal-time (Réaumur, 1735), budbreak and flowering models have only computed the accumulation of growth-effective temperature (i.e., growth degree days GDD). As the starting point is set close to the coldest time of the year (e.g., January 1st or July 1st usually chosen for convenience in the northern and southern hemispheres, respectively), these models provide relatively accurate results. However, this type of model is not effective in regions with warmer winters, where temperate crop species have been introduced (e.g. in North Africa, the Middle East or South America; Balandier et al., 1993). In this context, temperate perennial crops exhibit a lack of chilling and insufficient endodormancy release (Weinberger, 1950). The process of endodormancy, and the related chilling accumulation, was therefore introduced into the models (Vegis, 1964; Weinberger, 1956). Different chilling accumulation functions have been developed, depending on the species. An important difference is the consideration of a delaying effect on endodormancy release for warm temperature (e.g., Utah model; Richardson et al., 1974) or not (e.g., Chilling hours; Weinberger, 1967). In recent decades, naturally growing trees have also been affected by a reduction in chilling exposure throughout the winter, increasing interest in the endodormancy stage (Beil et al., 2021; Pater et al., 2015).

Phenological models using environmental variables as inputs have been developed to simulate the endodormancy release and budbreak dates (Caffarra, Donnelly, Chuine, & Jones, 2011a; Chuine et al., 2016). In perennial plants, the completion of one stage is concomitant with the onset of the following one (Hänninen & Tanino, 2011). However, the initial date for chilling accumulation (DCa) is usually set arbitrarily with various rules resulting in a large variability between studies (from late summer to late autumn). Here, I explored four different concepts of DCa to assess their effect on current and future predictions of endodormancy release and budbreak:

- fixed DCa,
- variable DCa through a simple climatic threshold,
- variable DCa through a mathematic function using temperature as the only variable,
- variable DCa through a mathematic function using interacting variables (temperature and photoperiod).

Based on what is known in the induction of endodormancy, data from 1975 until 2019 from different orchards across France for Juglans regia cv Franquette, were used along with different computations to simulate effects of the onset of chilling accumulation DCa on the predictive accuracy of endodormancy release and budbreak dates. Specifically, I tested whether the use of dynamic DCa could account for the delaying effect of warm temperature on endodormancy release by comparing positive and positive/negative chilling functions. In a second step, the best models were evaluated to predict endodormancy release and budbreak in future climate scenarios for France.

2 | MATERIAL AND METHODS

2.1 | Dormancy depth and endodormancy release

Endodormancy release dates were measured using the one-node-cutting “forcing” test of Rageau (1982). Sampling was performed every 3 weeks from October to March and 48 one-node cuttings were prepared per sampling date. On each sampling date, one-year-old stems were sampled from five individual trees and cut into 7-cm long pieces, bearing only one node at the top or within 1 cm below the upper end, for terminal and axillary buds, respectively. For axillary buds, the top of the cutting was covered with paraffin to prevent desiccation. If present, other buds were cut from the cutting with a razor blade to avoid cumulative inhibitions (Dennis, 2003). The bases of the cuttings were immersed in tap water and changed weekly. Forty-eight cuttings were exposed to forcing conditions (i.e. 16/8 h day/night and 25°C constant) and observed individually every 3 days. The mean time to budbreak (stage 09 BBCH; Meier, 2001) was computed as the average of the individual time to budbreak for each of the 48 cuttings. After endodormancy release, buds of J. regia cv Franquette break after 20 days or less under optimal conditions (Charrier et al., 2011; Maugé, 1980). Endodormancy release dates were obtained by linear interpolation between the two dates giving a time to budbreak greater than (or equal to) and less than (or equal to) 20 days, respectively.
2.2 | Budbreak dates

Budbreak dates were monitored every 2–3 days at the different sites on five individual trees until 50% of buds reached the BBCH stage 09. The different sites and number of annual observations are shown in Table 1.

2.3 | Climatic data

The models were fitted using the daily average and minimum temperatures observed by the weather stations, mostly located in the same orchard or within a 10 km distance (Table 1). For prediction, temperatures, calculated according to the CNRM-ALADIN52 model and corrected by a Q-Q method (Déqué et al., 2007), were used from 8462 sites across France (Safran grid at 64 km² spatial resolution; MétéoFrance). Four datasets were used as input variables: the reference period (1950–2005) and three climate scenarios (Representative Concentration Pathways RCP 2.6, RCP 4.5, and RCP 8.5) for the future period: short-term (2006–2051) and long-term (2051–2100). For each site, day length was computed as a function of latitude and day of the year.

2.4 | Endodormancy induction and onset of chilling accumulation

The initial date for chilling accumulation (DCA) was computed using different functions (see Table S1):

1. Fixed date as a day of the year (DOY).
2. Flexible date based on the threshold values reached by the minimum temperature (Tmin), the mean temperature (Tmean), the first frost (FF) or the photoperiod.
3. Date of minimum chilling units (CUmin) computed according to the Utah model (originally developed on Prunus persica L. Batsch), which computes the negative chilling effect for temperatures above 16°C (Richardson et al., 1974). Daily CUs were summed from DOY 182 until DOY 365 using the Utah_Model function (ChillR package; Luedeling, 2019) as follows:

\[
CU[Tmean] = \begin{cases} 
0 & \text{if } T_{\text{mean}} < 1.4 \\
0.5 \text{ if } 1.5 < T_{\text{mean}} < 2.4 \\
1 \text{ if } 2.5 < T_{\text{mean}} < 9.1 \\
0.5 \text{ if } 9.2 < T_{\text{mean}} < 12.4 \\
1 \text{ if } 12.5 < T_{\text{mean}} < 15.9 \\
-0.5 \text{ if } 16 < T_{\text{mean}} < 18 \\
-1 \text{ if } T_{\text{mean}} > 18 
\end{cases}
\]

with \( T_{\text{mean}} \) the daily mean temperature.

4. Predicted leaf fall dates (BBCH 97) were computed according to the thermal (LFT) and photothermal (LFPT) models developed by Delpierre et al. (2009) for Quercus and Quercus + Fagus, respectively. Below a critical photoperiod DLstart and for a temperature colder than a threshold T_b the variable RF, modulated by a photoperiod function in the case of the LFPT model, is summed daily up to a critical value (Ycri), corresponding to the leaf fall date and considered as DCA. Both LFT and LFPT models were computed using the original or optimized parameter sets: LF(P)Tadj and LF(P)Tadj respectively.

\[
R_{\text{sen}}[T_{\text{mean}}; \text{DL}] = \begin{cases} 
0 \text{ if } DL \geq DL_{\text{start}} \\
0 \text{ if } T_{\text{mean}} \geq T_b \\
T_{\text{mean}} - T_b \times \left(1 - \frac{DL}{DL_{\text{start}}}\right) \text{ if } T_{\text{mean}} < T_b
\end{cases}
\]
with $T_{\text{mean}}$ the daily mean temperature and DL the photoperiod. The parameter $y$ was set to 0 and 2 for LFT and LFPT models, respectively.

5. The endodormancy induction state (DS) was computed according to the DORMPHOT model developed for Betula pubescens Ehrh. by Caffarra, Donnelly, Chuine, and Jones (2011a). The two sigmoidal response functions to low temperature and photoperiod interact to compute DS. When the sum of daily DS reaches $D_{\text{crit}}$, the date is reported as $D_{\text{CA}}$. Both the original (DP$_{opt}$) and optimized (DP$_{adj}$) parameter sets were used.

$$DS[T_{\text{mean}}, DL] = \frac{1}{1 + e^{(T_{\text{mean}} - 60)}} \times \frac{1}{1 + e^{(24 - DL - D_{\text{crit}})}}$$  \hspace{1cm} (3)

with $T_{\text{mean}}$ the daily mean temperature, DL the photoperiod, $aD$ a coefficient for the effect of temperature, $bD$ a critical temperature, and $D_{\text{crit}}$ a critical photoperiod.

2.5 | Endodormancy release and budbreak

From the $D_{\text{CA}}$, the effect of chilling temperature was simulated according to the inverse of the function used for forcing accumulation in the original studies from Richardson et al. (1974). This function was defined as the best function predicting endodormancy release dates in walnut trees, although it does not take into account the negation of chilling at warm temperatures (Charrier, Chuine, et al., 2018a; Chuine et al., 2016). According to the sequential paradigm, the date at which the sum of CU reaches the critical $CU_{\text{crit}}$ threshold (arbitrary chilling units, CU) is the date of endodormancy release ($D_{\text{ER}}$), or the transition from endodormancy to ecodormancy:

$$CU[T_{\text{mean}}] = \max \{ \min (T_{\text{high}} - T_{\text{mean}}; T_{\text{high}} - T_{\text{low}}); 0 \}$$  \hspace{1cm} (4)

with $CU(t)$ the chilling unit at day $t$, $T_{\text{high}}$ the temperature above which $CU(t)$ is 0 and $T_{\text{low}}$ the temperature below which $CU(t)$ is maximum; $CU(t)$ is linear between $T_{\text{low}}$ and $T_{\text{high}}$.

Alternatively, the smoothed-Utah function, a smoothed version of the Utah function proposed by Richardson et al. (1974), takes into account the negation of chilling on warm days (Bonhomme et al., 2007).

$$CU[T_{\text{mean}}] = \begin{cases} 1 & \text{if } T_{\text{mean}} > T_{m1} \\ \frac{1}{1 + e^{-\left(\frac{T_{\text{mean}} - T_{m1}}{T_{opt} - T_{m1}}\right)}} & \text{if } T_{m1} < T_{\text{mean}} < T_{opt} \\ 0.5 \left(\frac{1}{T_{\text{mean}} - T_{opt}}\right)^2 & \text{if } T_{opt} < T_{\text{mean}} < T_{n2} \\ 1 - \left(1 - \min \left(\frac{T_{mean} - T_{opt}}{2(T_{n2} - T_{opt})^2}, \frac{T_{opt} - T_{\text{mean}}}{2(T_{opt} - T_{n2})^2} \right) \right) & \text{if } T_{opt} < T_{\text{mean}} < T_{n2} \\ \frac{1}{1 + e^{-\left(\frac{T_{\text{mean}} - T_{n2}}{T_{opt} - T_{n2}}\right)}} & \text{if } T_{\text{mean}} < T_{n2} \end{cases}$$  \hspace{1cm} (5)

with $CU(t)$ the chilling unit at day $t$, $T_{opt}$ the optimal temperature for chilling, $T_{m1}$ the slope of the cold efficiency at a colder temperature than $T_{opt}$, $T_{n2}$ the temperature warmer than $T_{opt}$, which has half the efficiency of $T_{opt}$ to release endodormancy; $min$ the effect of warm temperature to remove previously accumulated CU.

Ontogenetic development during the ecodormancy stage was modeled using a sigmoid function (Caffarra, Donnelly, Chuine, & Jones, 2011a). FU was summed daily from $D_{\text{ER}}$ until it reached the critical threshold $FU_{\text{crit}}$ (arbitrary forcing units, FU), considered as the budbreak date ($D_{\text{BB}}$).

$$FU[T_{\text{mean}}] = \frac{1}{1 + e^{-2\pi(T_{\text{mean}} - T_{50})}}$$  \hspace{1cm} (6)

with $FU(t)$ the forcing unit at day $t$, $SL$ the slope of the function at the temperature, inducing half of the maximal apparent growth rate $T_{50}$.

2.6 | Model calibration depending on the onset of chilling accumulation

For a given $D_{\text{CA}}$ rule, the date of endodormancy release was calibrated first and the best set of parameters was used to calibrate the bud break date. This sequential procedure was chosen to ensure that the date of endodormancy release would be realistic, which is not the case when a model is optimized only on budbreak dates (Chuine et al., 2016). For the endodormancy release model, in addition to the parameters defining $D_{\text{CA}}$ (between 1 [DOY and photoperiod] and 4 [LFT, LFPT, and DORMPHOT]; Table S2), three or five parameters were optimized for the reverse Richardson and the smoothed-Utah functions, respectively. For the ecodormancy model, one parameter was optimized: $FU_{\text{crit}}$ corresponding to the sum of forcing units for bud break. The endodormancy model used to predict $D_{\text{ER}}$ was the best from the previous step and the other parameters ($SL$ and $T_{50}$) set to the values described in Charrier, Chuine, et al. (2018a).

The nls function (using Gauss–Newton algorithm, R version 3.6.2; R development Core Team, 2019) was used to minimize the sums of squares between the observed and predicted values with different sets of starting values at the minimum, average, and maximum ranges of realistic parameter values. In order to maximize the variability within the datasets. The calibration was performed using approximately half of the observation per site for the calibration dataset and the other half for the validation dataset. Two independent calibration procedures were performed using at least one observation per site for the calibration (Tables S3 and S4). Most of the observations used in the calibration dataset #1 were used for validation in the second calibration and vice versa.

The quality of the fit and predictive ability of the models in relation to the $D_{\text{CA}}$ were assessed for calibration and validation datasets by several indexes independently for $D_{\text{ER}}$ and $D_{\text{BB}}$: Efficiency (Eff), Root Mean Square Error (RMSE), Predictive Root Mean Square Error (RMSEP), and Akaike Index Criterion (AIC$_C$; Akaike, 1974):
Eff = \frac{1}{n} \frac{\sum_{i=1}^{n} (\hat{y}_i - y_i)^2}{\sum_{i=1}^{n} (\bar{y} - y_i)^2} (7)

with $\hat{y}_i$ the predicted values for an observation $i$, $y_i$ the observed values for an observation $i$ and $\bar{y}$ the mean of observed values.

RMSE(P) = \sqrt{\frac{\sum_{i=1}^{n} (\hat{y}_i - y_i)^2}{n}} (8)

with $\hat{y}_i$ the predicted values for an observation $i$ and $y_i$ the observed values for an observation $i$.

AICC = 2n \log(\text{RMSE}) + \frac{k}{n-k-1} (9)

with $k$ the number of parameters, $n$ the number of observations.

2.7 Correlations between simulated and climate variables

A subset of the more efficient rules was selected based on their relative accuracy for the two datasets and the predicted dates (RMSE, RMSEP, and AICC $< 110\%$ of the minimum value for more than 9 of the 12 indexes shown on Tables 2 and 3). Parameters were optimized on the whole dataset for these relevant models and used to simulate $D_{CA}$, $D_{ER}$, and $D_{BB}$ from 1950 to 2005 per site (8462 sites at 64 km$^2$ spatial resolution). Correlations between the mean $D_{CA}$, $D_{ER}$, and $D_{BB}$ per site (8462 sites at 64 km$^2$ spatial resolution) and mean annual temperature were fitted by minimizing the sums of squares using a non-linear regression procedure (function nls in R). Different functions were tested: linear, sigmoid, exponential, power, second, third, or fourth degree polynomial) and selected according to RMSE and AICC.

3 RESULTS

3.1 Dormancy stages

During the induction stage of endodormancy, the time to budbreak generally increased by 20 days between August and October (onset of endodormancy) and reaches a maximum value (50–80 days: maximum endodormancy depth) between October and December (Figure 1A). The endodormancy release was observed when the time to breakbud gradually decreased to 20 days. The transition from endodormancy to ecodormancy was marked by a breakpoint in the curves between mid-December and mid-February. Significant linear correlations were observed between the onset of endodormancy and the date of maximum depth of dormancy ($F_{1,15} = 11.09; P = 0.005$; Figure 1B) and between the date of maximum depth of dormancy and the date of endodormancy release ($D_{ER}; F_{1,29} = 5.21; P = 0.030$; Figure 1C). However, no correlation was observed between the onset of endodormancy and $D_{ER}$ ($F_{1,15} = 0.79; P = 0.387$; Figure 1D).

3.2 Effects of $D_{CA}$ on endodormancy release date

With the exception of a few irrelevant rules, the use of different rules to compute the initial date for chilling accumulation ($D_{CA}$) had a relatively small effect on the accuracy of $D_{ER}$ prediction (Table 2). The use of a positive chilling function was overall more efficient than functions that take into account the delaying effect of warm temperature (positive and negative). Approximately 75% of the rules tested returned RMSE-values within a range of 2–3 days: between 11.5 and 13.3 days and between 7.2 and 9.5 days for datasets #1 and #2, respectively. However, the uses of first frost (FF) and the Utah model ($CU_{\text{min_ori}}$) were not effective for both datasets. Only four rules provided efficiencies higher than 0.5 for dataset #1 (LFT$\text{adj}$ and DP$\text{adj}$, positive only, and positive and negative for both), while 11 rules had similar performance for dataset #2. The predictive ability was relatively good for most of the $D_{CA}$ with 75% of the RMSEP between 8.3 and 11.6 days and between 12.9 and 14.4 days for datasets #1 and #2, respectively. Finally, only a few rules returned values below 125% of the minimum for RMSE, RMSEP, and AICC in both datasets: Photoperiod and LFPT$\text{adj}$ (positive only), $CU_{\text{min_adj}}$ (positive and negative), LFPT$\text{ori}$, DP$\text{ori}$, and DP$\text{adj}$ (positive only and positive and negative). By increasing the stringency to 110%, only DP$\text{adj}$ (positive only) could be considered more accurate and robust for all indices (RMSE, RMSEP, and AICC) and both datasets.

3.3 Effects of $D_{CA}$ on budbreak date

The accuracy of the fits was slightly better for the budbreak date ($D_{BB}$) than for the $D_{ER}$ (Table 3), although the effect of the different rules on the $D_{BB}$ was relatively similar to that observed for the $D_{ER}$. The positive chilling function was more effective than the positive and negative functions. For most of the $D_{CA}$, 75% of the RMSEs were within a 2–3 day range: between 7.4 and 9.6 days and between 6.8 and 8.6 days for datasets #1 and #2, respectively. The uses of FF and $CU_{\text{min_ori}}$ were also less efficient. Most rules provided efficiencies higher than 0.5 for datasets #1 and #2 (17 and 18, respectively). The predictive ability was less than 1 week for most of the $D_{CA}$ with 75% of the RMSEP between 6.7 and 9.3 days and between 6.9 and 8.2 days for datasets #1 and #2, respectively. Most rules returned values below 125% of the minimum for RMSE, RMSEP and AICC for both datasets, with the exception of FF and $CU_{\text{min_ori}}$. By increasing the stringency to 110%, several rules remained accurate and robust: DOY, photoperiod, LFPT$\text{adj}$ (positive only), LFPT$\text{ori}$ (positive and negative), LFPT$\text{ori}$ and DP$\text{ori}$ (positive only and positive and negative).
**TABLE 2** Performance of different rules to set the onset of chilling accumulation $D_{CA}$ on the prediction of endodormancy release dates ($D_{ER}$) for two different calibration datasets.

<table>
<thead>
<tr>
<th>Onset of chilling accumulation $D_{CA}$</th>
<th>Chilling effect</th>
<th>Dataset 1</th>
<th>Dataset 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>$k$</td>
<td>$n$</td>
</tr>
<tr>
<td>Day of year</td>
<td>Positive only</td>
<td>4</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>Positive and negative</td>
<td>6</td>
<td>18</td>
</tr>
<tr>
<td>Mean temp</td>
<td>Positive only</td>
<td>4</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>Positive and negative</td>
<td>6</td>
<td>18</td>
</tr>
<tr>
<td>Min temp</td>
<td>Positive only</td>
<td>4</td>
<td>18</td>
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<tr>
<td></td>
<td>Positive and negative</td>
<td>6</td>
<td>18</td>
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<tr>
<td>First frost</td>
<td>Positive only</td>
<td>3</td>
<td>18</td>
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<tr>
<td></td>
<td>Positive and negative</td>
<td>5</td>
<td>18</td>
</tr>
<tr>
<td>Photoperiod</td>
<td>Positive only</td>
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<td>18</td>
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<td></td>
<td>Positive and negative</td>
<td>6</td>
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<tr>
<td>$CU_{min}$ ori</td>
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<td>Positive and negative</td>
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<td>18</td>
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<tr>
<td>$CU_{min}$ adj</td>
<td>Positive only</td>
<td>7</td>
<td>18</td>
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<tr>
<td></td>
<td>Positive and negative</td>
<td>9</td>
<td>18</td>
</tr>
<tr>
<td>Leaf fall thermal ori</td>
<td>Positive only</td>
<td>3</td>
<td>18</td>
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<td></td>
<td>Positive and negative</td>
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<td>Leaf fall thermal adj</td>
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<td>Leaf fall photothermal ori</td>
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<td>Positive and negative</td>
<td>9</td>
<td>18</td>
</tr>
</tbody>
</table>

Note: RMSE, RMSEP, and AIC$_C$ lower than 110% of the minimum RMSE or RMSEP are indicated in bold. $D_{CA}$ were either fixed (DOY) or computed according to: Date of first frost (FF), minimum temperature ($T_{min}$), mean temperature ($T_{mean}$), photoperiod, minimum chilling unit ($CU_{min}$), leaf fall using temperature (LFT) or temperature and photoperiod (LFPT) and dormancy induction state using the DORMPHOT model (DP). The terms ori and adj refer to the original published version or adjusted to the data, respectively. Chilling effect were only positive, using the reverse Richardson function, or negative at warm temperature, using the smoothed Utah function. $k$ is the number of fitted parameters and $n$ the number of data used to fit the model.
TABLE 3 Performance of different rules to set the onset of chilling accumulation (D_{CA}) on the prediction of budbreak dates (D_{BB}) for two different calibration datasets

<table>
<thead>
<tr>
<th>Onset of chilling accumulation D_{CA}</th>
<th>Chilling effect</th>
<th>Dataset 1</th>
<th>Dataset 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>RMSE (days)</td>
<td>AIC_{C}</td>
</tr>
<tr>
<td>Day of year</td>
<td>Positive only</td>
<td>5</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td>Positive and negative</td>
<td>7</td>
<td>41</td>
</tr>
<tr>
<td>Mean temp</td>
<td>Positive only</td>
<td>5</td>
<td>41</td>
</tr>
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<td></td>
<td>Positive and negative</td>
<td>7</td>
<td>41</td>
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<tr>
<td>Min temp</td>
<td>Positive only</td>
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<td>41</td>
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<td></td>
<td>Positive and negative</td>
<td>7</td>
<td>41</td>
</tr>
<tr>
<td>First frost</td>
<td>Positive only</td>
<td>4</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td>Positive and negative</td>
<td>6</td>
<td>41</td>
</tr>
<tr>
<td>Photoperiod</td>
<td>Positive only</td>
<td>5</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td>Positive and negative</td>
<td>7</td>
<td>41</td>
</tr>
<tr>
<td>CU_{min} ori</td>
<td>Positive only</td>
<td>4</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td>Positive and negative</td>
<td>2</td>
<td>41</td>
</tr>
<tr>
<td>CU_{min} adj</td>
<td>Positive only</td>
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<td>41</td>
</tr>
<tr>
<td></td>
<td>Positive and negative</td>
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<tr>
<td>Leaf fall thermal ori</td>
<td>Positive only</td>
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<td>41</td>
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<tr>
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<td>Positive and negative</td>
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<td>41</td>
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<tr>
<td></td>
<td>Positive and negative</td>
<td>9</td>
<td>41</td>
</tr>
<tr>
<td>Leaf fall photothermal ori</td>
<td>Positive only</td>
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<td>Positive and negative</td>
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<tr>
<td>DORMPHOT ori</td>
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<td>Positive and negative</td>
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</tr>
</tbody>
</table>

Note: RMSE, RMSEP, and AIC_{C} lower than 110% of the minimum are indicated in bold. D_{CA} were either fixed (DOY) or computed according to date of first frost (FF), minimum temperature (T_{min}), mean temperature (T_{mean}), photoperiod, minimum chilling unit (CU_{min}), leaf fall using temperature (LFT), and DORMPHOT (DP). The terms ori and adj refer to the original published version or adjusted to the data, respectively. Chilling effect were only positive, using the reverse Richardson function, or negative at warm temperature, using the smoothed Utah function. k is the number of fitted parameters and n the number of data used to fit the model.
3.4 Predictions under current and future climates for *J. regia* cv Franquette

As shown in the previous section, most of the rules for setting $D_{CA}$ provided relatively accurate phenological predictions for $D_{ER}$ (RMSEP < 15 days) and $D_{BB}$ (RMSEP < 8 days), except for FF and $C_{U_{min,ori}}$. However, the predicted $D_{CA}$ was very different across rules, from late August (Photoperiod) to November (DP ori; Figure 2A), with Pearson’s correlation coefficients $r$ between -0.403 and 0.989 (Table S5). For most of the rules, the average $D_{CA}$ computed across France exhibited close and significant exponential relationships with the mean annual temperature (MAT; $P < 0.001$), except for DOY (defined as a constant; Figure 2B). The $D_{CA}$ predicted by $C_{U_{min}}$ and FF also exhibited a significant relationship with the mean annual temperature, although through different log-like (or linear) functions (Figure S1).

Despite the large variability in $D_{CA}$ (ca. 60 days difference in the median), the prediction of the $D_{ER}$ was highly reproducible for most rules, in mid-January (Figure 2C), with Pearson’s $r$ between 0.875 and 0.999 (Table S6). The relations between $D_{ER}$ and MAT fit exponential functions for all rules ($P < 0.001$), with almost no difference above 7°C. Below this value, three models deviate from the others: LFT ori and LFPT adj predicted earlier endodormancy release dates, whereas later dates for LFPT ori, LFT ini, (Figure 2D). For the budbreak date, predictions were almost identical for all rules with a prediction at the end of April, with Pearson’s $r$ between 0.960 and 0.999 (Table S7). The relations between $D_{BB}$ and MAT fit cubic functions and were not distinguishable from each other (Figure 2F). All rules returned a local minimum for MAT between (12.3°C [LFT ini] and 13.5°C [Photoperiod]). This temperature represents a tipping point above which budbreak dates is predicted to be delayed by warmer temperature.

$DP_{ori}$ (positive only) was selected as a representative model to explore current and future phenology trends since this rule had the highest average performance across 0.597. $D_{CA}$, $D_{ER}$, and $D_{BB}$ have a structured geographical distribution across France (Figure 3). $D_{CA}$ spanned a range of 43 days: earlier in the mountainous areas (mid-August) and later on the Mediterranean (South East; late September) and south-western coasts (late August–mid-September). $D_{ER}$ had a similar distribution but over a wider range (84 days): from the beginning of December in mountain areas to the end of February on the Mediterranean coast. $D_{BB}$ showed an opposite distribution over a period of 72 days: from mid-April in the southern and western regions to the end of June in the mountainous areas.

Warmer temperatures, as predicted by the different climate scenario, are therefore expected to delay the onset of chilling accumulation by 5–6 days until 2050 and, by the end of the century, by up to 20 days according to the RCP 8.5 scenario (Figures 4A,G and S2). Endodormancy release is projected to be delayed by a similar magnitude: 6–7 days until 2050 and, by the end of the century, up to 24 days under RCP 8.5 (Figures 4B,H and S3). However, the delay in the release of endodormancy did not directly affect the $D_{BB}$. The $D_{BB}$ would occur only 3–4 days earlier until 2050 (Figures 4C,I and S4). By the end of the century, budbreak is projected to be earlier under the RCP 4.5 scenario (~6.4 days) than under the warmer RCP 8.5 scenario (~3.5 days).

The relationship between $D_{BB}$ and temperature was not monotonic, exhibiting a tipping point, that is, a temperature above 13.2°C induces later $D_{BB}$ (Figure 2F). In the future climate, the relationships are similar, although the tipping point is slightly shifted toward a warmer temperature: 13.8°C in all scenarios between 2005 and 2050 and up to 14.9°C for the RCP 8.5 scenario (Figure 5C). Finally, a later budbreak than today is likely to occur in larger parts of France at the end of the 21st century: from 5.6°C (RCP 4.5) to 33.8°C (RCP 8.5) of French territory in 2051–2100 (Figure 6). A similar trend was observed using a fixed date (DOY) to define the onset of chilling accumulation with a tipping point between 13°C (current climate) and 14.9°C (RCP 8.5). Using the DOY rule, a later bud break than today is expected in between 4.0 (RCP 4.5) to 30.0% (RCP 8.5) of the French territory in 2051–2100.

The current annual variability of phenological stages is similar for $D_{CA}$ and $D_{ER}$ (standard deviation of about 5 days; Figure 4D,E). The future climate would increase the variance of $D_{CA}$ and $D_{ER}$ considerably, especially for RCP 8.5 in the period 2051–2100 (about 10 days). However, the pattern is reversed for $D_{BB}$, with a standard deviation of 10 days in the current period, while 5–7 days are expected in the future climate (Figure 5F). In both Protected Designation of Origin (PDO) areas, the variance in $D_{BB}$ would decrease by 2–3 days (RCP 8.5 scenario).
FIGURE 2  Predicted average dates of onset of chilling accumulation (A and B), endodormancy release (C and D) and budbreak (E and F) predicted across France under current climatic conditions using different rules for the onset of chilling accumulation. (A, C, E) The boxes represent the upper and lower quartile with the median indicated by a thick black line, the whiskers represents the 1st and 9th decile, outliers were not represented. (B, D, F) Average dates of onset of chilling accumulation (B), endodormancy release (D), and budbreak (F) depending on mean annual temperature.

FIGURE 3  Average dates of onset of chilling accumulation $D_{CA}$ (A), endodormancy release $D_{ER}$ (B), and budbreak $D_{BB}$ (C) predicted across France of *Juglans regia* cv Franquette under current climatic conditions using the DORMPHOT model (DPadj).
perennial organisms, such as trees, various empirical rules have been used so far. The onset of chilling accumulation during the endodormancy stage (DCA) had, for instance, been arbitrarily set using fixed dates regardless of year and location (Chuine et al., 2016) or based on environmental factors controlling the induction of endodormancy (Caffarra, Donnelly, & Chuine, 2011b). In the current study, long-term observations of phenological stages (endodormancy release DER and bud break DBB) were used to define the most efficient rule under various environmental conditions. For most of the computations, the different rules for defining the DCA did not have a large impact on the accuracy of the endodormancy release and budbreak dates (ca. 2–3 days; Tables 2 and 3). Overall, the use of a function that computes the negative effect of warm temperature, such as the Utah model, decreased the accuracy of the prediction. The Utah model, developed in Prunus does not apply to Juglans, as also shown by Chuine et al. (2016).

Across years and sites, the large ranges of variation in dates of endodormancy induction, maximum dormancy and endodormancy release (more than 2 month; Figure 1) suggest that they cannot be predicted by a simple trigger such as a fixed date or photoperiod (Caffarra, Donnelly, Chuine, & Jones, 2011a). Furthermore, the strong correlation between the onset of endodormancy (August–October) and the maximum depth of dormancy (October–December) indicates that the duration of endodormancy induction is generally 2 month with a relatively small effect of environmental conditions (Figure 1). In contrast, the maximum depth of endodormancy and endodormancy release are weakly, although significantly, correlated, with temperature being the main driver of endodormancy release (Weinberger, 1950). However, it is not clear whether chilling temperature actually acts only during endodormancy release or already during the induction of endodormancy.

Model optimization was used to understand the interaction between environmental factors and the induction of endodormancy. Optimization of the different DCA rules led to a wide range of variation in this variable but this was not reflected in the prediction of DER and DBB (Figure 2). However, not all the rules are effective in predicting DER and DBB. Among the rules tested, the date of the first frost event and the date of CUmin were less effective than the other rules (Tables 2 and 3). Although CUmin and FF returned similar average DCA than LFPT adj and Dpvec, respectively, their lower ability to predict DER and DBB suggest a minor role of temperature in setting the date of dormancy induction, as revealed by a different relationship with mean annual temperature (Figure S1). The relevant rules (DOY, DP, LFT, LFPT, and DORMPHOT) have indeed considered a potential effect of photoperiod, either directly or indirectly via the fixed date (Chuine & Régnière, 2017; Gauzere et al., 2019; Welling et al., 1997). The LF, LFPT, and DORMPHOT models, originally developed in Quercus sp., Fagus sp., and Betula sp., are also relevant for other deciduous species such as Juglans sp.

The relatively small effect of DCA on DER and DBB observed here could be the result of various factors such as an inadequacy of the dataset to reflect a wide range of variations in environmental

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**FIGURE 4** Distribution of the mean (A–C) and standard deviation (D and E) in the date of onset of chilling accumulation (A, D), endodormancy release (B, E) and budbreak (C, F) in the current period (Ref) or RCP scenario in the early (2006–2050) and late part of the XXI century (2051–2100) in France. Distribution of the variation compared to the reference period in the mean date of onset of chilling accumulation (G), endodormancy release (H), and budbreak (I). The box represents the upper and lower quartile with the median indicated by a thick black line, the whiskers represent the 1st and 9th decile, outliers were not represented. Different letters indicate a significantly different distribution across scenario according to the non-parametric Kruskal Wallis test (P < 0.05).

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**4 | DISCUSSION**

**4.1 | Defining the onset of chilling accumulation**

The definition of the initial date for the simulation of cyclical processes is a key issue. To predict the annual phenological cycle of...
conditions, endodormancy and budbreak dates. However, the calibration dataset was chosen to maximize environmental conditions for the $D_{\text{ER}}$ (MAT = 6.6 and 14.0°C for the coldest and warmest year, respectively), and the $D_{\text{BB}}$ (MAT = 6.6 and 15.0°C). In addition, most of the models were more accurate than the null model: RMSE and RMSEP were lower than the standard deviations for $D_{\text{ER}}$ and $D_{\text{BB}}$ (15.0 and 10.4 days, respectively). Furthermore, the two calibration procedures were in agreement. To my knowledge, the number of observations (i.e. 38 $D_{\text{ER}}$ and 77 $D_{\text{BB}}$) represents the largest dataset combining both phenological stages in the literature. For instance, in the studies cited in Table S1, only one paper combined more than 10 observation of both $D_{\text{ER}}$ and $D_{\text{BB}}$ (Chuine et al., 2016). According to their conclusions, the model optimization was performed in sequential order as the concomitant fitting of both dates would have given a higher weight to $D_{\text{BB}}$ (77 dates) compared to $D_{\text{ER}}$ (38 dates) leading to potentially biased results such as unrealistic dormancy release dates (Chuine et al., 2016).

### 4.2 Model optimization versus experimental evidence

Four rules suggest that $D_{\text{CA}}$ occurs in early September (DOY, DORMPHOT, LFT, and Photoperiod) whereas the others suggest that $D_{\text{CA}}$ occurs in late October (Figure 2), both periods being on the edge of observed onset of endodormancy (Figure 1). All relevant rules integrate the effect of photoperiod, interacting with temperature for some rules. Temperature and photoperiod are closely correlated over the seasons, and it is often difficult to consider their effect independently under natural conditions. As the induction of

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**FIGURE 5** (A–C) Average date of onset of chilling accumulation (A), endodormancy release (B), and budbreak (C) depending on mean annual temperature across France under different climatic scenarios using the DORMPHOT model (DPadj). Exponential (A, B) and cubic (C) functions were represented in black dashed lines.
endodormancy is a long process (ca. 2 month), perennial plants cannot rely solely on temperature changes that may be too sudden to induce winter dormancy in time (Caffarra, Donnelly, Chuine, & Jones, 2011a). The observations used in this study were performed in different orchards with large differences in MAT (9.7–16.9°C), but at a similar latitude (43.8–45.8° N) with low differences in photoperiod (16 min at solstice). It is therefore difficult to estimate the respective influence of these two factors in *Juglans*. Photoperiod and temperature variables affect the induction of endodormancy of perennial plants, although to different extents across species: photoperiod is dominant in *Populus* (Kalcsits et al., 2009) and *Vitis* (Fennell & Hoover, 1991), whereas temperature is dominant in *Malus*, *Pyrus* (Heide & Prestrud, 2005), and *Sorbus* (Heide, 2011). The interaction between photoperiod and temperature has been demonstrated in *Prunus* (Heide, 2008). In northern plants, Tanino et al. (2010) suggested the existence of two parallel pathways leading buds to dormancy, one under the control of cold temperature and the other under the control of photoperiod. It has been hypothesized that the modulation of photoperiod sensitivity by temperature might be related to the thermal effect on day length perception by phytochromes (Mølmann et al., 2005). The conceptual development of the DORMPHOT model is based on experimental results of dormancy combining the manipulation of photoperiod and temperature (Caffarra, Donnelly, & Chuine, 2011b), whereas other formalisms were based on empirical observations (e.g. leaf fall; Delpierre et al., 2009).

Finally, it is not possible to conclude whether buds actually integrate chilling information during the budset and the induction of endodormancy because models setting $D_{CA}$ in late summer or in late autumn do not diverge (Figure 2). From a modeling perspective, the use of temperature instead of (or in interaction with) photoperiod can lead to large differences in future climate projections. Delayed induction of endodormancy is likely to have profound consequences for autumn frost risks by delaying or reducing frost acclimation (Charrier, Chuine, et al., 2018a; Guàrdia et al., 2016). The use of experimental results remains essential to ensure that the factors included, and the responses fitted remain realistic (Charrier & Améglio, 2011; Charrier et al., 2018b; Chuine et al., 2016; Hänninen et al., 2019).

### 4.3 Predictions across France

Across the different rules, $D_{ER}$ predictions were relatively stable: during January across France. However, three rules diverged from the others at lower temperature than 7°C. $LFPT_{oa,Utah}$ predicts later endodormancy release than the other rules at cold temperature,
probably because the negative chilling units are accumulated in these locations immediately after the $D_{CA}$. Conversely, LFT$_{ori}$ and LFTP$_{adj}$ predict earlier dormancy than the other rules at cold temperature. The two rules have a significantly higher photoperiod threshold (>14.5 h) than the others, predicting earlier chilling accumulation in cold environment. However, these predictions, outside the calibration range (between 9.7 and 16.9°C; Table 1) should be considered highly putative. Furthermore, stations with mean annual temperature below 7°C represent only 3% of the French territory.

For budbreak, all the different rules provided strikingly similar predictions (Pearson’s $r > 0.961$; Table S7). All rules follow a cubic function, revealing a tipping point for $D_{BB}$ at a temperature warmer than 12.3–13.5°C (Figure 2F). Above this threshold, endodormancy release would be more delayed than ecodormancy hastened, resulting in delayed bud break compared to the current period. Under future climate conditions as predicted by the RCP scenarios, the tipping point would be reached in a larger fraction of France. Delayed bud break would thus cover up to one third of France under RCP 8.5 scenario in 2051–2100 using DORMPHOT rule (Figure 6). A similar proportion (30%) would also be observed using a fixed date DOY. The expected delay in $D_{BB}$ in the future climate would therefore be due to insufficient chilling exposure during endodormancy release rather than a delay in $D_{CA}$. Such a lack of chilling during endodormancy has also been assumed for apricot in the United Kingdom (Martínez-Lüscher et al., 2017) and would be even more exacerbated in subtropical area (Erez, 2000). The tipping point is shifted depending on the scenario (e.g. from 14.1 to 14.9°C. under current and RCP 8.5 in 2051–2100 projections using DOY to set $D_{CA}$) suggesting that although chilling requirements are delayed, a warmer spring than at present can eventually partly compensate for the induced delay.

Considering the main French production areas, that is, “Noix de Grenoble” (Middle East) and “Noix du Périgord” (Middle West) PDO areas, budbreak would be delayed in most of the “Noix du Périgord” area (96.8% in RCP 8.5 2051-2100) but not in the “Noix de Grenoble” area. These two PDO areas would indeed face distinct threats as they are on opposite sides of the tipping point. In Périgord, chilling requirements are likely not to be fulfilled and varieties with lower chilling requirements should be selected, as current varieties do not exhibit variability for this trait (Charrier et al., 2011). In Grenoble, earlier budbreak dates are expected, leading to greater exposure to late frost events (i.e. vulnerable to false springs) and varieties with higher forcing requirements can help stabilize production (Charrier, Chuine, et al., 2018a).

Interestingly, in the future climate, the annual variability of $D_{BB}$ is expected to be lower. The trend toward more uniform phenology in warm years has already been observed in recent decades for budbreak (Caffarra et al., 2014; Vitasse et al., 2018) and other phenological stages (Stemkovski et al., 2021). It is likely that the response to warm temperature is somewhat saturated with developmental functions reaching a plateau (Caffarra, Donnelly, Chuine, & Jones, 2011a) and eventually declining at even warmer temperature (Schoolfield et al., 1981). A more uniform phenology would act as a stabilizing factor for fruit production by synchronizing pollination and ripening. However, the lack of chilling temperature during endodormancy induces serious agronomic issues such as erratic patterns of blooming, floribondity, and potential dischronism with anthesis (Campoy et al., 2011).

5 | CONCLUSIONS AND PERSPECTIVES

The modeled approach suggests that the role of $D_{CA}$ is minor in predicting $D_{ER}$ and $D_{BB}$ explaining why many rules have been used for phenological modeling. A stronger role of photoperiod rather than temperature was shown, which is consistent with the experimental results. A tipping point of budbreak dates will probably be reached during the 21st century with chilling requirements likely to be fulfilled later or not at all. An accurate assessment of temperature and photoperiod responses during endodormancy is therefore necessary to complement the experimental data obtained during the ecodormancy stage (Charrier et al., 2011). Although the physiological mechanisms driving the onset of endodormancy may be profoundly altered by global change (Charrier et al., 2021; Hänninen & Tanino, 2011), they appear to have minimal impact on the way current models predict dormancy and bud break dates in walnut.

AUTHOR CONTRIBUTIONS

Data analysis, writing, and editing original manuscript: Guillaume Charrier.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Guillaume Charrier https://orcid.org/0000-0001-8722-8822
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